Ecological Engineering 108 (2017) 456–476

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Wetland management using microbial indicators

Hidetoshi Urakawa [a,*], Anne E. Bernhard [b]

[a] Department of Marine and Ecological Sciences, Florida Gulf Coast University, Fort Myers, FL, USA
[b] Biology Department, Connecticut College, New London, CT, USA

ARTICLE INFO

Article history:
Received 29 April 2017
Received in revised form 11 July 2017
Accepted 13 July 2017
Available online 1 September 2017

Keywords:
Wetland
Microbial indicator
Restoration
Management
High-throughput sequencing
16S rRNA amplicon sequencing

ABSTRACT

The use of biological indicators to monitor the health and functioning of wetlands has been an ongoing goal of wetland scientists and managers, and has focused primarily on monitoring the changes in macroorganisms, due to the relative ease of identifying and counting them. In recent years, the establishment of high-throughput sequencing techniques, development of assays for specific functional genes, and better quantitative measures are making it easier to get extensive diversity profiles and more robust abundance estimates of various microbial communities, and empowers us to explore wetland microbiomes and their role in ecosystem function. This heuristic search enables us to illuminate a spot light on minor populations of microbial communities, which were difficult to be scrutinized by more traditional molecular tools. Monitoring microbial indicators in response to nutrient loading, pollutants and redox potential is beneficial for wetland ecosystem management. Microbial populations can serve as the most sensitive and rapid bioindicator in response to various environmental changes. Evaluation of wetland condition and restoration cannot be met effectively by a single physical, chemical or biological parameter but a combination of multiple attributes is effective for robust wetland assessment and management. Various functional groups of microorganisms can be used as wetland assessment tools and provide a more profound understanding of microbial population dynamics and various direct microbial activity measurements. Understanding of the microbial communities controlling biogeochemical cycles in constructed wetlands could support optimizing performance of these promising treatment systems. This review focuses on a potential use of microorganisms as effective biological indicators for wetland management.

1. Introduction

Microorganisms play fundamental roles in wetland biogeochemistry through their versatile functions (Mitsch and Gosselink, 2015). Microbial communities respond to environmental alterations in a spatially and temporally highly dynamic fashion. In turn, microbial activity, biomass, and population dynamics may impact various chemical and physical conditions (e.g. pH, dissolved oxygen, nutrient availability and balance), and strongly shape wetland biomes and ecosystem functions (Fig. 1). It should be noted that wetlands can be an inorganic nutrient sink, a nutrient source, and a transformer of inorganic nutrients to organic nutrients (Mitsch and Gosselink, 2015). Therefore, an understanding of the impacts of nutrient inputs on biogeochemical processes, and the microbes that mediate the processes, is necessary to manage healthy wetland ecosystems.

Several lines of evidence have indicated that monitoring microorganisms as biological indicators in response to nutrient loading, pollutants, and redox potential is valuable for wetland management (Artman et al., 2008; Merkley et al., 2004; Paerl et al., 2003; Sims et al., 2013; Wright et al., 2009; Zhang et al., 2013). Due to their rapid growth rates and quick response to changes, microbial populations can serve as the most sensitive and rapid bioindicator in response to various pollutants (Parmar et al., 2016; Reddy and D'Angelo, 1997; Urakawa et al., 2012). Evaluation of wetland conditions and restoration efforts cannot be met effectively by a single physical, chemical or biological parameter, but a combination of multiple attributes is effective for robust wetland assessment and management (Mitsch and Gosselink, 2000; Sims et al., 2013). Various functional groups of microorganisms can be used as wetland assessment tools (Table 1), and a profound understanding of microbial population dynamics, functional redundancy and ecophysiology may support a strategic wetland assessment and management (Fig. 2).

Today 16S rRNA gene amplicon sequencing makes it easy to obtain comprehensive profiles of the phylogenetic diversity of microorganisms from various environmental samples, but 16S

* Corresponding author at: Florida Gulf Coast University, 10501 FGCU Blvd. S., Fort Myers, FL, 33965 USA.
E-mail address: hurakawa@fgcu.edu (H. Urakawa).

http://dx.doi.org/10.1016/j.ecoleng.2017.07.022
0925-8574/

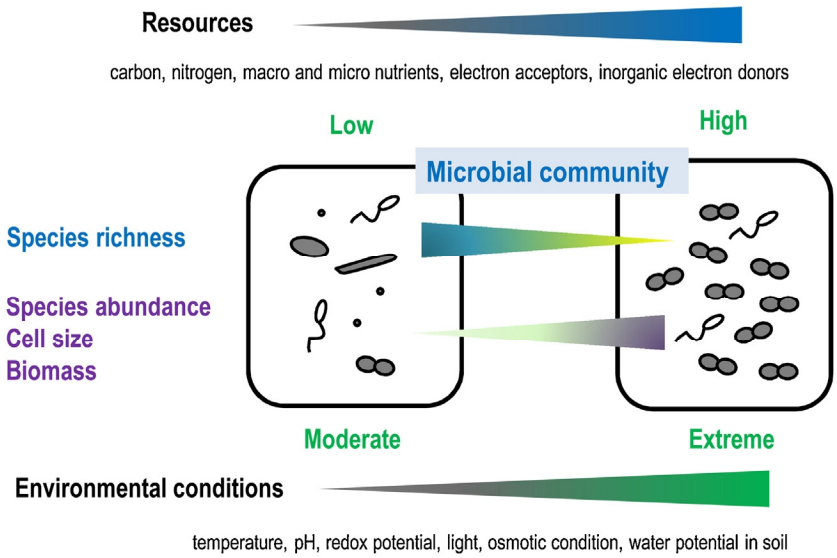

Fig. 1. Inputs of nutrient and other resources relevant to microbial communities in the wetland ecosystem. Species richness indicates the total number of different species present. Species abundance means the proportion of each species in the community. Moderate conditions may increase interactions among microbes, eukaryotic microbes and macro-organisms (e.g. plants, microbial predators). Extreme conditions (e.g. acid mine runoff, hypersaline lakes) decrease species richness but increase species abundance, cell size and biomass.

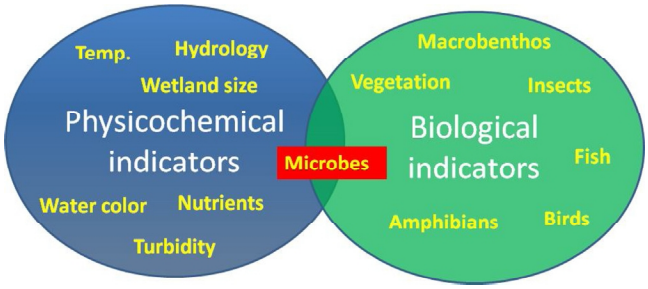

Fig. 2. Microbial indicators can be used for wetland management because they strongly couple with both physicochemical and biological indicators. Microbial indicators show rapid changes in response to the shift of environmental conditions and are extremely sensitive to environmental pollutants.

rRNA analyses do not necessarily relate to functional responses. To use microbes as bioindicators, genus-level ecotype identification (Fig. 3) and knowledge of ecophysiology of the microorganisms are necessary (Fig. 4). Since the vast majority of microorganisms have not yet been cultivated (Head et al., 1998), ecophysiology is often inferred from analysis of functional genes and transcripts. Phylogenetic and functional analyses using millions of sequences shall provide a detailed sketch of microbial diversity and functions in a wetland ecosystem. This review focuses on a potential use of microorganisms as an effective biological indicator for wetland management.

2. Microbial biomass and function

2.1. Bacterioplankton biomass and function

The biomass of bacterioplankton in wetlands may be regulated by available resources, habitats, and various environmental conditions in the ecosystem (Fig. 1). The abundance of bacterioplankton is also controlled by seasonal changes, and may be influenced by more long-term climate changes (Field et al., 1998). The total number of bacterioplankton is most accurately determined by the direct cell counting method using polycarbonate membrane filters, fluorochromes (e.g. 4′,6-diamidino-2-phenylindole [DAPI], SYBR Green I) and a fluorescence microscope (Faulwetter et al., 2009; Kepner and Pratt, 1994). With the combination of hybridization techniques (i.e. fluorescence *in situ* hybridization [FISH]) the number, morphology and spatial distribution of specific microbial populations can be selectively determined (Daims et al., 2015; Posch et al., 2009). The number of cells expected in wetland water columns is in the range of 10^5 to 10^6 cells/ml (Decamp and Warren, 2001; Hallberg and Johnson, 2005). The number of microbial cells may reach 10^7 cells/ml in nutrient-rich constructed wetlands or extreme conditions where microbial predation is limited (e.g. acid mine drainage) or there is very active decay of plants or animals (Fig. 1) (e.g. Decamp and Warren, 2001). Microbial biomass is also assessed by the compositional analyses of carbon, nitrogen and phosphorus. Wright et al. (2009) reported that microbial biomass P was somewhat more responsive to nutrient loading than biomass C and N, and can be a better marker to assess the level of eutrophication in the Everglades wetlands. It should be noted that bacteria in phosphate-limited freshwater environments can become a strong competitor of phytoplankton (Currie and Kalff, 1984), which may impact primary production. Under normal hydrological conditions, a large part of the water column is oxic, supporting high levels of aerobic heterotrophic activity, and constitutes one of the major microbial functions in the water column.

Bacterioplankton in some eutrophic surface waters may harbor a large fraction of Cyanobacteria. Because of their important role in primary production, their spatial and temporal abundance are of interest to researchers and freshwater monitoring programs (Paerl et al., 2016). The occurrence of massive cyanobacterial blooms in freshwater ecosystems is considered environmental pollution worldwide, and may be intensified by climate change (Paerl and Huisman, 2009; Paerl et al., 2016), so monitoring these populations is of critical importance (Fig. 5). Since commonly used chlorophyll *a* in vivo fluorescence cannot be used to accurately determine cyanobacterial abundance because their chlorophyll *a* locates in non-fluorescing photosystem I, analyzing phycobilin concentrations is preferred for detecting, quantifying, and monitoring cyanobacterial abundances (Seppälä et al., 2007). Generally, Cyanobacteria contain phycocyanin as an accessory pigment, and it can be used to fluorometrically differentiate Cyanobacteria from other eukaryotic algae by using narrow band interface filters that utilize excitation and emission wavelengths

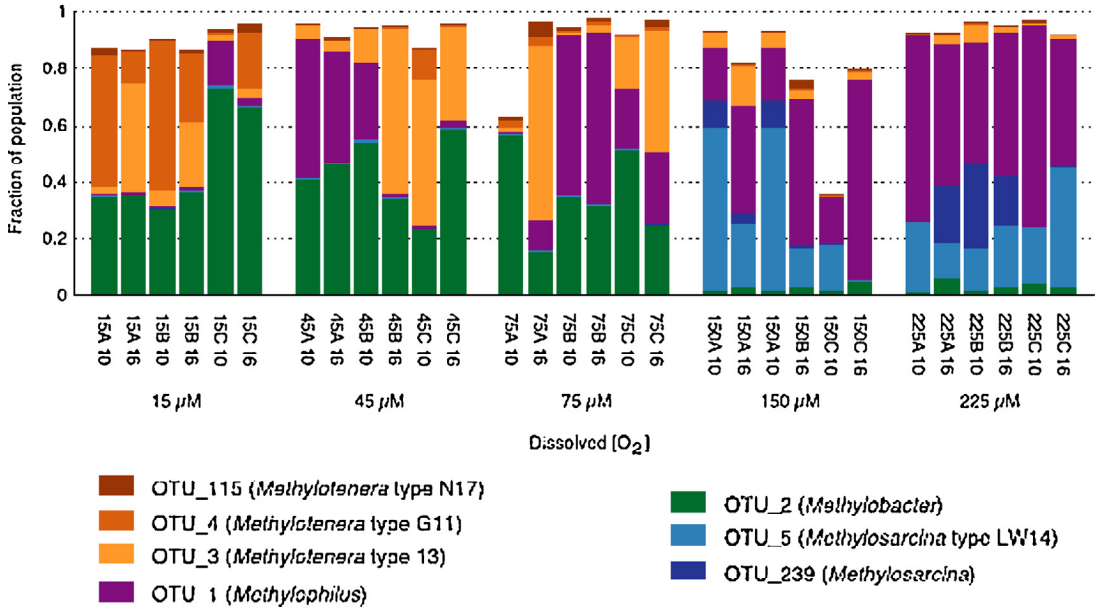

Fig. 3. Relative abundance of Methylococcaceae and Methylophilaceae in methane-fed microcosms under the different oxygen concentrations. Sample designations include oxygen tension, followed by the alphabetical name of a replicate and by the week of sampling. The figure is adapted from Hernandez et al. (2015).

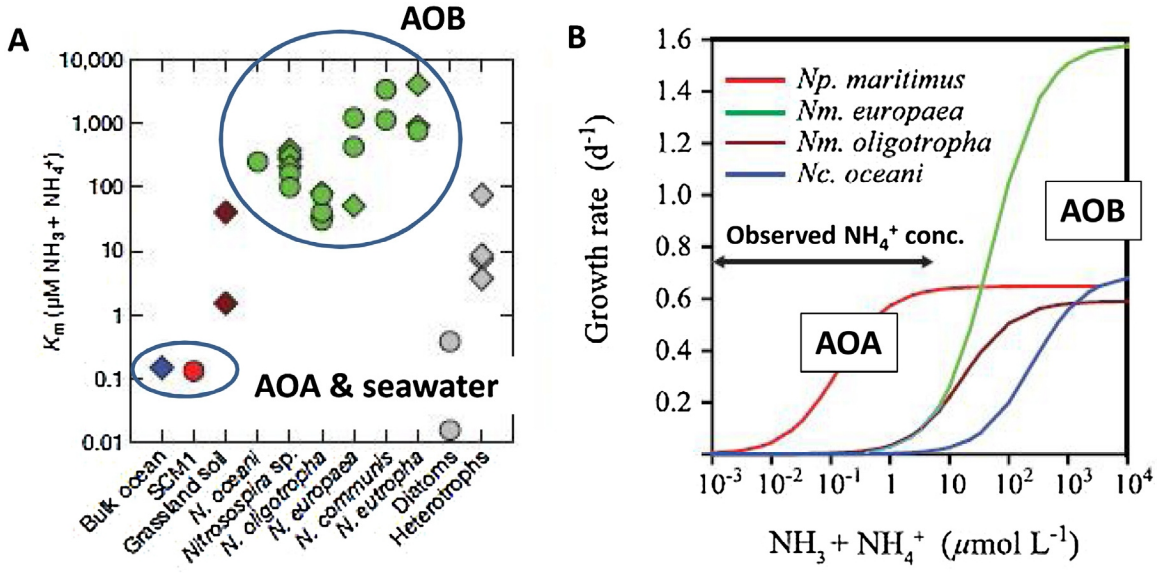

Fig. 4. Oligotrophic adaptation of *Nitrosopumilus maritimus* (AOA) is supported by the high-affinity ammonia oxidation (i.e. low K_m) (A) and the high growth rate under the low ammonium conditions (B). (A) Apparent K_m of SCM1 (red), the AOB strains *Nitrosococcus oceani*, *Nitrosospira* spp. cluster 0, 2 and 3, *Nitrosomonas oligotropha*, *Nitrosomonas europaea*, *Nitrosomonas communis*, *Nitrosomonas eutropha* (green), *in situ* nitrification in ocean water (blue) and soils (brown), as well as the lowest K_m for ammonium assimilation of diatoms and heterotrophic bacteria (grey). K_m values are given for activity measurements (circles) and growth (diamonds). (B) Growth rate model of ammonia oxidizers at different ammonium concentrations. The range of ammonium concentration observed in Puget Sound (WA, USA) is shown by the double-headed arrow. Np. indicates *Nitrosopumilus*; Nm., *Nitrosomonas*; Nc., *Nitrosococcus*. The figures are adapted and modified from Martens-Habbena et al. (2009) and Urakawa et al. (2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of 600 and 640 nm, respectively (Zamyadi et al., 2012). Generally cyanobacterial blooms can be managed by nutrient controls but also potentially regulated by a top-down control (Zhong et al., 2011). Wu et al. (2010) reported that cyanobacterial blooms can be controlled by biopond- wetland systems.

2.2. Biomass and activity of soil and sediment microbial communities

Sediments can maintain higher microbial abundance, function and diversity than those of the water column, thus the ecological roles of sediment microbial community are more likely to be prominent in shallow water environments, including wetlands. Although sediment microbial communities are influenced by water quality and the level of primary production, they are more likely controlled by the properties of soil/sediment (e.g. soil type, moisture, grain size and the degree of microbiologically available organic matter) (Tang et al., 2012; Wang et al., 2013). For example, sandy sediment typically contains a lower number of cells, while high silt-clay sediment may harbor more cells (Dale, 1974; Tang et al., 2012). Moisture is also a critical factor, and increases in moisture can lead to increased levels of microbiologically available organic matter

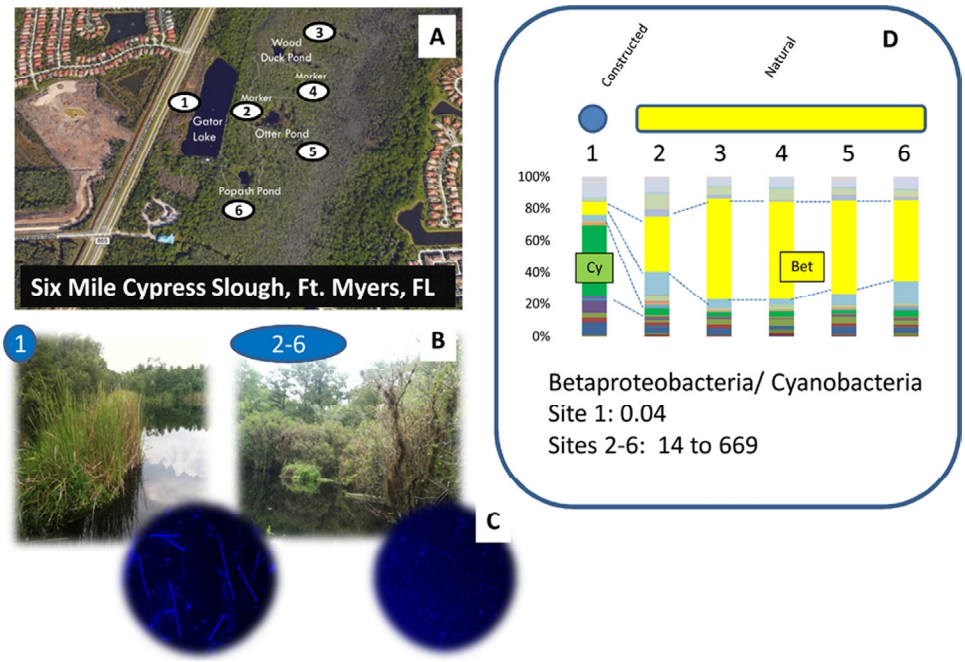

Fig. 5. Example of the use of microbial indicators for wetland management. Six Mile Cypress Slough Preserve, 14 kilometer long and 0.53 km wide, located in Fort Myers, FL (A), shoreline vegetation (B), fluorescence microscopy (C) and Illumina high-throughput sequencing at phylum level (Proteobacteria are shown as class) (D). Shoreline vegetation is different between natural ponds and a constructed lake, which was built more than 30 years ago. Some elongated cyanobacterial cells are occasionally found in the water samples of this constructed lake. Microbial cells were collected from surface water of one constructed lake (site 1), three natural ponds (sites 3, 4 and 6) and two boardwalk markers (sites 2 and 5). Microbial communities were similar among five natural sites where Betaproteobacteria dominated, but clearly distinguishable from that of the constructed lake, where the betaproteobacterial population was replaced by cyanobacterial populations. The ratio of Betaproteobacteria/Cyanobacteria was 0.04 at the constructed lake while it ranged from 14–669 at other sampling sites. The wetland system normally maintains an oligotrophic condition but water quality data of the constructed lake occasionally falls in mesotrophic. Currently a long term water quality monitoring by Lee County, FL is only conducted at the constructed lake and no other natural ponds within Six Mile Cypress Slough. The microbial indicator data (molecular fingerprinting) emphasize the importance of including other natural ponds in the future water monitoring plan.

and nutrients (Bai et al., 2004; Sleutel et al., 2008). As a consequence, microbial biomass and activity will increase accordingly (Sleutel et al., 2008; Tang et al., 2012). The reported total cell numbers in wetland soil/sediment ranged from 10^8 to 10^9 cells/g of soil or sediment (Ishida et al., 2006; Ivanova and Dedysh, 2012; Zhang et al., 2013). Cell numbers may be measured directly in sediments by fluorescence microscopy, although this can be challenging due to autofluorescence and particle interference (Lunau et al., 2005; Weinbauer et al., 1998), or cell numbers can be estimated based on copy number of genes measured by quantitative PCR (e.g. Humbert et al., 2012; Stoeva et al., 2014). In either case, measurements of cell numbers may be reported either as cells per gram, cells per milliliter, or they may be normalized to microgram of DNA (Urakawa et al., 2010).

A sharp oxic-anoxic gradient found in soil/sediment creates ideal habitats for functionally diverse microorganisms (Table 2). Multiple microbial activity measurements are needed to monitor various ecosystem services inasmuch as soil/sediment bacteria are functionally divergent (Fig. 6). Generally, the microbial biomass, diversity and activity in soil/sediment decrease with increasing soil/sediment depth (Wright et al., 2009; Zhen-Yu et al., 2010). Thus the monitoring of microbial communities in surface soil/sediment (e.g. 0–5 cm) is largely sufficient for freshwater wetland management tactics. On the other hand, in the case of coastal wetlands, the monitoring of sediment should be deeper (e.g. 0–30 cm) because of strong disturbance of sediments by tides and storm events. Recently Bernhard et al. (2015) showed recovery of nitrogen-cycling microbes in surface sediments after restoration in a salt marsh, while deeper sediments (6–8 cm) were still impacted.

Microbial activities are controlled by temperature and other abiotic and biotic factors, and may be altered by the currently changing climate (Palmer et al., 2012). Rate measurements such as nitrification and denitrification using *in situ* conditions and stable isotopes are the most accurate methods and should be employed if possible (Kellman and Hillaire-Marcel, 1998; Morse and Bernhardt, 2013). If these methods are not available, simple potential activity measurements are alternative methods (Bernhard et al., 2010; Castro et al., 2002; Hayashi et al., 2015; Palmer et al., 2012). What we have learned from many studies is how microbial activities span a dynamic range, sometimes varying as much as 1000 fold (Bachand and Horne, 1999a). These differences may be attributed to differences among wetlands, seasons and methods used. Thus, it is meaningful to quantitatively assess the success of wetland restoration projects through microbial functional activities. Particularly, production of methane, nitric and nitrous oxides and carbon dioxide, which are globally significant in wetland ecosystems (Faulwetter et al., 2009; Palmer et al., 2012). We anticipate that using transcript analysis as a proxy for microbial activity will be one of the promising methods (e.g. Nikolausz et al., 2008; Thomas et al., 2014).

3. Diversity, species composition and the relative abundance of environmental sequences

How do species richness and abundance of microorganisms vary along with multiple environmental parameters? (Fig. 1) This has been a century-old question for many microbial ecologists, and can now be intensively studied using high-throughput sequencing techniques. Although the composition of a microbial community can be analyzed at various taxonomic ranks (e.g. family and genus), a majority of studies has focused on phylum-level analysis. In general, great microbial diversity is considered as the sign of a pristine,

Table 1
Shifts of microbial populations with a gradient of environmental factors: A list of potential microbial indicators.

Type	Source	Low	High	Reference
Energy source	Ammonia	AOA *Nitrosospira*	AOB *Nitrosomonas*	Martens-Habbena et al. (2009), Sims et al. (2013), Schramm et al. (1998)
	Methane	Type Ia methanotrophs	Type II methanotrophs	Hanson and Hanson (1996)
Nutrient	Organic loading	*Nitrosospira* anammox bacteria Actinobacteria Acidobacteria	*Nitrosomonas* denitrifying bacteria Proteobacteria Betaproteobacteria	Urakawa et al. (2006a) Burgin and Hamilton (2007) Bell et al. (2013) Hartman et al. (2008)
	Fertilizer on rhizosphere	Deltaproteobacteria	Cytophagia	Huang et al. (2016)
Physicochemical factor	Land use alternation	Acidobacteria group I.1c Thaumarchaeota (Finnish Forest Soil (FFS) Archaea)		Peralta et al. (2013b) Bomberg (2016)
	pH	AOA	AOB	Nicol et al. (2008)
	Salinity	Betaproteobacteria	Alphaproteobacteria	Glöckner et al. (1999)
	Oxygen	*Methylotenera, Methylobacter*	*Methylosarcina, Methylophilus*	Hernandez et al. (2015)
Pollution	Hydrocarbon	Alphaproteobacteria Actinobacteria	Gammaproteobacteria Betaproteobacteria (Burkholderiales, Comamonadaceae, Rhodocyclaceae)	King et al. (2015) Bell et al. (2013)
		AOA beta-AOB	AOB gamma-AOB	Urakawa et al. (2012)
		AOA	AOB	Rodriguez-R et al. (2015)
	Methylene blue	AOA beta-AOB	AOB gamma-AOB	Sipos and Urakawa (2016)

AOA: ammonia-oxidizing archaea, AOB: ammonia-oxidizing bacteria. Beta-AOB: betaproteobacterial AOB, gamma-AOB, gammaproteobacterial AOB.

Table 2
Selected types of microbial oxidation-reduction reactions.

Process	Electron acceptor (EA)	End products	Moles of e^- per mole of EA	ΔG_o (kJ/mole of electron)	Redox potential (mV)
Aerobic respiration	O_2	H_2O	4	−125.1	300 to 700
Nitrate reduction	NO_3^-	N_2, N_2O, NO	5	−118.8	100 to 350
Manganese reduction	Mn^{4+}	Mn^{2+}	2	−94.5	−100 to 300
Iron reduction	Fe^{3+}	Fe^{2+}	1	−24.3	−100 to 200
Sulfate reduction	SO_4^{2-}	S^{2-}	8	−25.4	−200 to −100
Methanogenesis	CO_2	CO_2, CH_4	8	−23.2	−350 to −100

Source: Faulwetter et al. (2009) with minor modification.

healthy and balanced microbial community, while low microbial diversity is not favored and regarded as distressed community, in terms of ecosystem functioning (Bell et al., 2005, 2013; Delgado-Baquerizo et al., 2016). Thus, comparison of species richness indices obtained from DNA sequencing analyses may be directly used for the assessment of microbial communities (Fig. 1).

In nearly all freshwater wetlands, Proteobacteria dominate microbial communities at the phylum level (Bernhard et al., 2012; Ligi et al., 2014; Lv et al., 2014; Peralta et al., 2013b; Sánchez, 2016; Zhang et al., 2013). Proteobacteria are recognized as the largest phylum in the domain Bacteria and include five well-recognized classes and three recently-proposed classes as discussed later. Although Proteobacteria are nearly always the most abundant taxon, the following major taxonomic groups vary depending on the environmental settings. Bacteroidetes, Actinobacteria and Cyanobacteria are three common microbial groups at the phylum level in the water column (Sánchez, 2016; Schultz et al., 2013), while Bacteroidetes, Acidobacteria and Actinobacteria dominate in soil (Hartman et al., 2008; Ligi et al., 2014; Lv et al., 2014; Sánchez, 2016). Occasionally Acidobacteria make up a large fraction of microbial communities, but the overall relative abundance decreases by land use alterations and other environmental changes (Peralta et al., 2013b). Lv et al. (2014) examined the bacterial diversity using a total of 12,677 bacterial 16S rRNA gene sequences from a worldwide range of wetlands soil and sediment studies (Fig. 7). Although these sequences have been determined by Sanger DNA sequencing methods, these longer sequences are suitable to determine accurate taxonomic positions. Moreover, these conclusions are consistent with various high-throughput sequencing data. It is likely that the major taxa found in both "traditional" sequencing analysis and high-throughput sequencing are similar, but a clear difference is found in the discrimination of minor taxa. For example, Ligi et al. (2014) found 56 different bacterial phyla, which included candidate divisions, from soil and sediment microbial communities at the Olentangy River Wetland Research Park using high-throughput sequencing. On the contrary, Lv et al. (2014) reported only 31 known bacterial phyla from hundreds of independent wetland studies based on 16S rRNA gene clone library/denaturation gradient gel electrophoresis analyses. This comparison clearly indicates the limitation of "traditional" Sanger sequencing approaches and the superiority of high-throughput sequencing techniques, especially for detecting rare species (Sánchez, 2016; Sogin et al., 2006).

Today, high-throughput sequencing technologies have nearly completely replaced the 16S rRNA gene clone library analysis, which relies on Sanger DNA sequencing, and have greatly accelerated the data accumulation process along with the elimination of laborious workload (i.e. elimination of gene cloning step). As a consequence, numerous numbers of in-depth sequence data are created and stored as the sequence read archive (SRA) in the DNA databases (Leinonen et al., 2010). Although the new technology has a strong advantage (i.e. high-throughput), it is not perfect

(Quince et al., 2011). For example, two fundamental criteria of DNA sequencing technologies are the accuracy and the length of reads. In these two fundamental criteria, the classic Sanger sequencing exceeds those of high-throughput sequencing technologies. But in the present, the speed of the in-depth sequencing can help to find minor populations from the entire microbial communities and some of these may serve as important minor microbial indicators (Table 1).

As Proteobacteria are functionally and phylogenetically diverse, this phylum is often analyzed at the class level, while other taxa are handled at the phylum level (Fig. 5) (e.g. Deng et al., 2014; Urakawa et al., 2017; Zhang et al., 2013). At the class level, Deltaproteobacteria, Gammaproteobacteria and Betaproteobacteria are frequently the most prominent Proteobacteria in both sediment and soil of wetlands (Fig. 7) (Hartman et al., 2008; Ligi et al., 2014; Lv et al., 2014). It is well recognized that the abundance of Betaproteobacteria in microbial communities is very different between freshwater and marine environments: highly abundant in freshwater areas while minor in marine environments (Barberán and Casamayor, 2010). This tendency can be found both in real quantification (e.g. fluorescence *in situ* hybridization and quantitative real-time PCR assay) and in relative abundance (semi-quantitative) in 16S rRNA clone library analysis and high-throughput sequencing. Thus, Betaproteobacteria should serve as an excellent indicator to gauge the impact of salinity on estuarine wetlands (Table 1). In estuarine wetlands, salinity in a water column changes daily and seasonally. Therefore, the determination of the abundance of Betaproteobacteria in surficial sediment might be suitable to assess the impact of salinity on microbial communities. Sediment communities keep longer environmental records than bacterioplankton communities, which can be easily influenced by tidal rhythm and are more temporal and arbitrary (Urakawa et al., 2006a). Epsilonproteobacteria only dominate in hydrothermal vent ecosystems (López-García et al., 2003) and are rare in freshwater and wetland environments (Fig. 7) (Lv et al., 2014). More recently, the reclassification of this proteobacterial group was proposed (Waite et al., 2017). It should be noted that many high-throughput sequencing studies have reported the existence of unclassified or unidentified Proteobacteria from a wide range of environments (Uroz et al., 2010; Wang et al., 2012). The proportion of these unknown Proteobacteria is occasionally large (Madigan et al., 2015). Thus, it is reasonable that more unidentified classes of Proteobacteria exist in nature. At least three of these new Proteobacteria have been found recently: Zetaproteobacteria as a rare candidate class (Emerson et al., 2007; Fleming et al., 2013), Acidithiobacillia (Williams and Kelly, 2013) and Oligoflexia (Nakai et al., 2014; Nakai and Naganuma, 2015). Zetaproteobacteria can be found in freshwater environments as well as hydrothermal vent ecosystems but are only reported as minor populations (Emerson et al., 2007; Fleming et al., 2013; Lv et al., 2014). Apparently further detailed studies are needed for unclassified or unidentified Proteobacteria in wetlands.

Betaproteobacteria (beta I and beta II lineages) and Actinobacteria (acI lineages) are the most dominant bacterioplankton in freshwater lakes and ponds (Fig. 5) (Allgaier and Grossart, 2006; Warnecke et al., 2005; Urakawa et al., 2017; Zwart et al., 2002). These two groups of microbial populations may share the same substrate, but have different preferences of one or more environmental factors (e.g. light, UV) (Sharma et al., 2008, 2009; Warnecke et al., 2005). However, nutrient level is not a key factor determining their abundance (Warnecke et al., 2005). Apparently, the dominance of particular bacterial phylogenetic groups depends on the respective ecosystem (Allgaier and Grossart, 2006). Further studies are needed to use these cosmopolitan betaproteobacterial groups as useful freshwater microbial indicators.

Changes in the ratio of relative abundance of two different bacterial taxa may serve as a good index to assess the shift of microbial communities (Fig. 5) (Sims et al., 2013). For example, population dynamics between ammonia-oxidizing archaea (AOA) (Könneke et al., 2005) and bacteria (AOB) provide important insights into their ecological roles in different environments (Table 1). An ecophysiology study of AOA and AOB clearly indicated that ammonia availability shapes nitrifying communities, with AOA demonstrating lower K_m values for ammonia compared to AOB (Fig. 4) (Martens-Habbena et al., 2009; Urakawa et al., 2011, 2014). Later this eco-strategic concept was confirmed by a large number of field studies. For example, Sims et al. (2012b) reported that the temporal and spatial distributions of AOA and AOB and the higher AOA:AOB ratio can be used as an indicator of oligotrophic conditions in natural wetlands. Urakawa et al. (2014) reported that the ratio of AOA and AOB, but not the abundance, correlated with the ammonia concentration in coastal water. Dang et al. (2010) also found distinctly different communities of betaproteobacterial AOB that correlated with environmental conditions, and proposed that AOB community composition could serve as bioindicators of pollution (Table 1). Among the AOB, *Nitrosomonas* species typically dominate in more eutrophic conditions, while *Nitrosospira* dominate in more oligotrophic conditions (Beman and Francis, 2006; Gorra et al., 2007; Peng et al., 2013; Wei et al., 2011; Zhen-Yu et al., 2010). These studies demonstrate that healthy freshwater and coastal wetlands may harbor AOA as major nitrifiers, while the shift of populations from AOA to AOB may be found in more organic/nutrient rich environments (Sims et al., 2012a).

4. Microbes in the biogeochemical cycles

Bacteria and Archaea play fundamental roles in wetland biogeochemical cycles (Fig. 6). Wetland microbiomes and their activity are important because various microbial processes influence the water quality (e.g. Rea et al., 2015), greenhouse gas emissions (e.g. Li et al., 2016; Villa and Mitsch, 2014), and fertility of wetlands (Sánchez, 2016). Redox potential is a key factor that controls microbial function and activity of wetlands (Table 2). Manipulation of redox potential in the design of constructed wetlands may increase the performance of nutrient and pollutant removal. Currently the use of microbial indicators is not a common approach for wetland management. The complexity of microbial communities and required molecular microbiology tools and techniques that are not accessible to many users prevent the use of microbes as conventional ecological indicators to monitor the health of wetland ecosystems (Sims et al., 2013). However, the recent development of high-throughput sequencing techniques may greatly advance the use of microbial indicators as a valid tool of wetland health assessment in the future (Hartman et al., 2008; Sánchez, 2016). As microbial populations are evolutionarily and functionally diverse, a better understanding of each group is needed for adequate wetland management (Table 1).

4.1. Carbon cycle and associated microbes

4.1.1. Oxygenic phototrophs

The landscape of wetlands is mainly formed by macrophytes, which are major phototrophs in wetland ecosystems. Macrophytes play a key role in nutrient cycling and they create substrates for epiphytes, which contribute greatly in wetland primary production, and as major food source of primary consumers (Mitsch and Gosselink, 2015). Phytoplankton are good water quality indicators because their abundance and diversity are strongly influenced by nutrient conditions of ecosystems (Fig. 1) (Paerl et al., 2003). Succession of phytoplankton communities along with the changes of trophic level is a well-studied subject in limnology (Sommer et al., 1986) and beyond the focus of this review. Periphyton is a complex

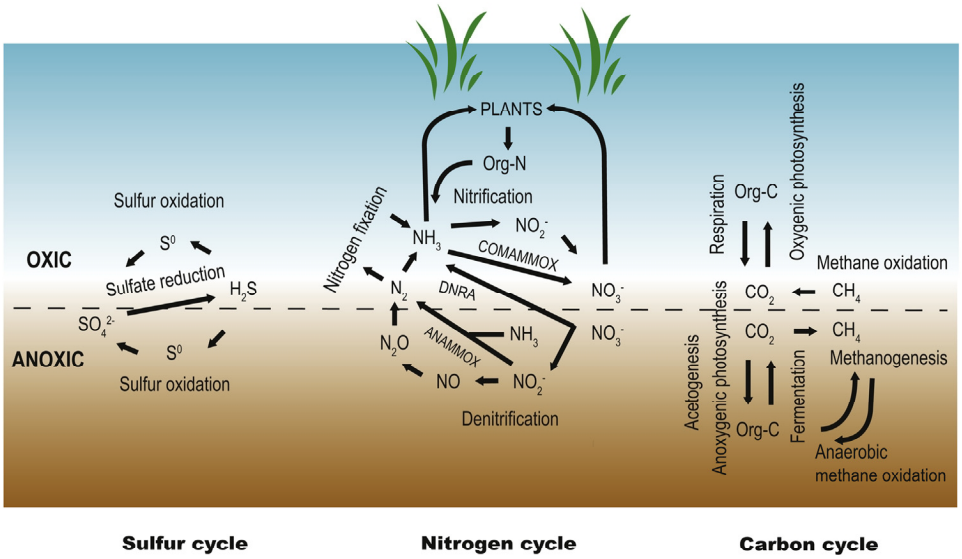

Fig. 6. Sediment biogeochemical cycles relevant to the wetland ecosystem. DNRA: dissimilatory nitrate reduction to ammonium; COMAMMOX: complete ammonia oxidation.

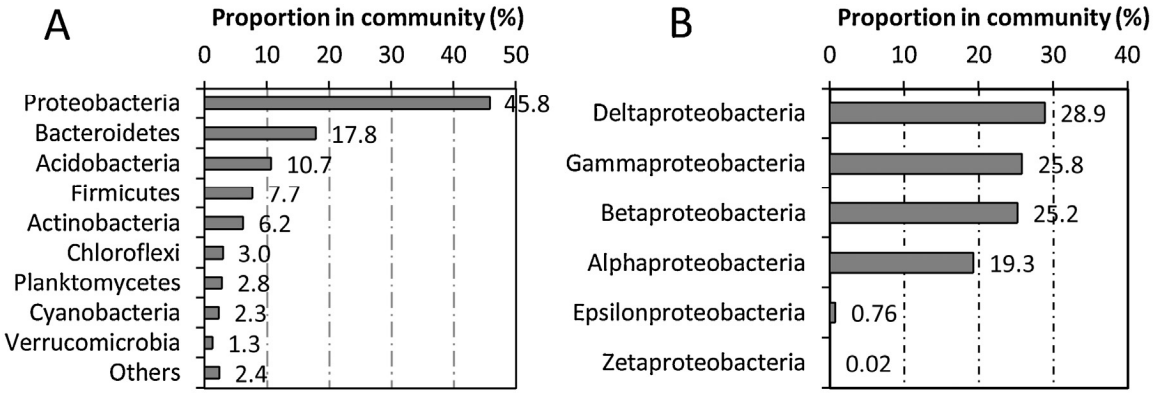

Fig. 7. Proportion in wetland soil/sediment community of Bacteria (A) and Proteobacteria (B). A total of 12583 bacterial sequences and 5637 proteobacterial sequences delivered from various wetlands are used. In order to avoid taxonomic uncertainties, sequences shorter than 250 bp were removed from the dataset. The source of data is from Lv et al. (2014).

mixture of eukaryotic algae (e.g. diatoms), cyanobacteria, heterotrophic bacteria, and detritus, which covers submerged surfaces in some oligotrophic wetland ecosystems (Hagerthey et al., 2011; Vymazal and Richardson, 1995). Not only does periphyton serve as an important food source for freshwater life, it can remove pollutants from the water column and limit their movement through the wetland environment (Gaiser et al., 2011). The periphyton can serve as an important water quality indicator and can be tested at a variety of scales representing physiological to community-level changes (McCormick and Stevenson, 1998; McCormick et al., 2006). For example, in the Florida Everglades, periphyton and floc frequently displayed greater sensitivity to alterations in environmental conditions than the underlying soil (Wright and Reddy, 2001).

There are also many bacterial primary producers, which carry out oxygenic photosynthesis in a similar fashion to that seen in macrophytes, and is summarized as:

$$6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6H_2O$$

Cyanobacteria are the primary oxygenic phototrophs among bacteria, and can be divided into 5 major morphological groups: 1) unicellular, 2) colonial, 3) filamentous containing heterocysts that are important in nitrogen fixation, 4) filamentous nonheterocystous, and 5) branching filamentous. They are represented by orders Oscillatoriales, Pleurocapsales, Chroococcales, Gloeobacterales, Stigonematales, and Nostocales, the latter two representing the heterocystous nitrogen-fixers (Madigan et al., 2015). A high diversity of cyanobacteria can be found in the water column and in the surface sediments of wetlands (Dorador et al., 2008b; Zhang et al., 2013). Since cyanobacteria are diverse, and do not represent a single monophyletic group, most studies target the bacterial 16S rRNA gene. Using a pyrosequencing approach, Zhang et al. (2013) found a decrease in cyanobacteria correlated with the degree of marsh degradation, while Jungblut et al. (2012) found evidence of broad environmental tolerance of cyanobacteria in Antarctic wetlands dominated by microbial mats. Others have targeted rRNA transcripts to monitor changes in cyanobacterial activity over diurnal cycles (Molina et al., 2016). Because of their role in both photosynthesis and nitrogen fixation, monitoring cyanobacterial diversity and abundance may help provide insight into both carbon and nitrogen cycling in wetland ecosystems.

4.1.2. Methanogenesis

Methanogenesis is an important process in wetlands, which are considered the largest natural source of methane emissions (Mitsch and Gosselink, 2015). The process of methanogenesis is carried out by members of the Archaea, forming one of the largest groups of Archaea. Currently six orders of

Table 3
Selected high-throughput sequencing applications for functional gene diversity analysis.

Functional group	Target	Target gene marker	Reference
Ammonia-oxidizing nitrifiers	Ammonia monooxygenase	*amoA*	Pester et al. (2012b)
Methanogenic archaea	Methyl-coenzyme M reductase	*mcrA*	Ellis et al. (2012)
Methane-oxidizing bacteria	Methane monooxygenase	*pmoA*	Lüke and Frenzel (2011)
Sulfate-reducing bacteria	Dissimilatory (bi)sulfite reductase	*dsrAB*	Bomberg et al. (2015)
Denitrifying bacteria	Nitrate reductase	*narG*	Palmer et al. (2012)
Denitrifying bacteria	Nitrite reductase	*nirK, nirS*	Palmer et al. (2012)
Denitrifying bacteria	Nitrous oxide reductase	*nosZ*	Palmer et al. (2012)
Nitrogen-fixing bacteria	Nitrogenase	*nifH*	Farnelid et al. (2001)
DNRA bacteria	Cytochrome C nitrite reductase	*nrfA*	Song et al. (2014a)

Currently 16S rRNA gene amplicon high-throughput sequencing is mainly used for microbial community analysis, but these functional genes have successfully been applied to microbial communities using high-throughput sequencing formats, as well as cloning and Sanger sequencing approaches. To our best of knowledge, the listed references are the first high-throughput sequencing applications for each functional gene. Although databases for sequence annotation are still primitive, the nature of high-throughput sequencing in which minor populations of microbial communities can be efficiently detected is suitable for functional gene diversity analysis. For *nifH* gene amplification, see Gaby and Buckley (2012).

methanogens have been recognized: Methanosarcinales, Methanomicrobiales, Methanococcales, Methanobacterales, Methanocellales and Methanopyrales (Madigan et al., 2015). The two leading sources of atmospheric methane include acetoclastic methanogenesis and hydrogenotrophic methanogenesis. Methanosarcinales can form methane from methylated compounds such as acetate (acetoclastic pathway), methanol and methylamines (methylotrophic pathway), summarized as:

$$H_3C\text{-}COOH \rightarrow CH_4 + CO_2$$

Other methanogens produce methane from the oxidation of hydrogen with carbon dioxide (hydrogenotrophic pathway).

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$$

The methyl-coenzyme M reductase (MCR) catalyzes heterodisulfide formation and subsequent release of methane by combining the hydrogen donor coenzyme B and methyl donor coenzyme M. MCR subunits are necessary for the production of cellular energy and are phylogenetically well-conserved within the lineages of methanogens. The protein is not found among Bacteria, Eukarya and other non-methanogenic Archaea (Madigan et al., 2015). Thus, methyl-coenzyme M reductase alpha subunit (*mcrA*) has been widely used as a suitable molecular marker for the detection and characterization of methanogenic archaeal communities in a wide range of natural and artificial environments and now it is ready to be used for high-throughput sequencing (Table 3). Methanogens are typically the most abundant Archaea in wetland sediment/soil (Lv et al., 2014), although in some salt marshes nitrogen-cycling Thaumarchaeota (formerly Crenarchaeota) may dominate (e.g. Nelson et al., 2009). In freshwater and wetland sediment, members of Methanomicrobiales and Methanosarcinales usually dominate the methanogenic community (He et al., 2015). Kao-Kniffin et al. (2010) examined the relationships of methanogenesis and nine wetland plant species and reported that methanogenic populations from *Juncus effusus* soils were dominated by acetoclastic archaea belonging to the family Methanosarcinaceae and Methanosaetaceae, while all other graminoid soils were primarily dominated by hydrogenotrophic archaea belong to the family Methanobacteriaceae. This differential distribution of methanogenic archaea among different habitats within wetlands indicates potential niche differentiation with the taxa, suggesting different ecophysiological traits and potential usefulness as microbial indicators.

4.1.3. Methanotrophs and methylotrophs

Methylotrophs are aerobic chemoorganotrophic bacteria that use organic compounds lacking C—C bonds as electron donors and carbon sources (Madigan et al., 2015). Some methylotrophs can use methane as an electron donor and carbon source, and are called methanotrophs. Thus, methanotrophy is a special case of methylotrophy. Since wetlands are an important source of methane to the atmosphere, these bacteria are common in wetland soil/sediment and greatly contribute in wetland carbon cycling (Fig. 6). The oxidation of methane to CO_2 is carried out in a series of steps, the first of which is catalyzed by the enzyme methane monooxygenase (MMO), producing formaldehyde from methane:

$$CH_4 \rightarrow CH_3OH \rightarrow CH_2O \rightarrow HCOO^- \rightarrow CO_2$$

Given the global importance of methane, its fate and the microbes responsible have been the target of many wetland studies. Oremland and Culbertson (1992) studied the activity of methane-oxidizing bacteria in lake and saltmarsh sediment and estimated that more than 90% of methane can be oxidized by methanotrophs; therefore only 10% of methane reaches the atmosphere. Siljanen et al. (2011) reported that the wettest area of a littoral wetland in a eutrophic boreal lake, comprising the highest methane oxidation, had the largest abundance and species richness of methanotrophic bacteria. Thus, it is important to study the dynamics of methanotrophic populations in wetland ecosystems as a process for global methane emission control. Abundance and diversity of methylotrophs and methanotrophs can be measured by targeting the *mxaF* gene and the *pmoA* gene, respectively. The *mxaF* gene codes for the large subunit of the enzyme, methanol dehydrogenase, which converts methanol to formaldehyde. Methanotrophs are typically characterized by the *pmoA* gene, which codes for the alpha-subunit of the particulate methane monooxygenase, and is evolutionarily related to the ammonia monooxygenase found in the AOB (Holmes et al., 1995). Both of these markers have been used successfully to study the abundance and diversity of methylotrophs/methanotrophs in wetland ecosystems (Siljanen et al., 2011).

Based on the differences of internal membrane structures, carbon assimilation pathways and methane monooxygenase genes, five types of methanotrophic bacteria are found. Type I methanotrophs are within the Gammaproteobacteria (Methylococcaeae and Crenotrichaceae) and use ribulose monophosphate as a carbon assimilation pathway. Type II methanotrophs belong to the Alphaproteobacteria (Methylocystaceae and Beijerinckiaceae) and use the serine pathway. Type X methanotrophs are classified in the Gammaproteobacteria and possess characteristics of both Type I and Type II methanotrophs. *Crenothrix polyspora*, a conspicuous uncultured filamentous bacterium, which is often found in drinking water systems, was recently identified as a methanotroph closely related to *Methylobacter* within the Gammaproteobacteria (Stoecker et al., 2006). This bacterium is characterized by its unique methane monooxygenase gene, which is more similar to ammonia monooxygenase genes of nitrifying bacteria than methane monooxygenase genes of other methanotrophs (Holmes

et al., 1995). One distant lineage of methanotrophic bacteria *Methylacidiphilum* belongs to Verrucomicrobiaceae and inhabits acidic geothermal environments (op den Camp et al., 2009).

Hanson and Hanson (1996) reported the ecophysiology of methanotrophs that set the foundation to use methanotrophs as microbial indicators. They described Type I methanotrophs (now regrouped as type Ia) as adapted to high oxygen and low methane conditions, while type II methanotrophs prefer high methane and low oxygen conditions, and type X methanotrophs (now regrouped as type Ib) possess characteristics of both Type Ia and Type II methanotrophs (Table 1). Siljanen et al. (2012) found the variation of methanotroph communities across seasons and associated hydrological conditions in boreal littoral wetlands. Type Ib freshwater-cluster methanotrophs were favored by the high water level condition while more stagnant hydrological conditions (i.e. low oxygen) during summer and fall induced the dominance of type II methanotrophs over type I methanotrophs. Chowdhury et al. (2014) found both Type I and II methanotrophs dominated in freshwater wetlands during winter. These observations suggest that the seasonal changes of diversity and activity of methanotrophic bacteria may serve as a new microbial indicator for wetland assessment (Table 1). Hernandez et al. (2015) attempted to understand the specific partnerships in methane oxidation between methanotrophs and methylotrophs using a microcosm experiment and 16S rRNA gene amplicon sequencing (Fig. 3). The methane-consuming populations were represented by two major types: the methanotrophs of the family Methylococcaceae and by non-methanotrophic methylotrophs of the family Methylophilaceae. The authors also found that different species persisted under different oxygen tensions. Examination of high initial oxygen tensions (150–225 μM) concluded major taxa were species of the genera *Methylosarcina* and *Methylophilus*. Comparatively, low initial oxygen tensions (15–75 μM) yielded dissimilar evidence; the major taxa were *Methylobacter* and *Methylotenera*. They concluded that oxygen availability is at least one major factor determining specific partnerships in methane oxidation and the possible oxygen gradient-dependent speciation within Methylococcaceae and Methylophilaceae. Based on our current understanding and detection abilities of methylotrophs and methanotrophs, they should both serve as important indicators in wetland ecosystems.

4.1.4. Anoxic methane oxidation

For a long time, biological methane oxidation was thought to require oxygen. Although all previously isolated methane oxidizers required oxygen to oxidize methane, this concept was not congruent with several sediment methane flux studies in which methane oxidation was observed in some anoxic marine and freshwater sediments (Reeburgh, 2007). Recent discoveries of anoxic methanotrophs backed up these environmental flux studies, and shed light on the hidden microbial functional diversities (Orphan et al., 2001). Currently it is estimated that almost 80% of methane produced from marine sediment is anaerobically oxidized (Reeburgh, 2007). The first discovery of an anoxic methanotroph (ANME) was associated with a unique consortium of two microorganisms: methanotrophic archaeum and sulfate-reducing bacterium (Orphan et al., 2001), with the overall reaction summarized as:

$$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O$$

The newly identified Archaea used methane as an electron donor and were phylogenetically closely related to other methanogens in the phylum Euryarchaeota. The electrons produced are transferred to the sulfate-reducing bacterium, which uses electrons to reduce sulfate to hydrogen sulfide. Although ANME is believed to oxidize methane to carbon dioxide by reversing the steps of methanogenesis, and electrons are transferred to the sulfate-reducing bacterium in some organic compounds, the complete mechanism of anoxic methane oxidation is unsolved (Hallam et al., 2004). Later variations of consortia formed were not with sulfate-reducing bacteria, but different microorganisms such as anammox and NC10 bacteria (Haroon et al., 2013; Raghoebarsing et al., 2006). NC10 bacteria can couple methane oxidation with nitrite reduction:

$$3CH_4 + 8NO_2^- + 8H^+ \rightarrow 3CO_2 + 4N_2 + 10H_2O$$

The second major discovery of anoxic methanotrophy was reported as a methane-oxidizing denitrifying consortium found in freshwater sediment where methane and nitrate are in sufficient supply (Ettwig et al., 2010). In these consortia, some contained ANME-associated methanotrophs while others were totally free of an archaeal partner. This newly found bacterium called *Methylomirabilis oxyfera* oxidizes methane with nitrate as an electron acceptor:

$$CH_4 + 4NO_3^- + 8H^+ \rightarrow CO_2 + 4NO_2^- + 2H_2O$$

But both the reduction of nitrate and the oxidation of methane are unique; nitrate is reduced to make nitric oxide without forming nitrous oxide as an intermediate and then nitric oxide is split into nitrogen gas and oxygen. This intracellularly-produced oxygen is used for the oxidation of methane to carbon dioxide. It should be noted that *M. oxyfera* was isolated from a small polluted canal in the Netherlands (Ettwig et al., 2010). Few studies in wetlands to date have investigated anoxic methane oxidation, although Prasse et al. (2015) reported ubiquitous distribution of ANME in restored tidal freshwater wetlands, based on analysis of 16S rRNA pyrosequencing data. As wetlands are the chief natural source of atmospheric methane, further ecological studies of anoxic methane oxidation are strongly required for better understanding of wetland methane dynamics (Segarra et al., 2015).

4.2. Nitrogen cycle and associated microbes

4.2.1. Ammonia-oxidizing bacteria and archaea

Ammonia-oxidizing microorganisms have been well characterized in both terrestrial and marine environments, as well as natural and artificial environments (Urakawa et al., 2011). This microbial functional group includes ammonia-oxidizing bacteria (AOB) and archaea (AOA). The oxidation of ammonia to nitrite is the first, and rate-limiting, step in the complete oxidation of ammonia to nitrate. In the well-characterized AOB, the process consists of two reactions that are catalyzed by two different enzymes.

$$1)NH_3 + O_2 + 2e^- \rightarrow NH_2OH + 2H_2O$$

$$2)NH_2OH + H_2O \rightarrow NO_2^- + 5H^+ + 4e^-$$

The first reaction is catalyzed by the ammonia monooxygenase (AMO), coded for the *amo* operons (*amoCAB*). The alpha subunit of the *amo* is the most frequently targeted functional gene marker (*amoA*), and is found in all known AOB. Hydroxylamine has been shown to be a product of both the bacterial and archaeal AMO (Vajrala et al., 2013) in this first reaction. The second reaction is catalyzed by hydroxylamine oxidoreductase (HAO) in AOB, however, characterized archaeal ammonia oxidizers lack homologs of the hydroxylamine oxidoreductase (Walker et al., 2010), suggesting that the oxidation of hydroxylamine to nitrite may be carried out by a novel enzyme system that possibly involves periplasmic multicopper oxidases (Walker et al., 2010; Urakawa et al., 2011).

Currently AOB include four genera, *Nitrosospira* and *Nitrosomonas* in the Betaproteobacteria and *Nitrosococcus* and "*Candidatus* Nitrosoglobus" in the *Gammaproteobacteria* (Hayatsu et al., 2017). AOA belong to *Thaumarchaeota* group I.1a (*Nitrosopumilus*, "*Ca*. Nitrosoarchaeum", "*Ca*. Nitrosotenuis"), group I.1a-associates

("*Ca.* Nitrosotalea"), group I.1b (*Nitrososphaera,* "*Ca.* Nitrosocosmicus") and "*Candidatus* Nitrosocaldus" (HWCG III) (de la Torre et al., 2008). Although AOA and AOB share a similar range of substrates (i.e. ammonia and urea), these two groups are phylogenetically distant. As they are phylogenetically easily differentiated, various molecular microbiology techniques have been developed and applied for the estimation of diversity (clone library analysis, high-throughput sequencing) and quantity (quantitative PCR assay) of these microorganisms by using 16S rRNA and ammonia monooxygenase genes as phylogenetic and functional markers, respectively (Rotthauwe et al., 1997; Francis et al., 2005). Moreover, studies of ecophysiology of isolated/enriched microorganisms have greatly facilitated a better understanding of their ecological adaptation and strategies (Martens-Habbena et al., 2009; Prosser and Nicol, 2012). Culture-dependent studies have also revealed mixotrophic growth properties of some AOA (Qin et al., 2014), and possible interactions between AOA and helper microorganisms through hydrogen peroxide production and consumption (Kim et al., 2016).

A large number of field studies have demonstrated that (1) AOA fit more oligotrophic conditions than AOB (Jia and Conrad, 2009; Verhamme et al., 2011; Zhou et al., 2016), (2) AOA show better adaptation to low pH soil than AOB (Lehtovirta-Morley et al., 2016), (3) AOA are more sensitive to pollutants than AOB (Rodriguez-R et al., 2015; Sipos and Urakawa, 2016; Urakawa et al., 2012). Thus, the study of functional redundancy of AOA and AOB can serve as the best example of the use of microbial indicators for wetland ecosystem management (Table 1). The dominance of AOA as the primary nitrifiers has been documented from a wide range of environments (Beman et al., 2012; Urakawa et al., 2014). Particularly, the contribution of AOA in nitrification is maximized in pelagic zones where nutrient levels are very low and AOB abundance is negligible (Fig. 4) (Beman et al., 2008; Santoro et al., 2010). An increase of salinity is likely a barrier for betaproteobacterial AOB to adapt in marine environments; AOB decreases with the increase of salinity (Bernhard et al., 2007), as well as other Betaproteobacteria (Glöckner et al., 1999). Thus, the diversity and abundance of AOA and AOB, and *Nitrosomonas* and *Nitrosospira* could serve as microbial indicators (Table 1). For example, the soil AOA/AOB ratio can be used to infer eutrophic or oligotrophic status in wetland conditions (Sims et al., 2013). Urakawa et al. (2014) reported that ammonia availability was a major factor to determine the AOA and AOB distribution and nitrification activity in coastal water. Before the discovery of AOA, ecological K- and r-strategists were discussed within *Nitrosospira* and *Nitrosomonas*, respectively (Schramm et al., 1998). It was thought that *Nitrosomonas* species were more adapted to eutrophic environments while *Nitrosospira* species preferred more oligotrophic environments. Taylor and Bottomley (2006) reported that low extractable ammonia levels in soil may drive the dominance of *Nitrosospira* in major soil environments, while *Nitrosomonas* may be poised to take advantage of much higher extractable ammonia level. Since now AOA are considered as an indicator of oligotrophic adaptation (Jia and Conrad, 2009; Martens-Habbena et al., 2009; Verhamme et al., 2011), functional redundancy between AOA and *Nitrosospira* needs to be addressed more carefully in the future. Zhou et al. (2016) reported that *Nitrosospira* were less abundant than *Nitrosomonas* in a polluted Chinese artificial canal where AOA abundance and the contribution to potential nitrification activity were limited due to its eutrophic condition. It has been reported that *Nitrosomonas*, not *Nitrosospira*, were major nitrifiers in highly-polluted marine sediments in Japan (Urakawa et al., 2006a, 2006b). These results were in contrast to the case in salt marsh studies, in which *Nitrosospira* were the major AOB (Bernhard et al., 2005; Francis et al., 2003), although in highly fertilized salt marshes, *Nitrosomonas* dominated (Peng et al., 2013). In addition, the recent discovery of non-halophilic and acid-adapted gammmaproteobacterial ammonia oxidizing bacterium, "*Candidatus* Nitrosoglobus terrae" from acidic agricultural soil may change the current view of niche differentiation between AOA and AOB in acidic soil (Hayatsu et al., 2017).

4.2.2. Nitrite-oxidizing bacteria

Nitrite oxidation is the second step in the complete nitrification of ammonia to nitrate and is summarized by the following equation:

$$NO_2^- + \tfrac{1}{2}O_2 \rightarrow NO_3^-$$

Nitrite-oxidizing bacteria (NOB) utilize the enzyme nitrite oxidoreductase to catalyze the reaction. In many textbooks *Nitrobacter* are coined as representative NOB in nature. However, multiple molecular ecology studies have demonstrated that *Nitrospira* are more abundant, and are likely key players of nitrite oxidation in natural and engineered ecosystems (Juretschko et al., 1998; Schramm et al., 1998), although more recently, Pelissari et al. (2017) used next-generation sequencing of 16S rRNA genes and found *Nitrobacter* to be the dominant nitrite-oxidizers in a constructed wetland. One recent exciting finding was that nitrite oxidation was discovered in the lineage of phylum *Chloroflexi* (Sorokin et al., 2012), although their metabolic versatility is only partially understood (Koch et al., 2015). The members of *Nitrospira* are generally considered to favor oligotrophic environments in comparison with *Nitrobacter* (Nowka et al., 2015). It should be noted that not all *Nitrospirae* detected by 16S rRNA at the phylum level or Nitrospira at the class level are nitrite-oxidizers. The phylum *Nitrospirae* includes functionally different groups such as sulfate-reducing bacteria (*Thermodesulfovibrio*) and iron-oxidizing bacteria (*Leptospirillum*). The phylum *Nitrospirae* is formed by only one class (*Nitrospira*), one order (*Nitrospirales*) and one family (*Nitrospiraceae*). The reason for the confusion is from the identical taxon name of *Nitrospira* (class) and *Nitrospira* (genus). Thus, genus-level identification is required to use 16S rRNA sequence data to attribute them to nitrogen cycle. Compared to other microbes involved in the nitrogen cycle, nitrite-oxidizing bacteria have been the least well-studied, likely due to their low abundance and lack of a well-characterized functional gene as a target. The few studies conducted in wetlands have often quantified NOB based on their relative abundance in bacterial 16S rRNA gene sequencing datasets (Pelissari et al., 2017) or by qPCR analysis of 16S rRNA genes using primers specific for *Nitrospira* or *Nitrobacter* 16S rRNA genes (e.g. Ke et al., 2015).

4.2.3. Complete ammonia oxidizers (COMAMMOX)

In every textbook, nitrification has been explained as a biogeochemical process driven by two functionally distinct groups of microorganisms, the ammonia-oxidizing microorganisms and the nitrite-oxidizing bacteria (Fig. 6). For more than 125 years, this textbook knowledge was the foundation for hundreds of studies on nitrification in various environments, including wetland studies. However, the recent discovery of complete ammonia oxidizers (comammox) changed the more than 100-year dogma of nitrification (Daims et al., 2015; van Kessel et al., 2015). Taxonomically they are characterized as within the phylum *Nitrospira* and have unique ammonia monooxygenase genes (Daims et al., 2015; van Kessel et al., 2015). The first isolation of a comammox bacterium, "*Candidatus* Nitrospira inopinata", was cultivated from a biofilm on the walls of a pipe from a deep oil exploration well, and is a moderate thermophile (Daims et al., 2015). Since the discovery of comammox, metagenomic queries have revealed that comammox is widely distributed, but the process was simply overlooked. The only environment where no comammox genes were detected was oceanic environments, suggesting comammox may be more important in freshwater wetlands compared to salt marshes. There are

currently primer sets available that target the comammox ammonia monooxygenase gene (Daims et al., 2015), but it is too soon to know much about their activity and abundance in wetlands.

4.2.4. Denitrifiers

Denitrification is the primary process removing nitrate from overlying wetland waters and pore waters in sediment (e.g. Bachand and Horne, 1999a, 1999b), and can be summarized by the following reaction:

$$NO_3^- + 6\,H^+ + 6\,e^- \rightarrow \tfrac{1}{2}N_2 + 3H_2O$$

It is considered as a primary path of nitrogen loss from most kinds of wetlands (Fig. 6). Most denitrification is thought to be carried out by prokaryotes spanning broad phylogenetic groups (Shapleigh, 2005), although there has been a report of eukaryotic denitrification (Risgaard-Petersen et al., 2006). Despite denitrification is one of the most important microbial processes in wetlands, the monitoring of denitrifying microorganisms using 16S rRNA gene is problematic. Since denitrifiers do not compose specific 16S rRNA groups, the tracking of functional genes is a widely accepted alternative approach to elucidate the biodiversity of denitrifiers in nature. Copper-containing nitrite reductase (*nirK*) and heme-containing nitrite reductase (*nirS*) are two key enzymes for denitrification, and are widely used as molecular gene markers (Table 3) (Braker et al., 1998; Hallin and Lindgren, 1999). To date, the two genes are mutually exclusive and appear to have differential distributions in wetland sediments (Desnues et al., 2007; Nogales et al., 2002; Priemé et al., 2002; Santoro et al., 2006), so surveys for both genes should be done to fully characterize denitrifiers. A third functional gene for the nitrous oxide reductase (*nosZ*) has also been used frequently to detect and characterize denitrifying bacteria (Henry et al., 2006), although not all denitrifiers have this enzyme, and are therefore not capable of denitrifying all the way to N_2. By computing ratios of *nosZ* to *nirS* and/or *nirK*, one can identify the proportion of denitrifiers that produce N_2O instead of N_2. For management objectives, abundance and biodiversity of functional genes can be measured between restored and natural wetlands (Peralta et al., 2010, 2013a; Bernhard et al., 2015).

Sediments with high organic matter and anoxic conditions provide an ideal environment for denitrification, and not surprisingly, high denitrification rates have been recorded in salt marshes (see Seitzinger, 1988 for review). Abundance of denitrifying bacteria has been reported to vary seasonally in wetland sediments, as the availability of substrate fluctuates (Lisa et al., 2015). Despite the high rates and importance of the process, relatively few studies of the diversity of denitrifying bacteria have been conducted in wetlands. A few studies in salt marshes have revealed high diversity based on *nir*S genes (Bowen et al., 2011, 2013; Bernhard et al., 2015), as well as significant responses to disturbance.

Although there is a high diversity of denitrifiers in many environments, direct denitrification activity measurements may also be helpful to assess this important ecosystem service performed by soil/sediment microorganisms. It is reported that hydrologic history may influence denitrification activity; potential denitrification rates significantly increased under wetter conditions (Peralta et al., 2013a). In wetland studies, an acetylene blocking method has been widely used (Bastviken et al., 2003; Hernandez and Mitsch 2007; Song et al., 2014b) and provided the direct evidence for the existence of certain kinds of denitrifiers and a rough estimate of their density (Faulwetter et al., 2009). Nowadays, the use of ^{15}N stable isotope is considered as more accurate and highly encouraged (Bergsma et al., 2002; Morse and Bernhardt, 2013). There are some problems when the acetylene blocking technique is used to determine denitrification rates, including the inhibition of nitrification, removal of free sulfide during the exchange of gas phase, disruption of the sediment redox gradients and the incorrect assumption that all N_2O produced is the result of denitrification (i.e. ignoring DNRA) (Burgin and Hamilton, 2007). Nevertheless, because nitrate diffusion rates in wetland soils are seven times faster than ammonium diffusion rates, ammonium diffusion and subsequent nitrification appear to limit the entire process of nitrogen loss by denitrification (Mitsch and Gosselink, 2015).

4.2.5. Anaerobic ammonium oxidation (ANAMMOX)

In 1999, a bacterial group that mediates ammonia oxidation under anaerobic conditions was discovered (Strous et al., 1999a). In this microbiological process, nitrite and ammonium are converted directly into nitrogen gas, thus two nitrogen species are simultaneously removed from the system, as summarized by the equation:

$$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$$

It has been reported that this process may be responsible for 30–50% of the nitrogen gas produced in the oceans (Devol, 2003). The bacteria that perform the anammox process belong to the phylum Planctomycetes. Currently, five anammox genera have been discovered from freshwater (*Brocadia*, *Kuenenia*, *Anammoxoglobus* and *Jettenia*) and marine environments (*Scalindua*) (Jetten et al., 2009), and three of these (*Brocadia, Kuenenia, and Scalindua*) have been found in wetland ecosystems (Ligi et al., 2014). All recognized species possess one anammoxosome, a membrane-bound compartment inside the cytoplasm, which plays a central role in the anammox catabolism. A unique ecological feature of anammox bacteria is their extremely slow doubling time (7–22 days) (Kartal et al., 2013) and they have a high affinity for their substrates (ammonium and nitrite) to support their low nutrient adaptation (Strous et al., 1999b). Though these bacteria are commercially used in wastewater treatments, their fastidious nature (i.e. slow growth, oligotrophic) has prevented us from deploying anammox bacteria into constructed wetlands aiming at reducing nitrogen loads (Paredes et al., 2007).

Although our current understanding of anammox abundance and diversity in wetland environments is in its infancy, recent research on anammox bacteria in wetlands, employing a variety of techniques, has begun to fill the knowledge gap. Koop-Jakobsen and Giblin (2009) measured low anammox activity relative to denitrification along a salinity gradient in salt marsh sediments receiving high nitrogen loads, reporting highest anammox activity in the freshwater end. Similarly, Jiang et al. (2017) found highest anammox activity and abundance at low salinity in slurry experiments using intertidal wetland sediments. Anammox diversity, based on 16S rRNA gene sequencing, however, increased along the salinity gradient. In coastal wetlands in China, Hou et al. (2015) reported that temperature was the strongest driver of anammox diversity and abundance, using isotope tracing techniques and 16S rRNA gene sequencing. Additional studies have employed the use of the marker gene, hydrazine oxidoreductase (*hzo*) as an alternative method for monitoring anammox bacteria (Li et al., 2010), and a recent study in a North Carolina estuary reported significant seasonal variation of anammox activity, but not gene abundance as measured by the *hzo* gene (Lisa et al., 2014). As additional studies of anammox in wetlands are conducted, the utility of the different markers may become more clear (Burgin and Hamilton, 2007).

4.2.6. Dissimilatory nitrate reduction to ammonium

Like denitrification, dissimilatory nitrate reduction to ammonium (DNRA) is another respiratory pathway in the microbial nitrogen cycle. But unlike denitrification, which leads to the loss of nitrogen from the system, DNRA returns the nitrogen in the form of ammonium to the environment (Fig. 6). Thus the balance of DNRA

to denitrification can have a significant impact on the availability of nitrogen. The process can be summarized as follows:

$$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+$$

The conversion of nitrite to ammonium is a 6-electron step:

$$NO_2^- + 6[H] + 2H^+ \rightarrow NH_4^+ + 2H_2O$$

and is catalyzed by the cytochrome C nitrite reductase (NRF). The protein is coded for by the gene (*nrfA*) and serves as a target gene to measure abundance and diversity of microbes capable of carrying out DNRA (Table 3). Microbes that carry out DNRA are diverse, and include members in the Proteobacteria, Bacteroidetes, Firmicutes, and Planctomycetes (Mohan et al., 2004; Simon and Klotz, 2013). Studies of DNRA in wetlands are limited, particularly those that have targeted the microbes responsible, but several recent studies have begun to suggest that DNRA may be an important microbially-mediated process in some coastal environments (Tobias et al., 2001; An and Gardner, 2002; Koop-Jakobsen and Giblin, 2010; Dong et al., 2011). It is thought that certain conditions, such as high C/N ratios, high sulfide, and high salinity may favor DNRA over denitrification (Burgin and Hamilton, 2007; Giblin et al., 2013). Recently, Song et al. (2014a) using high-throughput sequencing of the *nrfA* genes and DNRA activity measurements in a shallow lagoon estuary system, found a correlation between *nrfA* diversity and DNRA activity, which also corresponded to higher organic matter. Based on their findings, Song et al. (2014a) proposed that the abundance of bacteria capable of DNRA may be an important regulator for the process in aquatic systems. With the recent development of methods to track the abundance of DNRA bacteria, more studies should be expected and should help elucidate the complex fate of nitrogen in wetland environments.

4.2.7. Nitrogen fixation

Nitrogen is an essential element for all life, but a majority of it is in the form of nitrogen gas, which is extremely stable (triple bonds in N_2) and the most common element in the earth's atmosphere (78% of air). Some prokaryotes have the capability to tap this nitrogen resource through the process called nitrogen fixation in which nitrogen gas is enzymatically converted to ammonia:

$$N_2 + 8H^+ \rightarrow 2NH_3 + H_2$$

Nitrogen fixation is a vital process for sustaining life on Earth through the supply of sufficient amount of nitrogen for other life forms. The function of nitrogen fixation is dispersed widely in the lineages of Bacteria and Archaea, but it has not been discovered in Eukarya (Zehr et al., 2003). Nitrogen-fixation bacteria are called diazotrophs and divided into two groups: one is mutualistic bacteria and the other is free-living bacteria (Bodelier et al., 2006). In wetlands, both types of bacteria flourish and play a fundamental role in nitrogen cycle (Bodelier et al., 2006; Šantrůčková et al., 2010). Symbiotic nitrogen fixation can be found in a wide variety of aquatic plant rhizospheres including *Spartina alterniflora* (Chelius and Lepo, 1999; Whiting et al., 1986), *Kandelia obovata* (Weng et al., 2013), *Oryza sativa* (Roger and Ladha, 1992; Sun et al., 2008; Ueda et al., 1995a, 1995b) and *Azolla* spp. (Lumpkin and Plucknett, 1980).

Nitrogen fixation is catalyzed by an enzyme complex called nitrogenase, which is formed by two proteins, dinitrogenase and dinitrogenase reductase (Seefeldt et al., 2009). Both proteins require iron while dinitrogenase additionally requests molybdenum to form iron-molybdenum cofactor. The reaction center of the nitrogenase is able to cleave the extraordinarily stable nitrogen molecule. Nitrogen fixation is inhibited by molecular oxygen because dinitrogenase reductase is sensitive to oxygen. Since many diazotrophs are obligate aerobes, nitrogenase is protected from oxygen inactivation by means of slime layer production and rapid respiration (Madigan et al., 2015). Heterocysts, differentiated cells that specialize in nitrogen fixation found in some cyanobacterial species, are a good example of how cells protect nitrogenase from oxygen exposure.

Molecular analyses targeting the nitrogenase reductase gene (*nifH*), encoding the conserved iron–protein subunit of the nitrogenase enzyme complex, has been widely used in microbial ecology including wetland studies (Bodelier et al., 2006; Chelius and Lepo, 1999; Gaby and Buckley, 2012; Lovell et al., 2000; Ueda et al., 1995a, 1995b; Zehr et al., 1997, 2003) and successfully used in the 454 pyrosequencing platform (Farnelid et al., 2011) (Table 3). One high-throughput sequencing study using *nifH* gene for invasive *Spartina* rhizosphere showed that invasive plants may alter not only the landscape of wetlands, but also the nitrogen balance of wetlands (Huang et al., 2016). All research indicates the importance of Proteobacteria as diazotrophs of wetland plant rhizospheres.

4.3. Sulfur cycle and associated microbes

Sulfur is a popular target of bioremediation in constructed wetlands because it is highly reactive, redox-sensitive, and harmful for aquatic life when it is reduced (Sturman et al., 2008). Sulfur is used as a sole energy source by some chemolithotrophic bacteria and archaea (Fig. 6). Widely dispersed dissimilative sulfur metabolism on the evolutionary tree of life is supported by the chemical diversity of sulfur compounds found in nature. Sulfur has eight oxidation states that range from its most oxidative form, sulfate (SO_4^{2-} [oxidation state of +6]) to thiosulfate ($S_2O_3^{2-}$ [+2]), to elemental sulfur (S^0 [0]), to hydrogen sulfide (H_2S [−2]) as its most reduced form. Sulfur compounds have diverse forms including inorganic sulfur compounds, organosulfur compounds, and metal sulfides.

4.3.1. Sulfate-reducing bacteria

Microbial sulfate reduction is one of the essential biogeochemical processes within the sulfur cycle (Fig. 6). Sulfate-reducing bacteria (SRB) use sulfate as a terminal electron acceptor, and produce hydrogen sulfide, carbon dioxide and water via anaerobic respiration. SRB are an assembly of anaerobic bacteria that can acquire energy by oxidizing molecular hydrogen or organic compounds while reducing sulfate to hydrogen sulfide.

$$SO_4^{2-} + 2CH_2O + 2H+ \rightarrow H_2S + 2CO_2 + 2H_2O$$

SRB can establish diverse life styles, such as sulfidogenic, acetogenic, and hydrogenogenic metabolism (Plugge et al., 2011). Prokaryotes capable of sulfate reduction occur in both bacterial and archaeal lineages. Thus, sulfate reducers are also known as SRP (sulfate-reducing prokaryotes) or SRM (sulfate-reducing microorganisms) (Castro et al., 2002; Pester et al., 2012a). SRB occur in four bacterial phyla (Proteobacteria, Firmicutes, Nitrospirae and Thermodesulfobacteria) that contain more than 60 genera and 220 species (Parte, 2014). Due to their great ecological importance, SRB studies have intensified in the last few decades (Muyzer and Stams, 2008). For example, SRB act as important mediators of various processes in biogeochemical cycles, including mercury (Han et al., 2010; Kim and Zoh, 2012) and anaerobic methane oxidation (Orphan et al., 2001). As dissimilatory sulfate reducers, the bacteria can be found in marine sediments where they perform nearly half of all organic mineralization (Plugge et al., 2011). Park et al. (2009) reported that SRB reached up to 40% of the total bacteria, indicating the importance of SRB in sulfate reduction and overall biochemical processes in constructed wetland sediments (Pester et al., 2012a). Since SRB rely on anaerobic respiration, their abundance and activity are higher in wet sediment than dry soil (Zhang et al., 2013). Molecular analyses using *dsrAB* as marker genes demonstrated that members of novel phylogenetic lineages, which are unrelated to

currently recognized SRB, exist in wetland sediment and may play an important role as a part of the autochthonous wetland microbiota (Table 3).

4.3.2. Sulfur-oxidizing bacteria

Reduced sulfur compounds, such as hydrogen sulfide, elemental sulfur, sulfite and thiosulfate are mainly oxidized as electron donors in energy conservation by three phyla of Bacteria (Aquificae, Deinococcus-Thermus, and Proteobacteria) and a lineage of Archaea (Crenarchaeota) (Madigan et al., 2015). Hydrogen sulfide, elemental sulfur, and thiosulfate are the most common compounds used as electron donors. When sulfide is the substrate, the final product may be either sulfate or sulfur:

$$H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+$$

$$HS\text{-} + 1½O_2 + H+ \rightarrow S^0 + 2H_2O$$

When sulfur or thiosulfate is used as the substrate, the final product is also sulfate:

$$S^0 + H_2O + 1½O_2 \rightarrow SO_4^{2-} + 2H^+$$

$$S_2O_3^{2-} + H_2O + 2O_2 \rightarrow 2SO_4^{2-} + 2H^+$$

In an aerobic environment, these dissimilative sulfur oxidizers use oxygen as an electron acceptor but nitrate is often used in anoxic conditions. In general, the size of sulfur-oxidizing bacteria is larger than other bacteria and it allows the sulfur-oxidizing bacteria to store sufficient nitrate, sulfur granules, carboxysomes, and calcium carbonate into their cells. Some groups of sulfur-oxidizing bacteria are filamentous (e.g. *Thiothrix*, *Thioploca*, *Beggiatoa*). Notably the largest bacterium ever reported is also a sulfur oxidizer, *Thiomargarita namibiensis*, which was discovered off the Namibian coast, southwest Africa (Schulz and Schulz, 2005). Microbial mats of sulfur-oxidizing bacteria are common in organic rich estuarine wetlands (i.e. mangrove forests, tape-grass beds, salt marshes). But if white microbial mats are found in freshwater wetlands, it indicates the sediment is anoxic and highly organic rich (e.g. polluted ditch, canal, shallow lake sediment) or a source of water is acidic or includes high concentrations of hydrogen sulfide (e.g. streams of mine drainage or sulfur rich groundwater) (Nicomrat et al., 2006). Since hydrogen sulfide produced by SRB is toxic for most of life forms, detoxification of hydrogen sulfide by sulfur-oxidizing bacteria is a remarkable ecosystem service (Stubner et al., 1998; Urakawa et al., 2017). Using most probable number assays and cultivation techniques, sulfur-oxidizers were shown to be important in the functioning of an artificial wetland constructed to remediate wastewater from a tannery (Aguilar et al., 2008). More recently, Thomas et al. (2014) investigated sulfur oxidizer diversity and transcriptional activity in salt marsh sediments using 16S rRNA amplicon sequencing and two marker genes of the S-oxidation pathway, sulfate thiohydrolase (*soxB*) and reverse sulfite reductase (*rdsrAB*). They found that S-oxidizer transcripts were particularly abundant on roots, confirming the importance of S-oxidation for removing toxic hydrogen sulfide from plants and surrounding sediments.

4.3.3. Anoxygenic phototrophs

Anoxygenic phototrophs are widely spread out within bacterial lineages and play an important role in the anaerobic sulfur cycling process (Fig. 6). These anoxygenic phototrophs include purple sulfur bacteria (Gammaproteobacteria), purple non-sulfur bacteria (Alphaproteobacteria and Betaproteobacteria), green sulfur bacteria (Chlorobi), green non-sulfur bacteria (Chloroflexi) and a few other phototrophic bacteria Heliobacteria [Firmicutes], *Chloracidobacterium* (Acidobacteria) (Madigan et al., 2015).

Purple sulfur bacteria are a group of microorganisms that use hydrogen sulfide as an electron donor for anoxygenic photosynthesis:

$$H_2S + CO_2 + \text{light} \rightarrow S + CH_2O$$

These bacteria belong to the order Chromatiales in the Gammaproteobacteria. Purple sulfur bacteria are often observed in high density in meromictic lakes and change the color of water to bright red, which is caused by their carotenoids contained in the cell (Baatar et al., 2016; Brocks and Schaeffer, 2008; Ovreås et al., 1997). Two groups of purple sulfur bacteria are recognized based on the different patterns of sulfur granule accumulation and internal cell photosynthetic membranes. The members of the family Chromatiaceae do not have the internal cell photosynthetic membranes but maintain the globules of elemental sulfur inside the cells. The members of the family Ectothiorhodospiraceae have intracellular photosynthetic membrane systems and sulfur granules are deposited outside the cells. Many of these species are extremely halophilic or alkaliphilic and common in saline lakes, soda lakes and salterns (Madigan et al., 2015).

Purple non-sulfur bacteria are the most metabolically versatile of all microorganisms and potentially play a significant role in wetland ecosystems. They are morphologically and phylogenetically diverse and belong to the Alphaproteobacteria and Betaproteobacteria. Purple non-sulfur bacteria use low concentrations of hydrogen sulfide as an electron donor for the reduction of carbon dioxide. Under a dark, oxic condition, photosynthetic machinery is repressed by oxygen; organic compounds or hydrogen are used as electron donors. Under the light, purple non-sulfur bacteria subsist in two ways. One is photoheterotrophy, and the other is photoautotrophy ($CO_2 + H_2/CO_2$ + low level of H_2S). They can also fix nitrogen. *Rhodopseudomonas*, *Rhodospirillum* and *Rhodobacter* are well recognized genera in this group.

Green sulfur bacteria (Chlorobi) are non-motile anoxygenic phototrophs and utilize hydrogen sulfide as an electron donor, oxidizing it first to elemental sulfur and then to sulfate. The sulfur is deposited outside the cell. Most species can assimilate a few organic compounds in the light (photoheterotrophy). Green non-sulfur bacteria (Chloroflexi) are evolutionarily old and considered the oldest phototrophs. This filamentous anoxygenic phototroph has hybrid photosynthetic features of green sulfur bacteria and purple bacteria. It can grow faster as photoheterotrophs than as phototrophs, and can grow aerobically in the dark on a wide variety of carbon sources. They have unique membrane lipids containing 1,2-dialcohols instead of glycerol. As other unique features, they have a hydroxypropionate cycle and lack peptidoglycan (Madigan et al., 2015).

Heliobacteria are the only firmicutes known to conduct photosynthesis. They are phylogenetically assigned within Clostridia and form heat-resistant endospores as well as other members of Clostridia but interestingly they are gram-negative. The primary pigment involved is bacteriochlorophyll *g*. The heliobacteria are nitrogen-fixing phototrophs, requiring organic carbon sources. They are obligate anaerobes and grow without light by fermentation. The members of heliobacteria have been found in waterlogged soils, suggesting their importance in wetlands (Madigan and Ormerod, 1995). One more phototrophic bacterial lineage was recently discovered in the phylum Acidobacteria (*Chloracidobacterium*) (Bryant et al., 2007).

A variety of anoxygenic phototrophs have been documented in wetland environments and their role in coastal microbial mats has been recently reviewed (Hubas et al., 2011). Urakawa et al. (2017) reported a remarkable diversity of sulfate reducers and anoxygenic phototrophs in the rhizosphere of floating treatment wetland plants and suggested potential production and consump-

tion of hydrogen sulfide in a water column beneath the floating treatment wetland. Using a high-throughput sequencing approach, Abed et al. (2014) found frequent occurrence of both purple sulfur and purple non-sulfur bacteria in a cyanobacterial mats in a constructed freshwater wetland for remediation of oil-polluted waters, and found the bacterial communities to be impacted most by oil and ammonia levels. These microbial mats play important roles in both carbon and sulfur cycling in coastal wetlands, thus contributing to the overall biogeochemistry of the ecosystem.

5. Human impacts, wetland management and wetland microbiology

5.1. Assessment of wetland restoration projects

Wetland losses transpire as a result of both anthropological activity and natural processes. Many constructed wetlands have been made worldwide and offer an effective means for treatment of wastewater from a variety of sources (Henry-Silva and Camargo, 2006; Vymazal, 2007). With the Everglades as an example, some natural wetlands are very sensitive to human-induced environmental changes, but on the other hand, many wetlands located on human-populated areas play a role as a buffer zone contributing to nutrient removal. Some types of constructed wetlands are classified by the difference of hydraulic designs, such as surface flow, horizontal subsurface flow and vertical flow (Vymazal, 2007). Wetland mitigation is implemented to substitute ecosystem functions delivered by natural wetlands; however, restoration efforts often fail to rebuild equivalent levels of ecosystem services (Fig. 5) (Peralta et al., 2010). Understanding of the microbial communities controlling biogeochemical cycles in constructed wetlands could provide insight into how to optimize the performance of these promising treatment systems (Faulwetter et al., 2009; Peralta et al., 2010; Wei et al., 2011). Wetland landscape restoration may alter previous soil/sediment properties, hydrology and water quality conditions. Based on the restoration strategy, various environmental parameters such as nutrient level, pH, oxygen level, and salinity may be altered and these changes should be sharply reflected by microbial communities (Sims et al., 2012a). Acidity of soil is recognized as a strong driving force in shaping unique microbial communities (Hartman et al., 2008; Peralta et al., 2013b). For example, soil AOA (Thaumarchaeota I.1a) has been reported as a major ammonia oxidizer in acidic soil environments (Zhao et al., 2015). In addition, the I.1c Thaumarchaeota, a group of uncultured slow-growing organotrophs, prefers low pH soil environments (pH 5 or below) and is influenced by the presence of plant roots and mycorrhizal fungi (Bomberg, 2016). Thus, microbial indicators may serve as one of the core elements of wetland management and protection.

Although there are many other macrobiological indicators currently in use (see Sims et al., 2013 for a review), microorganisms have some advantages over macroorganisms (Fig. 2). Due to their rapid growth rates, microorganisms are poised to respond very quickly to changes in the environmental conditions and can be very sensitive to certain pollutants (e.g. Urakawa et al., 2012). However, assessment of wetland conditions cannot be effectively achieved by a single physical, chemical or biological factor, but a combination of multiple indices is useful for wetland assessment (Sims et al., 2013). Microbial indicators have a potential application in the management of wetland restoration projects because microbial communities differ according to wetland types, restoration status and land uses (Hartman et al., 2008; Peralta et al., 2013b; Sims et al., 2013). Constructed wetlands may have lower microbial diversity and functions in comparison with natural wetlands (Hartman et al., 2008). Therefore, the success of restoration projects may be evaluated by means of diversity, activities and biomass of microbial communities between the restored sites and reference sites (i.e. natural or original wetlands) (Faulwetter et al., 2013; Prasse et al., 2015; Sims et al., 2012a). Hartman et al. (2008) found wetland restoration lowered the microbial diversity so that the community was dominated by a few large taxa and altered the normalized ratio of Proteobacteria to Acidobacteria, suggesting the incompleteness of the restoration project. In contrast, Card and Quideau (2010) reported a similar microbial community composition and biomass between the restored sites (7–11 years) and the reference sites of the Prairie Pothole Region of Canada, indicating the success of restoration efforts. Similarly, Bernhard et al. (2012) reported no difference in bacterial community composition in restored marshes after 30 years, but found significant differences in community variability of the restored marshes compared to undisturbed marshes, suggesting a potential long-term effect. Additionally, significantly higher abundances of nitrogen cycle microbes were found in subsurface salt marsh sediments 30 years after restoration, indicating that full recovery had not been achieved (Bernhard et al., 2015). A recent study has shown that while bacterial community structures varied significantly between restored and reference (i.e. natural) wetlands, denitrifying microbial assemblages were similar among reference sites, where the highest denitrification potential was found (Peralta et al., 2010). The results indicate that wetland restoration efforts could benefit from increased denitrification mediated by denitrifying bacteria in natural wetlands. It is also important to note that establishing whether a wetland is recovered is very complex and cannot be determined from a single metric, and in many cases, some aspects may show strong recovery, while others are much less resilient.

5.2. Wetland landscape management: aquatic vegetation and associated microorganisms

Aquatic vegetation plays an essential role in wetland landscape scenery (Mitsch and Gosselink, 2015). In wetland ecosystems, the largest part of biologically available organic matter is provided by aquatic vegetation. Among the various aquatic plants that are used for restored wetlands, emergent plants are found to decay more slowly than floating (free-floating and floating-leaf plants) and submersed plants (Godshalk and Wetzel, 1978). In general, 70–80% of biomass loss of common aquatic macrophytes occurs within the first 60 days (Odum and Heywood, 1978); the decay rates of plants are correlated with total fiber content (i.e. hemicellulose, cellulose, lignin) and temperature (Godshalk and Wetzel, 1978). Ibekwe et al. (2007) reported that the experimental constructed wetland cells with 50% plant cover had as high as 96·3% nitrate removal, whereas, the nitrate removal in the 100% plant cover cells was about 11·4%. In accordance with the performance of nitrate removal, microbial diversity was also higher in the wetland cells with 50% plant density than the 100%. A high oxygen level is a key factor in maximizing the degradation of organic matter in wetlands and the microbial community should serve as an excellent indicator to monitor the biological and chemical responses of the wetland to variable oxygen levels (Godshalk and Wetzel, 1978; Ibekwe et al., 2007).

Nearly all wetland restoration projects include landscape management through vegetation control, but less attention has been paid to the soil/sediment bacteria and rhizosphere microbiomes. Microbial communities in the rhizosphere are quite important for the healthy growth of wetland plants. The rhizosphere normally positively influences the abundance of microorganisms (Nihorimbere et al., 2011; Zhen-Yu et al., 2010) and harbors phylogenetically more diverse groups of microorganisms than bulk soil/sediment (He et al., 2015; Zhang et al., 2013). Rhizosphere bacteria can increase soil fertility and promote the growth of roots, thus helping the establishment of wetland vegetation (Ehrenfeld et al., 2005). As rhizosphere microbial diversity decreases, plant

growth may be negatively affected. Therefore, it is difficult to assess the bioremediation roles of vegetation without considering rhizosphere microbiomes. In order to improve the quality of wetlands and maintain their ecosystem function, efforts to control the plant diversity and quantity are necessary (Bachand and Horne, 1999b; Ibekwe et al., 2007).

Although the origin of microbial communities in plant root systems is considered to be bulk soil, microbial populations between rhizosphere and bulk soils are generally distinctive, suggesting the existence of selective forces on microbial communities in the rhizosphere through plant-microbe interaction (e.g. excretion of rhizodeposits from plant roots) (el Zahar Haichar et al., 2008, 2014; Ibekwe et al., 2007). However, little is known about the source of microbial communities in the aquaponic rhizosphere (Tanaka et al., 2012). For example, Urakawa et al. (2017) studied rhizosphere microbiomes of a floating treatment wetland and found the oxic-anoxic gradient was formed and this environmental gradient assisted to extend the complex biogeochemical processes that include carbon, nitrogen and sulfur. Many different groups of SRB were detected through 16S rRNA gene high-throughput sequencing from the rhizospheres exposed in oxic water. Zhang et al. (2013) compared the rhizospheres of *Phragmites australis* (common reed) grown in three different soil conditions (swamp, salt meadow and dune) and found that SRB were only found in the swamp rhizospheres. These observations showed the potential ubiquitous nature of sulfate reducers in the aquatic rhizosphere. Therefore, monitoring of plant-associated microbial communities may be used as an effective tool for the assessment of plant restoration work in the wetland landscape. Monitoring sulfate reducers is particularly important to assess the impact of submergence on rhizospheres in constructed wetlands.

5.3. Environmental disturbance and microbial responses, Deepwater Horizon oil spill as example

Historically, wetlands have been the subject of multiple human-induced disturbances. Wetlands have been an easy target of a wide range of land developments; nearly half of them have already been drained (Mitsch and Gosselink, 2015). Another type of human induced disturbance to the wetlands is the introduction of pollutants. When metals, oil, or other toxic organic compounds are the pollutants, adverse effects on the wetland ecosystem can be devastating, such as in the 2010 Deepwater Horizon oil spill, where about 690 km of northern Gulf of Mexico coastal wetlands, which are dominated by salt marshes, were affected (Michel et al., 2013). The response and resilience of wetland microbial communities to oil spills depend on multiple factors, including the physical condition of the oil (i.e. weathered), water temperature, salinity, nutrients (i.e. nitrogen and phosphorus), soil moisture and the availability of oxygen, and the presence of hydrocarbon-degrading microorganisms (Bernhard et al., 2016; King et al., 2015; Marton et al., 2015). In addition, vegetation patterns, sediment deposition rates, and tidal flooding can collectively contribute to enhance the process of oil degradation or subsurface oil sequestration (King et al., 2015; Mendelssohn et al., 2012). Microbial hydrocarbon degradation occurs more rapidly under oxic conditions than it does under anoxic conditions. Although the majority of wetland soil is anoxic, a few millimeters of surface sediment and rhizosphere is oxic. Numerous macrofaunal burrows created by crustaceans, bivalves and polychaete worms can also expand the oxygen penetration of wetland soil. The existence of these aerobic environments may provide increases resilience of the wetland ecosystem to oil pollution. Beazley et al. (2012) provided a comprehensive view of the succession of microbial community structure and functional dynamics within oil perturbed salt marsh ecosystems. An increase in the relative abundances of hydrocarbon-degrading Proteobacteria, Actinobacteria, and Bacteroidetes was observed after the oil spill. These oil-eating bacteria decreased once hydrocarbons were below detection levels. Firmicutes, however, continuously increased in relative richness and abundance after hydrocarbon concentrations were below detection. Functional genes involved in hydrocarbon degradation were augmented in oiled sediments then declined significantly once hydrocarbon concentrations diminished. A greater decline in hydrocarbon concentrations among marsh grass sediments compared to bare sediments suggests that the marsh rhizosphere microbial communities may play a role in hydrocarbon degradation. Lighter oil compounds tend to degrade quickly, while the heavier oil fractions still remain and higher organic matter inputs overall enhance the key microbial processes associated with SRB (Natter et al., 2012; Overton et al., 2016). Boopathy et al. (2012) reported that significant degradation of oil occurred under sulfate-reducing and nitrate-reducing conditions. Marton et al. (2015) reported no difference in nitrification activities between oiled and unoiled salt marshes two years after the Deepwater Horizon oil spill. Lastly, the positive response of hydrocarbon-degrading fungi in oiled salt marshes suggests a potentially important contribution to hydrocarbon degradation. However, the importance of fungi in the process of oil degradation is largely unknown (King et al., 2015).

5.4. The influence of climate change on microbial communities

The influence of global warming will impact the future of wetlands. Generally, wetlands are considered the largest non-anthropogenic source of atmospheric methane, but they can also be a sink by changing the level of the water table (Hanson and Hanson, 1996). Some of the methane produced is oxidized in sediments/soils by methanotrophic bacteria (Fig. 6). Net methane emission is determined by the balance of production and oxidation, which is governed by the physicochemical factors of soil, sediment, vegetation, hydrology and climate (Kayranli et al., 2010). Methane is slowly released from bogs as the permafrost melts, caused by global warming. With increasing global temperatures, the expanse of permafrost thaws out and the release of methane continue to surge (Walter et al., 2006). In high latitude wetlands, the melting of ice and associated environmental changes will alter microbial activity and communities (Palmer et al., 2012). In the arctic tundra, nitrous gas emission patterns from acidic peat soils were strongly influenced by the cryoturbation cycle, which leads to breakdown of decomposable soil aggregates and activates microbial activities (Palmer et al., 2012). In the case of nitrification, temperature was a strong driving force in shifting the species composition (Avrahami et al., 2003; Avrahami and Conrad, 2005; Fierer et al., 2009; Urakawa et al., 2008). Increasing lines of evidence suggests that the diversity of AOA in cold environments exceeds that of AOB (Alves et al., 2013; Hayashi et al., 2015; Urakawa et al., 2008), which may have important implications to the nitrogen cycle as temperatures change. Nitrification rates in wetlands dropped rapidly once temperatures decreased below 6 °C (Werker et al., 2002). In other studies, only small differences in nitrogen removal between warmer and colder periods were reported (Mæhlum and Stålnacke, 1999). The cultivation studies clearly indicate that growth rates under low temperatures varies at the species level. For example, *Nitrosomonas* cluster 6a, the most dominant *Nitrosomonas* group in various freshwater environments, does not include a cold adapted species (i.e. psychrophilic or psychrotolerant species) in previously cultured microorganisms (Speksnijder et al., 1998). On the other hand, *Nitrosomonas cryotolerans* can grow below 0 °C in seawater (Jones et al., 1988). *Nitrosospira* also includes one psychrotolerant species, *Nitrosospira lacus* (Urakawa et al., 2015). A high-throughput sequencing effort of bacterial *amoA* gene from arctic soils revealed that all six major operational taxonomic units identified belonged

to the *Nitrosospira*-Mount Everest cluster (Table 3) (Hayashi et al., 2015; Zhang et al., 2009). Therefore it is likely that a variable cold temperature response in nitrification activity is attributed to the difference in species composition of nitrifiers. Therefore, cold-adapted microorganisms may serve as microbial indicators of global warming.

Coastal wetlands, especially estuarine and marine wetlands, are natural targets of alteration by high energy events such as coastal erosion and storm events (Nicholls, 2004). The impacts of these processes may be intensified by climate change and associated sea-level rise (Nicholls et al., 1999). Estuarine wetlands have a capability to protect the coastline from erosion and flooding, but if sea level increases and urban development and shoreline armoring prevent the inland migration of wetlands, more wetlands will be under the sea (up to 22% of the world's coastal wetlands by the 2080s) (Nicholls et al., 1999). Sea-level rise also influences the dynamics of coastal groundwater. The sensitivity of certain plant and microbial populations to salt-waterlogging and subsequent soil chemical changes could influence species composition and biogeochemical cycling, and result in a shift of vegetation zones. Belowground, the death and decay of plant roots will be stimulated by the intrusion of seawater; soil compaction will be hastened (Nyman et al., 1994; Reed, 1995). The major changes of soil and groundwater microbial communities may be induced by an increase in the availability of sulfate and the subsequent prominence of sulfur cycling (Craft et al., 2009). The increase in the availability of sulfate will change the major terminal oxidation process of organic matter from methanogenesis to sulfate reduction (Table 2). The sea-level rise and subsequent salt-waterlogging could decrease the methane emission from soil and also could limit the diversity of methanogenic archaea and expand the abundance and diversity of SRB. Thus methanogenic and sulfate-reducing microbial populations could be good microbial indicators to assess the impacts of sea-level rise on wetland and subsequent soil/groundwater alternations. Sediment microbial activities and physiochemistry have been used as progress indicators of salt marsh restoration processes (Duarte et al., 2012).

6. Conclusion

Microbial indicators have a potential application in the management of wetland restoration projects because microbial communities differ according to wetland types, restoration status and land uses. They can serve as the most sensitive and rapid bioindicator in response to various environmental changes. With the control of redox potential, the retention time of water, and the selection of soil and vegetation, we might create a desired constructed wetland, which has elevated performance in nutrient and pollutant removal. High-throughput sequencing methods can be comprehensive monitoring tools for microorganisms, making them valuable wetland indicators. More knowledge of these microbial populations, through family or genus level ecotype identification and ecophysiological assessment, is necessary to better use them as indicators (Hernandez et al., 2015; Martens-Habbena et al., 2009).

Acknowledgments

We thank I. L. Sanchez and M. E. Feeney (Florida Gulf Coast University) for their critical reading of the manuscript. We thank J.C. Gaby, D. H. Buckley (Cornell University) and S. Iwai (Second Genome) for sharing the discussion about the high-throughput sequencing of functional genes. We also deeply acknowledge the effort and time of two anonymous reviewers. This publication was assisted by U.S. National Science Foundation (NSF) grant CBET-1619948 with project title: U.S. Science International Collaborations and Contributions to EcoSummit 2016 'Sustainability: Engineering Change'. A part of this research was supported by NSF Division of Environmental Biology Ecosystem Science Cluster grant DEB-1664052 to H.U. This work was also supported via funding provided by the Office of Research and Graduate Studies of Florida Gulf Coast University (H. U.) and funding from the Gulf of Mexico Research Initiative through the Alabama Center for Ecological Resilience administered by the Dauphin Island Sea Lab (H. U.) and the Coastal Waters Consortium (A. E. B.). Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org.

References

Šantrůčková, H., Rejmánková, E., Pivničková, B., Snyder, J.M., 2010. Nutrient enrichment in tropical wetlands: shifts from autotrophic to heterotrophic nitrogen fixation. Biogeochemistry 101, 295–310.
Abed, R.M.M., Al-Kharusi, S., Prigent, S., Headley, T., 2014. Diversity, distribution and hydrocarbon biodegradation capabilities of microbial communities in oil-contaminated cyanobacterial mats from a constructed wetland. PLoS One 9, e114570.
Aguilar, J.R.P., Cabriales, J.J.P., Vega, M.M., 2008. Identification and characterization of sulfur-oxidizing bacteria in an artificial wetland that treats wastewater from a tannery. Int. J. Phytoremediation 10, 359–370.
Allgaier, M., Grossart, H.-P., 2006. Diversity and seasonal dynamics of Actinobacteria populations in four lakes in northeastern Germany. Appl. Environ. Microbiol. 72, 3489–3497.
Alves, R.J.E., Wanek, W., Zappe, A., Richter, A., Svenning, M.M., Schleper, C., Urich, T., 2013. Nitrification rates in Arctic soils are associated with functionally distinct populations of ammonia-oxidizing archaea. ISME J. 7, 1620–1631.
An, S.M., Gardner, W.S., 2002. Dissimilatory nitrate reduction to ammonium (DNRA) as a nitrogen link, versus denitrification as a sink in a shallow estuary (Laguna Madre/Baffin Bay, Texas). Mar. Ecol. Prog. Ser. 237, 41–50.
Avrahami, S., Conrad, R., 2005. Cold-temperate climate: a factor for selection of ammonia oxidizers in upland soil? Can. J. Microbiol. 51, 709–714.
Avrahami, S., Liesack, W., Conrad, R., 2003. Effects of temperature and fertilizer on activity and community structure of soil ammonia oxidizers. Environ. Microbiol. 5, 691–705.
Baatar, B., Chiang, P.-W., Rogozin, D.Y., Wu, Y.-T., Tseng, C.-H., Yang, C.-Y., Chiu, H.-H., Oyuntsetseg, B., Degermendzhy, A.G., Tang, S.-L., 2016. Bacterial communities of three saline meromictic lakes in Central Asia. PLoS One 11, e0150847.
Bachand, P.A.M., Horne, A.J., 1999a. Denitrification in constructed free-water surface wetlands: i. Very high nitrate removal rates in a macrocosm study. Ecol. Eng. 14, 9–15.
Bachand, P.A.M., Horne, A.J., 1999b. Denitrification in constructed free-water surface wetlands: II. Effects of vegetation and temperature. Ecol. Eng. 14, 17–32.
Bai, J., Deng, W., Zhu, Y., Wang, Q., 2004. Spatial variability of nitrogen in soils from land/inland water ecotones. Commun. Soil Sci. Plant Anal. 35, 735–749.
Barberán, A., Casamayor, E.O., 2010. Global phylogenetic community structure and β-diversity patterns in surface bacterioplankton metacommunities. Aquat. Microb. Ecol. 59, 1–10.
Bastviken, S.K., Eriksson, P.G., Martins, I., Neto, J.o.M., Leonardson, L., Tonderski, K., 2003. Potential nitrification and denitrification on different surfaces in a constructed treatment wetland. J. Environ. Qual. 32, 2414–2420.
Beazley, M.J., Martinez, R.J., Rajan, S., Powell, J., Piceno, Y.M., Tom, L.M., Andersen, G.L., Hazen, T.C., Van Nostrand, J.D., Zhou, J., 2012. Microbial community analysis of a coastal salt marsh affected by the deepwater horizon oil spill. PLoS One 7, e41305.
Bell, T., Newman, J.A., Silverman, B.W., Turner, S.L., Lilley, A.K., 2005. The contribution of species richness and composition to bacterial services. Nature 436, 1157–1160.
Bell, T.H., Yergeau, E., Maynard, C., Juck, D., Whyte, L.G., Greer, C.W., 2013. Predictable bacterial composition and hydrocarbon degradation in Arctic soils following diesel and nutrient disturbance. ISME J. 7, 1200–1210.
Beman, J.M., Francis, C.A., 2006. Diversity of ammonia-oxidizing archaea and bacteria in the sediments of a hypernutrified subtropical estuary: bahia del Tobari, Mexico. Appl. Environ. Microbiol. 72, 7767–7777.
Beman, J.M., Popp, B.N., Francis, C.A., 2008. Molecular and biogeochemical evidence for ammonia oxidation by marine Crenarchaeota in the Gulf of California. ISME J. 2, 429–441.
Beman, J.M., Popp, B.N., Alford, S.E., 2012. Quantification of ammonia oxidation rates and ammonia-oxidizing archaea and bacteria at high resolution in the Gulf of California and eastern tropical North Pacific Ocean. Limnol. Oceanogr. 57, 711–726.
Bergsma, T.T., Robertson, G.P., Ostrom, N.E., 2002. Influence of soil moisture and land use history on denitrification end-products. J. Environ. Qual. 31, 711–717.

Bernhard, A.E., Donn, T., Giblin, A.E., Stahl, D.A., 2005. Loss of diversity of ammonia-oxidizing bacteria correlates with increasing salinity in an estuary system. Environ. Microbiol. 7, 1289–1297.
Bernhard, A.E., Tucker, J., Giblin, A.E., Stahl, D.A., 2007. Functionally distinct communities of ammonia-oxidizing bacteria along an estuarine salinity gradient. Environ. Microbiol. 9, 1439–1447.
Bernhard, A.E., Landry, Z.C., Blevins, A., de la Torre, J.R., Giblin, A.E., Stahl, D.A., 2010. Abundance of ammonia-oxidizing archaea and bacteria along an estuarine salinity gradient in relation to potential nitrification rates. Appl. Environ. Microbiol. 76, 1285–1289.
Bernhard, A.E., Marshall, D., Yiannos, L., 2012. Increased variability of microbial communities in restored salt marshes nearly 30 years after tidal flow restoration. Estuaries Coasts 35, 1049–1059.
Bernhard, A.E., Dwyer, C., Idrizi, A., Bender, G., Zwick, R., 2015. Long-term impacts of disturbance on nitrogen-cycling bacteria in a New England salt marsh. Front. Microbiol. 6, 46.
Bernhard, A.E., Sheffer, R., Giblin, A.E., Marton, J.M., Roberts, B.J., 2016. Population dynamics and community composition of ammonia oxidizers in salt marshes after the Deepwater Horizon oil spill. Front. Microbiol. 7, 854.
Bodelier, P.L.E., Frenzel, P., Drake, H.L., Hurek, T., Küsel, K., Lovell, C., Megonigal, P., Reinhold-Hurek, B., Sorrell, B., 2006. Ecological aspects of microbes and microbial communities inhabiting the rhizosphere of wetland plants. In: Wetlands and Natural Resource Management. Springer, pp. 205–238.
Bomberg, M., Nyyssönen, M., Pitkänen, P., Lehtinen, A., Itävaara, M., 2015. 2015, Active microbial communities inhabit sulphate-methane interphase in deep bedrock fracture fluids in Olkiluoto, Finland. BioMed Res. Int., 979517 (Article ID 979530).
Bomberg, M., 2016. The elusive boreal forest Thaumarchaeota. Agronomy 6, 36.
Boopathy, R., Shields, S., Nunna, S., 2012. Biodegradation of crude oil from the BP oil spill in the marsh sediments of southeast Louisiana, USA. Appl. Biochem. Biotechnol. 167, 1560–1568.
Braker, G., Fesefeldt, A., Witzel, K.-P., 1998. Development of PCR primer systems for amplification of nitrite reductase genes (*nirK* and *nirS*) to detect denitrifying bacteria in environmental samples. Appl. Environ. Microbiol. 64, 3769–3775.
Brocks, J.J., Schaeffer, P., 2008. Okenane, a biomarker for purple sulfur bacteria (Chromatiaceae), and other new carotenoid derivatives from the 1640 Ma Barney Creek Formation. Geochim. Cosmochim. Acta 72, 1396–1414.
Bryant, D.A., Costas, A.M.G., Maresca, J.A., Chew, A.G.M., Klatt, C.G., Bateson, M.M., Tallon, L.J., Hostetler, J., Nelson, W.C., Heidelberg, J.F., 2007. *Candidatus* Chloracidobacterium thermophilum: an aerobic phototrophic acidobacterium. Science 317, 523–526.
Burgin, A.J., Hamilton, S.K., 2007. Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. Front. Ecol. Environ. 5, 89–96.
Card, S.M., Quideau, S.A., 2010. Microbial community structure in restored riparian soils of the Canadian prairie pothole region. Soil Biol. Biochem. 42, 1463–1471.
Castro, H., Reddy, K.R., Ogram, A., 2002. Composition and function of sulfate-reducing prokaryotes in eutrophic and pristine areas of the Florida Everglades. Appl. Environ. Microbiol. 68, 6129–6137.
Chelius, M.K., Lepo, J.E., 1999. Restriction fragment length polymorphism analysis of PCR-amplified nifH sequences from wetland plant rhizosphere communities. Environ. Technol. 20, 883–889.
Chowdhury, T.R., Mitsch, W.J., Dick, R.P., 2014. Seasonal methanotrophy across a hydrological gradient in a freshwater wetland. Ecol. Eng. 72, 116–124.
Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H., Machmuller, M., 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Front. Ecol. Environ. 7, 73–78.
Currie, D.J., Kalff, J., 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. Limnol. Oceanogr. 29, 298–310.
Daims, H., Lebedeva, E.V., Pjevac, P., Han, P., Herbold, C., Albertsen, M., Jehmlich, N., Palatinszky, M., Vierheilig, J., Bulaev, A., 2015. Complete nitrification by Nitrospira bacteria. Nature 528, 504–509.
Dale, N.G., 1974. Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr. 19, 509–518.
Dang, H.Y., Li, J., Chen, R.P., Wang, L., Guo, L.Z., Zhang, Z.N., Klotz, M.G., 2010. Diversity, abundance, and spatial distribution of sediment ammonia-oxidizing betaproteobacteria in response to environmental gradients and coastal eutrophication in Jiaozhou Bay, China. Appl. Environ. Microbiol. 76, 4691–4702.
Decamp, O., Warren, A., 2001. Abundance, biomass and viability of bacteria in wastewaters: impact of treatment in horizontal subsurface flow constructed wetlands. Water Res. 35, 3496–3501.
Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat. Commun. 7, 10541.
Deng, Y., Cui, X., Hernández, M., Dumont, M.G., 2014. Microbial diversity in hummock and hollow soils of three wetlands on the Qinghai-Tibetan Plateau revealed by 16S rRNA pyrosequencing. PLoS One 9, e103115.
Desnues, C., Michotey, V.D., Wieland, A., Zhizang, C., Fourcans, A., Duran, R., Bonin, P.C., 2007. Seasonal and diel distributions of denitrifying and bacterial communities in a hypersaline microbial mat (Camargue, France). Water Res. 41, 3407–3419.
Devol, A.H., 2003. Nitrogen cycle: solution to a marine mystery. Nature 422, 575–576.
Dong, L.F., Sobey, M.N., Smith, C.J., Rusmana, I., Phillips, W., Stott, A., Osborn, A.M., Nedwell, D.B., 2011. Dissimilatory reduction of nitrate to ammonium, not denitrification or anammox, dominates benthic nitrate reduction in tropical estuaries. Limnol. Oceanogr. 56, 279–291.
Duarte, B., Freitas, J., Cacador, I., 2012. Sediment microbial activities and physic-chemistry as progress indicators of salt marsh restoration processes. Ecol. Indic. 19, 231–239.
Ehrenfeld, J.G., Ravit, B., Elgersma, K., 2005. Feedback in the plant-soil system. Annu. Rev. Environ. Resour. 30, 75–115.
Ellis, J.T., Tramp, C., Sims, R.C., Miller, C.D., 2012. Characterization of a methanogenic community within an algal fed anaerobic digester. ISRN Microbiol. 2012, 753812 (Article ID 753892) http://dx.doi.org/753810.755402/752012/753892.
Emerson, D., Rentz, J.A., Lilburn, T.G., Davis, R.E., Aldrich, H., Chan, C., Moyer, C.L., 2007. A novel lineage of Proteobacteria involved in formation of marine Fe-oxidizing microbial mat communities. PLoS One 2, e667.
Ettwig, K.F., Butler, M.K., Le Paslier, D., Pelletier, E., Mangenot, S., Kuypers, M.M.M., Schreiber, F., Dutilh, B.E., Zedelius, J., de Beer, D., 2010. Nitrite-driven anaerobic methane oxidation by oxygenic bacteria. Nature 464, 543–548.
Farnelid, H., Andersson, A.F., Bertilsson, S., Al-Soud, W.A., Hansen, L.H., Sørensen, S., Steward, G.F., Hagström, Å., Riemann, L., 2001. Nitrogenase gene amplicons from global marine surface waters are dominated by genes of non-cyanobacteria. PLoS One 6, e19223.
Faulwetter, J.L., Gagnon, V., Sundberg, C., Chazarenc, F., Burr, M.D., Brisson, J., Camper, A.K., Stein, O.R., 2009. Microbial processes influencing performance of treatment wetlands: a review. Ecol. Eng. 35, 987–1004.
Faulwetter, J.L., Burr, M.D., Parker, A.E., Stein, O.R., Camper, A.K., 2013. Influence of season and plant species on the abundance and diversity of sulfate reducing bacteria and ammonia oxidizing bacteria in constructed wetland microcosms. Microb. Ecol. 65, 111–127.
Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281, 237–240.
Fierer, N., Carney, K.M., Horner-Devine, M.C., Megonigal, J.P., 2009. The biogeography of ammonia-oxidizing bacterial communities in soil. Microb. Ecol. 58, 435–445.
Fleming, E.J., Davis, R.E., McAllister, S.M., Chan, C.S., Moyer, C.L., Tebo, B.M., Emerson, D., 2013. Hidden in plain sight: discovery of sheath-forming iron-oxidizing Zetaproteobacteria at Loihi Seamount, Hawaii, USA. FEMS Microbiol. Ecol. 85, 116–127.
Francis, C.A., O'Mullan, G.D., Ward, B.B., 2003. Diversity of ammonia monooxygenase (amoA) genes across environmental gradients in Chesapeake Bay sediments. Geobiology 1, 129–140.
Francis, C.A., Roberts, K.J., Beman, J.M., Santoro, A.E., Oakley, B.B., 2005. Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean. Proc. Natl. Acad. Sci. U. S. A. 102, 14683–14688.
Gaby, J.C., Buckley, D.H., 2012. A comprehensive evaluation of PCR primers to amplify the nifH gene of nitrogenase. PLoS One 7, e42149.
Gaiser, E.E., McCormick, P.V., Hagerthey, S.E., Gottlieb, A.D., 2011. Landscape patterns of periphyton in the Florida Everglades. Crit. Rev. Environ. Sci. Technol. 41, 92–120.
Glöckner, F.O., Fuchs, B.M., Amann, R., 1999. Bacterioplankton compositions of lakes and oceans: a first comparison based on fluorescence in situ hybridization. Appl. Environ. Microbiol. 65, 3721–3726.
Godshalk, G.L., Wetzel, R.G., 1978. Decomposition of aquatic angiosperms. I. Dissolved components. Aquat. Bot. 5, 281–300.
Gorra, R., Coci, M., Ambrosoli, R., Laanbroek, H.J., 2007. Effects of substratum on the diversity and stability of ammonia-oxidizing communities in a constructed wetland used for wastewater treatment. J. Appl. Microbiol. 103, 1442–1452.
Hagerthey, S.E., Bellinger, B.J., Wheeler, K., Gantar, M., Gaiser, E., 2011. Everglades periphyton: a biogeochemical perspective. Crit. Rev. Environ. Sci. Technol. 41, 309–343.
Hallam, S.J., Putnam, N., Preston, C.M., Detter, J.C., Rokhsar, D., Richardson, P.M., DeLong, E.F., 2004. Reverse methanogenesis: testing the hypothesis with environmental genomics. Science 305, 1457–1462.
Hallberg, K.B., Johnson, D.B., 2005. Microbiology of a wetland ecosystem constructed to remediate mine drainage from a heavy metal mine. Sci. Total Environ. 338, 53–66.
Hallin, S., Lindgren, P.-E., 1999. PCR detection of genes encoding nitrite reductase in denitrifying bacteria. Appl. Environ. Microbiol. 65, 1652–1657.
Han, S., Narasingarao, P., Obraztsova, A., Gieskes, J., Hartmann, A.C., Tebo, B.M., Allen, E.E., Deheyn, D.D., 2010. Mercury speciation in marine sediments under sulfate-limited conditions. Environ. Sci. Technol. 44, 3752–3757.
Hanson, R.S., Hanson, T.E., 1996. Methanotrophic bacteria. Microbiol. Rev. 60, 439–471.
Haroon, M.F., Hu, S., Shi, Y., Imelfort, M., Keller, J., Hugenholtz, P., Yuan, Z., Tyson, G.W., 2013. Anaerobic oxidation of methane coupled to nitrate reduction in a novel archaeal lineage. Nature 500, 567–570.
Hartman, W.H., Richardson, C.J., Vilgalys, R., Bruland, G.L., 2008. Environmental and anthropogenic controls over bacterial communities in wetland soils. Proc. Natl. Acad. Sci. U. S. A. 105, 17842–17847.
Hayashi, K., Shimomura, Y., Morimoto, S., Uchida, M., Nakatsubo, T., Hayatsu, M., 2015. Characteristics of ammonia oxidation potentials and ammonia oxidizers in mineral soil under Salix polaris–moss vegetation in Ny-Ålesund, Svalbard. Polar Biol. 39, 725–741.
Hayatsu, M., Tago, K., Uchiyama, I., Toyoda, A., Wang, Y., Shimomura, Y., Okubo, T., Kurisu, F., Hirono, Y., Nonaka, K., 2017. An acid-tolerant ammonia-oxidizing γ-proteobacterium from soil. ISME J. 11, 1130–1141.

He, S., Malfatti, S.A., McFarland, J.W., Anderson, F.E., Pati, A., Huntemann, M., Tremblay, J., del Rio, T.G., Waldrop, M.P., Windham-Myers, L., 2015. Patterns in wetland microbial community composition and functional gene repertoire associated with methane emissions. mBio 6, e00066–00015.
Head, I.M., Saunders, J.R., Pickup, R.W., 1998. Microbial evolution, diversity, and ecology: a decade of ribosomal RNA analysis of uncultivated microorganisms. Microb. Ecol. 35, 1–21.
Henry, S., Bru, D., Stres, B., Hallet, S., Philippot, L., 2006. Quantitative detection of the nosZ gene, encoding nitrous oxide reductase, and comparison of the abundances of 16S rRNA, narG, nirK, and nosZ genes in soils. Appl. Environ. Microbiol. 72 (8), 5181–5189.
Henry-Silva, G.G., Camargo, A.F.M., 2006. Efficiency of aquatic macrophytes to treat Nile tilapia pond effluents. Scientia Agricola 63, 433–438.
Hernandez, M.E., Mitsch, W.J., 2007. Denitrification potential and organic matter as affected by vegetation community, wetland age, and plant introduction in created wetlands. J. Environ. Qual. 36, 333–342.
Hernandez, M.E., Beck, D.A.C., Lidstrom, M.E., Chistoserdova, L., 2015. Oxygen availability is a major factor in determining the composition of microbial communities involved in methane oxidation. PeerJ 3, e801.
Holmes, A.J., Costello, A., Lidstrom, M.E., Murrell, J.C., 1995. Evidence that particulate methane monooxygenase and ammonia monooxygenase may be evolutionarily related. FEMS Microbiol. Lett. 132, 203–208.
Hou, L.J., Zheng, Y.L., Liu, M., Li, X.F., Lin, X.B., Yin, G.Y., Gao, J., Deng, F.Y., Chen, F., Jiang, X.F., 2015. Anaerobic ammonium oxidation and its contribution to nitrogen removal in China's coastal wetlands. Sci. Rep. 5, 15621.
Huang, J., Xu, X., Wang, M., Nie, M., Qiu, S., Wang, Q., Quan, Z., Xiao, M., Li, B., 2016. Responses of soil nitrogen fixation to Spartina alterniflora invasion and nitrogen addition in a Chinese salt marsh. Sci. Rep. 6, 20384.
Hubas, C., Jesus, B., Passarelli, C., Jeanthon, C., 2011. Tools providing new insight into coastal anoxygenic purple bacterial mats: review and perspectives. Res. Microbiol. 162, 858–868.
Humbert, S., Zopfi, J., Tarnawski, S.-E., 2012. Abundance of anammox bacteria in different wetland soils. Environ. Microbiol. Rep. 4, 484–490.
Ibekwe, A.M., Lyon, S.R., Leddy, M., Jacobson-Meyers, M., 2007. Impact of plant density and microbial composition on water quality from a free water surface constructed wetland. J. Appl. Microbiol. 102, 921–936.
Ishida, C.K., Kelly, J.J., Gray, K.A., 2006. Effects of variable hydroperiods and water level fluctuations on denitrification capacity, nitrate removal, and benthic-microbial community structure in constructed wetlands. Ecol. Eng. 28, 363–373.
Ivanova, A.O., Dedysh, S.N., 2012. Abundance, diversity, and depth distribution of Planctomycetes in acidic northern wetlands. Front. Microbiol. 3, 5.
Jetten, M.S.M., v. Niftrik, L., Strous, M., Kartal, B., Keltjens, J.T., op den Camp, H.J.M., 2009. Biochemistry and molecular biology of anammox bacteria. Crit. Rev. Biochem. Mol. Biol. 44, 65–84.
Jia, Z., Conrad, R., 2009. Bacteria rather than Archaea dominate microbial ammonia oxidation in an agricultural soil. Environ. Microbiol. 11, 1658–1671.
Jiang, X.F., Hou, L.J., Zheng, Y.L., Liu, M., Yin, G.Y., Gao, J., Li, X.F., Wang, R., Yu, C.D., Lin, X.B., 2017. Salinity-driven shifts in the activity, diversity, and abundance of anammox bacteria of estuarine and coastal wetlands. Phys. Chem. Earth. 97, 46–53.
Jones, R.D., Morita, R.Y., Koops, H.-P., Watson, S.W., 1988. A new marine ammonium-oxidizing bacterium, Nitrosomonas cryotolerans sp. nov. Can. J. Microbiol. 34, 1122–1128.
Jungblut, A.D., Wood, S.A., Hawes, I., Webster-Brown, J., Harris, C., 2012. The pyramid trough wetland: environmental and biological diversity in a newly created Antarctic protected area. FEMS Microb. Ecol. 82, 356–366.
Juretschko, S., Timmermann, G., Schmid, M., Schleifer, K.-H., Pommerening-Röser, A., Koops, H.-P., Wagner, M., 1998. Combined molecular and conventional analyses of nitrifying bacterium diversity in activated sludge: nitrosococcus mobilis and nitrospira-like bacteria as dominant populations. Appl. Environ. Microbiol. 64, 3042–3051.
Könneke, M., Bernhard, A.E., de la Torre, J.R., Walker, C.B., Waterbury, J.B., Stahl, D.A., 2005. Isolation of an autotrophic ammonia-oxidizing marine archaeon. Nature 437, 543–546.
Kao-Kniffin, J., Freyre, D.S., Balser, T.C., 2010. Methane dynamics across wetland plant species. Aquat. Bot. 93, 107–113.
Kartal, B., de Almeida, N.M., Maalcke, W.J., den Camp, H.J.M.O., Jetten, M.S.M., Keltjens, J.T., 2013. How to make a living from anaerobic ammonium oxidation. FEMS Microbiol. Rev. 37, 428–461.
Kayranli, B., Scholz, M., Mustafa, A., Hedmark, Å., 2010. Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30, 111–124.
Ke, X., Lu, W., Conrad, R., 2015. High oxygen concentration increases the abundance and acticvity of bacterial rather than archaeal nitrifiers in rice field soil. Microb. Ecol. 70, 961–970.
Kellman, L., Hillaire-Marcel, C., 1998. Nitrate cycling in streams: using natural abundances of NO_3-$\delta^{15}N$ to measure in-situ denitrification. Biogeochemistry 43, 273–292.
Kepner, R.L., Pratt, J.R., 1994. Use of fluorochromes for direct enumeration of total bacteria in environmental samples: past and present. Microbiol. Rev. 58, 603–615.
Kim, M.-K., Zoh, K.-D., 2012. Fate and transport of mercury in environmental media and human exposure. J. Prev. Med. Pub. Health 45, 335–343.
Kim, J.-G., Park, S.-J., Damsté, J.S.S., Schouten, S., Rijpstra, W.I.C., Jung, M.-Y., Kim, S.-J., Gwak, J.-H., Hong, H., Si, O.-J., 2016. Hydrogen peroxide detoxification is a key mechanism for growth of ammonia-oxidizing archaea. Proc. Natl. Acad. Sci. U. S. A. 113, 7888–7893.
King, G.M., Kostka, J.E., Hazen, T.C., Sobecky, P.A., 2015. Microbial responses to the Deepwater Horizon oil spill: from coastal wetlands to the deep sea. Annu. Rev. Mar. Sci. 7, 377–401.
Koch, H., Lücker, S., Albertsen, M., Kitzinger, K., Herbold, C., Spieck, E., Nielsen, P.H., Wagner, M., Daims, H., 2015. Expanded metabolic versatility of ubiquitous nitrite-oxidizing bacteria from the genus *Nitrospira*. Proc. Natl. Acad. Sci. U. S. A. 112, 11371–11376.
Koop-Jakobsen, K., Giblin, A.E., 2009. Anammox in tidal marsh sediments: the role of salinity, nitrogen loading, and marsh vegetation. Estuar. Coasts 32, 238–245.
Koop-Jakobsen, K., Giblin, A.E., 2010. The effect of increased nitrate loading on nitrate reduction via denitrification and DNRA in salt marsh sediments. Limnol. Oceanogr. 55, 789–802.
López-García, P., Duperron, S., Philippot, P., Foriel, J., Susini, J., Moreira, D., 2003. Bacterial diversity in hydrothermal sediment and epsilonproteobacterial dominance in experimental microcolonizers at the Mid-Atlantic Ridge. Environ. Microbiol. 5, 961–976.
Lüke, C., Frenzel, P., 2011. Potential of *pmoA* amplicon pyrosequencing for methanotroph diversity studies. Appl. Environ. Microbiol. 77, 6305–6309.
Lehtovirta-Morley, L.E., Sayavedra-Soto, L.A., Gallois, N., Schouten, S., Stein, L.Y., Prosser, J.I., Nicol, G.W., 2016. Identifying potential mechanisms enabling acidophily in the ammonia-oxidizing archaeon *Candidatus* Nitrosotalea devanaterra. Appl. Environ. Microbiol. 82, 2608–2619.
Leinonen, R., Sugawara, H., Shumway, M., 2010. The sequence read archive. Nucleic Acids Res. 39, D19–D21.
Li, M., Hong, Y.G., Klotz, M.G., Gu, J.D., 2010. A comparison of primer sets for detecting 16S rRNA and hydrazine oxidoreductase genes of anaerobic ammonium-oxidizing bacteria in marine sediments. Appl. Microbiol. Biotechnol. 86, 781–790.
Ligi, T., Oopkaup, K., Truu, M., Preem, J.-K., Nõlvak, H., Mitsch, W.J., Ü. Mander, Truu, J., 2014. Characterization of bacterial communities in soil and sediment of a created riverine wetland complex using high-throughput 16S rRNA amplicon sequencing. Ecol. Eng. 72, 56–66.
Lisa, J.A., Song, B., Tobias, C.R., Duernberger, K.A., 2014. Impacts of freshwater flushing on anammox community structure and activities in the New River Estuary, USA. Aquatic Microb. Ecol. 72, 17–31.
Lisa, J.A., Song, B., Tobias, C.R., Hines, D.E., 2015. Genetic and biogeochemical investigation of sedimentary nitrogen cycling communities responding to tidal and seasonal dynamics in Cape Fear River Estuary. Estuarine Coastal Shelf Sci. 167, A313–A323.
Lovell, C.R., Piceno, Y.M., Quattro, J.M., Bagwell, C.E., 2000. Molecular analysis of diazotroph diversity in the rhizosphere of the smooth cordgrass, Spartina alterniflora. Appl. Environ. Microbiol. 66, 3814–3822.
Lumpkin, T.A., Plucknett, D.L., 1980. *Azolla*: botany, physiology, and use as a green manure. Econ. Bot. 34, 111–153.
Lunau, M., Lemke, A., Walther, K., Martens-Habbena, W., Simon, M., 2005. An improved method for counting bacteria from sediments and turbid environments by epifluorescence microscopy. Environ. Microbiol. 7, 961–968.
Lv, X., Yu, J., Fu, Y., Ma, B., Qu, F., Ning, K., Wu, H., 2014. A meta-analysis of the bacterial and archaeal diversity observed in wetland soils. Sci. World J., 437612 (Article ID 437684).
Mæhlum, T., Stålnacke, P., 1999. Removal efficiency of three cold-climate constructed wetlands treating domestic wastewater: effects of temperature, seasons, loading rates and input concentrations. Water Sci. Technol. 40, 273–281.
Madigan, M.T., Ormerod, J.G., 1995. Taxonomy, Physiology and Ecology of Heliobacteria Anoxygenic Photosynthetic Bacteria. Springer, pp. 17–30.
Madigan, M.T., Martinko, J.M., Bender, Kelly S., Buckley, D.H., Stahl, D.A., Brock, T., 2015. Brock Biology of Microorganisms, 14th edition.
Martens-Habbena, W., Berube, P.M., Urakawa, H., de la Torre, J., Stahl, D.A., 2009. Ammonia oxidation kinetics determine niche separation of nitrifying Archaea and Bacteria. Nature 461, 976–979.
Marton, J.M., Roberts, B.J., Bernhard, A.E., Giblin, A.E., 2015. Spatial and temporal variability of nitrification potential and ammonia-oxidizer abundances in Louisiana salt marshes. Estuar. Coasts 38, 1824–1837.
McCormick, P.V., Stevenson, R.J., 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. J. Phycol. 34, 726–733.
McCormick, P.V., Shuford, R.B.E., Chimney, M.J., 2006. Periphyton as a potential phosphorus sink in the Everglades Nutrient Removal Project. Ecol. Eng. 27, 279–289.
Mendelssohn, I.A., Andersen, G.L., Baltz, D.M., Caffey, R.H., Carman, K.R., Fleeger, J.W., Joye, S.B., Lin, Q., Maltby, E., Overton, E.B., 2012. Oil impacts on coastal wetlands: implications for the Mississippi River Delta ecosystem after the Deepwater Horizon oil spill. Bioscience 62, 562–574.
Merkley, M., Rader, R.B., McArthur, J.V., Eggett, D., 2004. Bacteria as bioindicators in wetlands: bioassessment in the Bonneville Basin of Utah, USA. Wetlands 24, 600–607.
Michel, J., Owens, E.H., Zengel, S., Graham, A., Nixon, Z., Allard, T., Holton, W., Reimer, P.D., Lamarche, A., White, M., 2013. Extent and degree of shoreline oiling: deepwater Horizon oil spill, Gulf of Mexico, USA. PLoS One 8, e65087.
Mitsch, W.J., Gosselink, J.G., 2000. The value of wetlands: importance of scale and landscape setting. Ecol. Econ. 35, 25–33.
Mitsch, W.J., Gosselink, J.G., 2015. Wetlands, 5th edition. John Wiley & Sons, Hoboken, New Jersey.

Molina, V., Hernandez, K., Dorador, C., Eissler, Y., Hengst, M., Perez, V., Harrod, C., 2016. Bacterial active community cycling in response to solar radiation and their influence on nutrient changes in a high-altitude wetland. Frontiers in Microbiology 7, 1823.

Mohan, S.B., Schmid, M., Jetten, M., Cole, J., 2004. Detection and widespread distribution of the *nrfA* gene encoding nitrite reduction to ammonia, a short circuit in the biological nitrogen cycle that competes with denitrification. FEMS Microbiol. Ecol. 49, 433–443.

Morse, J.L., Bernhardt, E.S., 2013. Using ^{15}N tracers to estimate N_2O and N_2 emissions from nitrification and denitrification in coastal plain wetlands under contrasting land-uses. Soil Biol. Biochem. 57, 635–643.

Muyzer, G., Stams, A.J.M., 2008. The ecology and biotechnology of sulphate-reducing bacteria. Nat. Rev. Microbiol. 6, 441–454.

Nakai, R., Naganuma, T., 2015. Oligoflexia, the newest class of the phylum Proteobacteria, consisting of only one cultured species and uncultured bacterial phylotypes from diverse habitats. J. Phylogenet. Evol. Biol., 3–141.

Nakai, R., Nishijima, M., Tazato, N., Handa, Y., Karray, F., Sayadi, S., Isoda, H., Naganuma, T., 2014. *Oligoflexus tunisiensis* gen. nov, sp. nov., a Gram-negative, aerobic, filamentous bacterium of a novel proteobacterial lineage, and description of *Oligoflexaceae* fam. nov., *Oligoflexales* ord. nov. and *Oligoflexia* classis nov. Int. J. Syst. Evol. Microbiol. 64, 3353–3359.

Natter, M., Keevan, J., Wang, Y., Keimowitz, A.R., Okeke, B.C., Son, A., Lee, M.-K., 2012. Level and degradation of Deepwater Horizon spilled oil in coastal marsh sediments and pore-water. Environ. Sci. Technol. 46, 5744–5755.

Nelson, K.A., Moin, N.S., Bernhard, A.E., 2009. Archaeal diversity and the prevalence of Crenarchaeota in salt marsh sediments. Appl. Environ. Microbiol. 75, 4211–4215.

Nicholls, R.J., Hoozemans, F.M.J., Marchand, M., 1999. Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. Global Environ. Change 9, S69–S87.

Nicholls, R.J., 2004. Coastal flooding and wetland loss in the 21 st century: changes under the SRES climate and socio-economic scenarios. Global Environ. Change 14, 69–86.

Nicol, G.W., Leininger, S., Schleper, C., Prosser, J.I., 2008. The influence of soil pH on the diversity, abundance and transcriptional activity of ammonia oxidizing archaea and bacteria. Environ. Microbiol. 10 (November (11)), 2966–2978.

Nicomrat, D., Dick, W.A., Tuovinen, O.H., 2006. Assessment of the microbial community in a constructed wetland that receives acid coal mine drainage. Microb. Ecol. 51, 83–89.

Nihorimbere, V., Ongena, M., Smargiassi, M., Thonart, P., 2011. Beneficial effect of the rhizosphere microbial community for plant growth and health. Biotechnol. Agron. Soci. Environ. 15, 327–337.

Nikolausz, M., Kappelmeyer, U., Székely, A., Rusznyák, A., Márialigeti, K., Kästner, M., 2008. Diurnal redox fluctuation and microbial activity in the rhizosphere of wetland plants. Eur. J. Soil Biol. 44, 324–333.

Nogales, B., Timmis, K.N., Nedwell, D.B., Osborn, A.M., 2002. Detection and diversity of expressed denitrification genes in estuarine sediments after reverse transcription-PCR amplification from mRNA. Appl. Environ. Microbiol. 68, 5017–5025.

Nowka, B., Off, S., Daims, H., Spieck, E., 2015. Improved isolation strategies allowed the phenotypic differentiation of two *Nitrospira* strains from widespread phylogenetic lineages. FEMS Microbiol. Ecol. 91 (fiu031).

Nyman, J.A., Carloss, M., DeLaune, R.D., Patrick, W.H., 1994. Erosion rather than plant dieback as the mechanism of marsh loss in an estuarine marsh. Earth Surf. Processes Landforms 19, 69–84.

Odum, W.E., Heywood, M.A., 1978. Decomposition of Intertidal Freshwater Marsh Plants Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, pp. 89–97.

Oremland, R.S., Culbertson, C.W., 1992. Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor. Nature 356, 421–423.

Orphan, V.J., House, C.H., Hinrichs, K.-U., McKeegan, K.D., DeLong, E.F., 2001. Methane-consuming archaea revealed by directly coupled isotopic and phylogenetic analysis. Science 293, 484–487.

Overton, E.B., Wade, T.L., Radović, J.R., Meyer, B.M., Miles, M.S., Larter, S.R., 2016. Chemical composition of Macondo and other crude oils and compositional alterations during oil spills. Oceanography 29, 50–63.

Ovreås, L., Forney, L., Daae, F.L., Torsvik, V., 1997. Distribution of bacterioplankton in meromictic Lake Saelenvannet, as determined by denaturing gradient gel electrophoresis of PCR-amplified gene fragments coding for 16S rRNA. Appl. Environ. Microbiol. 63, 3367–3373.

Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1, 27–37.

Paerl, H.W., Dyble, J., Moisander, P.H., Noble, R.T., Piehler, M.F., Pinckney, J.L., Steppe, T.F., Twomey, L., Valdes, L.M., 2003. Microbial indicators of aquatic ecosystem change: current applications to eutrophication studies. FEMS Microbiol. Ecol. 46, 233–246.

Paerl, H.W., Gardner, W.S., Havens, K.E., Joyner, A.R., McCarthy, M.J., Newell, S.E., Qin, B., Scott, J.T., 2016. Mitigating cyanobacterial harmful algal blooms in aquatic ecosystems impacted by climate change and anthropogenic nutrients. Harmful Algae 54, 213–222.

Palmer, K., Biasi, C., Horn, M.A., 2012. Contrasting denitrifier communities relate to contrasting N_2O emission patterns from acidic peat soils in arctic tundra. ISME J. 6, 1058–1077.

Paredes, D., Kuschk, P., Stange, F., Müller, R.A., Köser, H., 2007. Model experiments on improving nitrogen removal in laboratory scale subsurface constructed wetlands by enhancing the anaerobic ammonia oxidation. Water Sci. Technol. 56, 145–150.

Park, N., Lee, J., Chon, K., Kang, H., Cho, J., 2009. Investigating microbial activities of constructed wetlands with respect to nitrate and sulfate reduction. Desalin. Water Treat. 1, 172–179.

Parmar, T.K., Rawtani, D., Agrawal, Y.K., 2016. Bioindicators: the natural indicator of environmental pollution. Front. Life Sci. 9, 110–118.

Parte, A.C., 2014. LPSN-list of prokaryotic names with standing in nomenclature. Nucleic Acids Res. 42(D1, D613–D616.

Pelissari, C., Guivernau, M., Vinas, M., de Souza, S.S., Garcia Sezerino, J.P.H., Avila, C., 2017. Unraveling the active microbial populations involved in nitrogen utilization in a vertical subsurface flow constructed wetland treating urban wastewater. Sci. Total Environ. 584, 642–650.

Peng, X.F., Yando, E., Hildebrand, E., Dwyer, C., Kearney, A., Waciega, A., Valiela, I., Bernhard, A.E., 2013. Differential responses of ammonia-oxidizing archaea and bacteria to long-term fertilization in a New England salt marsh. Front. Microbiol. 3, 445.

Peralta, A.L., Matthews, J.W., Kent, A.D., 2010. Microbial community structure and denitrification in a wetland mitigation bank. Appl. Environ. Microbiol. 76, 4207–4215.

Peralta, A.L., Ludmer, S., Kent, A.D., 2013a. Hydrologic history influences microbial community composition and nitrogen cycling under experimental drying/wetting treatments. Soil Biol. Biochem. 66, 29–37.

Peralta, R.M., Ahn, C., Gillevet, P.M., 2013b. Characterization of soil bacterial community structure and physicochemical properties in created and natural wetlands. Sci. Total Environ. 443, 725–732.

Pester, M., Knorr, K.-H., Friedrich, M.W., Wagner, M., Loy, A., 2012a. Sulfate-reducing microorganisms in wetlands – fameless actors in carbon cycling and climate change. Front. Microbiol. 3, 72.

Pester, M., Rattei, T., Flechl, S., Gröngröft, A., Richter, A., Overmann, J., Reinhold-Hurek, B., Loy, A., Wagner, M., 2012b. *amoA*-based consensus phylogeny of ammonia-oxidizing archaea and deep sequencing of *amoA* genes from soils of four different geographic regions. Environ. Microbiol. 14, 525–539.

Plugge, C.M., Zhang, W., Scholten, J.C.M., Stams, A.J.M., 2011. Metabolic flexibility of sulfate-reducing bacteria. Front. Microbiol. 2, 81.

Posch, T., Franzoi, J., Prader, M., Salcher, M.M., 2009. New image analysis tool to study biomass and morphotypes of three major bacterioplankton groups in an alpine lake. Aquat. Microb. Ecol. 54, 113–126.

Prasse, C.E., Baldwin, A.H., Yarwood, S.A., 2015. Site history and edaphic features override the influence of plant species on microbial communities in restored tidal freshwater wetlands. Appl. Environ. Microbiol. 81, 3482–3491.

Priemé, A., Braker, G., Tiedje, J.M., 2002. Diversity of nitrite reductase (*nirK* and *nirS*) gene fragments in forested upland and wetland soils. Appl. Environ. Microbiol. 68, 1893–1900.

Prosser, J.I., Nicol, G.W., 2012. Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. Trends Microbiol. 20, 523–531.

Qin, W., Amin, S.A., Martens-Habbena, W., Walker, C.B., Urakawa, H., Devol, A.H., Ingalls, A.E., Moffett, J.W., Armbrust, E.V., Stahl, D.A., 2014. Marine ammonia-oxidizing archaeal isolates display obligate mixotrophy and wide ecotypic variation. Proc. Natl. Acad. Sci. U. S. A. 111, 12504–12509.

Quince, C., Lanzen, A., Davenport, R.J., Turnbaugh, P.J., 2011. Removing noise from pyrosequenced amplicons. BMC Bioinf. 12, 38.

Raghoebarsing, A.A., Pol, A., Van de Pas-Schoonen, K.T., Smolders, A.J.P., Ettwig, K.F., Rijpstra, W.I.C., Schouten, S., Damsté, J.S.S., den Camp, H.J.M.O., Jetten, M.S.M., 2006. A microbial consortium couples anaerobic methane oxidation to denitrification. Nature 440, 918–921.

Rea, C.L., Bisesi, M.S., Mitsch, W., Andridge, R., Lee, J., 2015. Human health-related ecosystem services of avian-dense coastal wetlands adjacent to a Western Lake Erie swimming beach. Ecohealth 12, 77–87.

Reddy, K.R., D'Angelo, E.M., 1997. Biogeochemical indicators to evaluate pollutant removal efficiency in constructed wetlands. Water Sci. Technol. 35, 1–10.

Reeburgh, W.S., 2007. Oceanic methane biogeochemistry. Chem. Rev. 107, 486–513.

Reed, D.J., 1995. The response of coastal marshes to sea-level rise: survival or submergence? Earth Surf. Processes Landforms 20, 39–48.

Risgaard-Petersen, N., Langezaal, A.M., Ingvardsen, S., Schmid, M.C., Jetten, M.S.M., den Camp, H.J.M.O., Derksen, J.W.M., Pina-Ochoa, E., Eriksson, S.P., Nielsen, L.P., 2006. Evidence for complete denitrification in a benthic foraminifer. Nature 443, 93–96.

Rodriguez-R, L.M., Overholt, W.A., Hagan, C., Huettel, M., Kostka, J.E., Konstantinidis, K.T., 2015. Microbial community successional patterns in beach sands impacted by the Deepwater Horizon oil spill. ISME J. 9, 1928–1940.

Roger, P.-A., Ladha, J.K., 1992. Biological N2 fixation in wetland rice fields: estimation and contribution to nitrogen balance. Plant Soil 141, 41–55.

Rotthauwe, J.-H., Witzel, K.-P., Liesack, W., 1997. The ammonia monooxygenase structural gene *amoA* as a functional marker: molecular fine-scale analysis of natural ammonia-oxidizing populations. Appl. Environ. Microbiol. 63, 4704–4712.

Sánchez, O., 2016. Constructed wetlands revisited: microbial diversity in the –omics era. Microb. Ecol. 73, 722–733.

Santoro, A.E., Boehm, A.B., Francis, C.A., 2006. Denitrifier community composition along a nitrate and salinity gradient in a coastal aquifer. Appl. Environ. Microbiol. 72, 2102–2109.

Santoro, A.E., Casciotti, K.L., Francis, C.A., 2010. Activity, abundance and diversity of nitrifying archaea and bacteria in the central California Current. Environ. Microbiol. 12, 1989–2006.
Schramm, A., de Beer, D., Wagner, M., Amann, R., 1998. Identification and activities *in situ* of *Nitrosospira* and *Nitrospira* spp: as dominant populations in a nitrifying fluidized bed reactor. Appl. Environ. Microbiol. 64, 3480–3485.
Schultz Jr., G.E., Kovatch, J.J., Anneken, E.M., 2013. Bacterial diversity in a large, temperate, heavily modified river, as determined by pyrosequencing. Aquat. Microb. Ecol. 70, 169–179.
Schulz, H.N., Schulz, H.D., 2005. Large sulfur bacteria and the formation of phosphorite. Science 307, 416–418.
Seefeldt, L.C., Hoffman, B.M., Dean, D.R., 2009. Mechanism of Mo-dependent nitrogenase. Annu. Rev. Biochem 78, 701–722.
Segarra, K.E.A., Schubotz, F., Samarkin, V., Yoshinaga, M.Y., Hinrichs, K.U., Joye, S.B., 2015. High rates of anaerobic methane oxidation in freshwater wetlands reduce potential atmospheric methane emissions. Nat. Commun., 6 (Article number: 7477).
Seitzinger, S.P., 1988. Denitrification in freshWater and coastal marine ecosystems – ecological and geochemical significance. Limnol. Oceanogr. 33, 702–724.
Seppälä, J., Ylöstalo, P., Kaitala, S., Hällfors, S., Raateoja, M., Maunula, P., 2007. Ship-of-opportunity based phycocyanin fluorescence monitoring of the filamentous cyanobacteria bloom dynamics in the Baltic Sea. Estuarine. Coast. Shelf Sci. 73, 489–500.
Shapleigh, J.P., 2005. The denitrifying prokaryotes. In: Dworkin, M. (Ed.), The Prokaryotes: An evolving electronic resource for the microbiological community. Springer-Verlag, New York.
Sharma, A.K., Zhaxybayeva, O., Papke, R.T., Doolittle, W.F., 2008. Actinorhodopsins: proteorhodopsin-like gene sequences found predominantly in non-marine environments. Environ. Microbiol. 10, 1039–1056.
Sharma, A.K., Sommerfeld, K., Bullerjahn, G.S., Matteson, A.R., Wilhelm, S.W., Jezbera, J., Brandt, U., Doolittle, W.F., Hahn, M.W., 2009. Actinorhodopsin genes discovered in diverse freshwater habitats and among cultivated freshwater Actinobacteria. ISME J. 3, 726–737.
Siljanen, H.M.P., Saari, A., Krause, S., Lensu, A., Abell, G.C.J., Bodrossy, L., Bodelier, P.L.E., Martikainen, P.J., 2011. Hydrology is reflected in the functioning and community composition of methanotrophs in the littoral wetland of a boreal lake. FEMS Microbiol. Ecol. 75, 430–445.
Siljanen, H.M.P., Saari, A., Bodrossy, L., Martikainen, P.J., 2012. Seasonal variation in the function and diversity of methanotrophs in the littoral wetland of a boreal eutrophic lake. FEMS Microbiol. Ecol. 80, 548–555.
Simon, J., Klotz, M.G., 2013. Diversity and evolution of bioenergetic systems involved in microbial nitrogen compound transformations. Biochim. Biophys. Acta (BBA)-Bioenerget. 1827, 114–135.
Sims, A., Gajaraj, S., Hu, Z., 2012a. Seasonal population changes of ammonia-oxidizing organisms and their relationship to water quality in a constructed wetland. Ecol. Eng. 40, 100–107.
Sims, A., Horton, J., Gajaraj, S., McIntosh, S., Miles, R.J., Mueller, R., Reed, R., Hu, Z., 2012b. Temporal and spatial distributions of ammonia-oxidizing archaea and bacteria and their ratio as an indicator of oligotrophic conditions in natural wetlands. Water Res. 46, 4121–4129.
Sims, A., Zhang, Y., Gajaraj, S., Brown, P.B., Hu, Z., 2013. Toward the development of microbial indicators for wetland assessment. Water Res. 47, 1711–1725.
Sipos, A.J., Urakawa, H., 2016. Differential responses of nitrifying archaea and bacteria to methylene blue toxicity. Lett. Appl. Microbiol. 62, 199–206.
Sleutel, S., Moeskops, B., Huybrechts, W., Vandenbossche, A., Salomez, J., De Bolle, S., Buchan, D., De Neve, S., 2008. Modeling soil moisture effects on net nitrogen mineralization in loamy wetland soils. Wetlands 28, 724–734.
Sogin, M.L., Morrison, H.G., Huber, J.A., Welch, D.M., Huse, S.M., Neal, P.R., Arrieta, J.M., Herndl, G.J., 2006. Microbial diversity in the deep sea and the underexplored rare biosphere. Proc. Natl. Acad. Sci. U. S. A. 103, 12115–12120.
Sommer, U., Gliwicz, Z.M., Lampert, W., Duncan, A., 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106, 433–471.
Song, B., Lisa, J.A., Tobias, C.R., 2014a. Linking DNRA community structure and activity in a shallow lagoonal estuarine system. Front. Microbiol. 5, 460.
Song, K., Hernandez, M.E., Batson, J.A., Mitsch, W.J., 2014b. Long-term denitrification rates in created riverine wetlands and their relationship with environmental factors. Ecol. Eng. 72, 40–46.
Sorokin, D.Y., Lücker, S., Vejmelkova, D., Kostrikina, N.A., Kleerebezem, R., Rijpstra, W.I.C., Damsté, J.S.S., Le Paslier, D., Muyzer, G., Wagner, M., 2012. Nitrification expanded: discovery, physiology and genomics of a nitrite-oxidizing bacterium from the phylum Chloroflexi. ISME J. 6, 2245–2256.
Speksnijder, A.G.C.L., Kowalchuk, G.A., Roest, K., Laanbroek, H.J., 1998. Recovery of a *Nitrosomonas*-like 16S rDNA sequence group from freshwater habitats. Syst. Appl. Microbiol. 21, 321–330.
Stoecker, K., Bendinger, B., Schöning, B., Nielsen, P.H., Nielsen, J.L., Baranyi, C., Toenshoff, E.R., Daims, H., Wagner, M., 2006. Cohn's *Crenothrix* is a filamentous methane oxidizer with an unusual methane monooxygenase. Proc. Natl. Acad. Sci. U. S. A. 103, 2363–2367.
Stoeva, M.K., Aris-Brosou, S., Chételat, J., Hintelmann, H., Pelletier, P., Poulain, A.J., 2014. Microbial community structure in lake and wetland sediments from a high Arctic polar desert revealed by targeted transcriptomics. PLoS One 9, e89531.
Strous, M., Fuerst, J.A., Kramer, E.H.M., Logemann, S., Muyzer, G., van de Pas-Schoonen, K.T., Webb, R., Kuenen, J.G., Jetten, M.S.M., 1999a. Missing lithotroph identified as new planctomycete. Nature 400, 446–449.
Strous, M., Kuenen, J.G., Jetten, M.S.M., 1999b. Key physiology of anaerobic ammonium oxidation. Appl. Environ. Microbiol. 65, 3248–3250.
Stubner, S., Wind, T., Conrad, R., 1998. Sulfur oxidation in rice field soil: activity, enumeration, isolation and characterization of thiosulfate-oxidizing bacteria. Syst. Appl. Microbiol. 21, 569–578.
Sturman, P.J., Stein, O.R., Vymazal, J., Kröpfelová, L., 2008. Sulfur Cycling in Constructed Wetlands. Wastewater Treatment, Plant Dynamics and Management in Constructed and Natural Wetlands. Springer, Netherlands, pp. 329–344 (310.1007/1978-1001-4020-8235-1001_1029).
Sun, L., Qiu, F., Zhang, X., Dai, X., Dong, X., Song, W., 2008. Endophytic bacterial diversity in rice (Oryza sativa L.) roots estimated by 16S rDNA sequence analysis. Microb. Ecol. 55, 415–424.
Tanaka, Y., Tamaki, H., Matsuzawa, H., Nigaya, M., Mori, K., Kamagata, Y., 2012. Microbial community analysis in the roots of aquatic plants and isolation of novel microbes including an organism of the candidate phylum OP10. Microb. Environ. 27, 149–157.
Tang, J., Ding, X., Wang, L., Xu, Q., Yang, Z., Zhao, J., Sun, Q., Feng, S., Zhang, J., 2012. Effects of wetland degradation on bacterial community in the Zoige Wetland of Qinghai-Tibetan Plateau (China). World J. Microbiol. Biotechnol. 28, 649–657.
Taylor, A.E., Bottomley, P.J., 2006. Nitrite production by *Nitrosomonas europaea* and *Nitrosospira* sp. AV in soils at different solution concentrations of ammonium. Soil Biol. Biochem. 38, 828–836.
Thomas, F., Giblin, A.E., Cardon, Z.G., Sievert, S.M., 2014. Rhizosphere heterogeneity shapes abundance and activity of sulfur-oxidizing bacteria in vegetated salt marsh sediments. Front. Microbiol. 5, 309.
Tobias, C.R., Macko, S.A., Anderson, I.C., Canuel, E.A., Harvey, J.W., 2001. Tracking the fate of a high concentration groundwater nitrate plume through a fringing marsh: a combined groundwater tracer and *in situ* isotope enrichment study. Limnol. Oceanogr. 46, 1977–1989.
Ueda, T., Suga, Y., Yahiro, N., Matsuguchi, T., 1995a. Remarkable N_2-fixing bacterial diversity detected in rice roots by molecular evolutionary analysis of *nifH* gene sequences. J. Bacteriol. 177, 1414–1417.
Ueda, T., Suga, Y., Yahiro, N., Matsuguchi, T., 1995b. Genetic diversity of N_2-fixing bacteria associated with rice roots by molecular evolutionary analysis of a *nifD* library. Can. J. Microbiol. 41, 235–240.
Urakawa, H., Kurata, S., Fujiwara, T., Kuroiwa, D., Maki, H., Kawabata, S., Hiwatari, T., Ando, H., Kawai, T., Watanabe, M., Kohata, K., 2006a. Characterization and quantification of ammonia-oxidizing bacteria in eutrophic coastal marine sediments using polyphasic molecular approaches and immunofluorescence staining. Environ. Microbiol. 8, 787–803.
Urakawa, H., Maki, H., Kawabata, S., Fujiwara, T., Ando, H., Kawai, T., Hiwatari, T., Kohata, K., Watanabe, M., 2006b. Abundance and population structure of ammonia-oxidizing bacteria that inhabit canal sediments receiving effluents from municipal wastewater treatment plants. Appl. Environ. Microbiol. 72, 6845–6850.
Urakawa, H., Tajima, Y., Numata, Y., Tsuneda, S., 2008. Low temperature decreases the phylogenetic diversity of ammonia-oxidizing archaea and bacteria in aquarium biofiltration systems. Appl. Environ. Microbiol. 74, 894–900.
Urakawa, H., Martens-Habbena, W., Stahl, D.A., 2010. High abundance of ammonia-oxidizing Archaea in coastal waters, determined using a modified DNA extraction method. Appl. Environ. Microbiol. 76, 2129–2135.
Urakawa, H., Martens-Habbena, W., Stahl, D.A., 2011. Physiology and genomics of ammonia-oxidizing archaea. In: Ward, B.B., Arp, D.J., Klotz, M.G. (Eds.), Nitrification. ASM Press, p. 460.
Urakawa, H., Garcia, J.C., Barreto, P.D., Molina, G.A., Barreto, J.C., 2012. A sensitive crude oil bioassay indicates that oil spills potentially induce a change of major nitrifying prokaryotes from the Archaea to the Bacteria. Environ. Pollut. 164, 42–45.
Urakawa, H., Martens-Habbena, W., Huguet, C., de la Torre, J.R., Ingalls, A.E., Devol, A.H., Stahl, D.A., 2014. Ammonia availability shapes the seasonal distribution and activity of archaeal and bacterial ammonia oxidizers in the Puget Sound Estuary. Limnol. Oceanogr. 59, 1321–1335.
Urakawa, H., Garcia, J.C., Nielsen, J.L., Le, V.Q., Kozlowski, J.A., Stein, L.Y., Lim, C.K., Pommerening-Röser, A., Martens-Habbena, W., Stahl, D.A., 2015. *Nitrosospira lacus* sp. nov, a psychrotolerant, ammonia-oxidizing bacterium from sandy lake sediment. Int. J. Syst. Evol. Microbiol. 65, 242–250.
Urakawa, H., Dettmar, D.L., Thomas, S., 2017. The uniqueness and biogeochemical cycling of plant root microbial communities in a floating treatment wetland. Ecol. Eng., https://doi.org/10.1016/j.ecoleng.2017.06.066 http://www.sciencedirect.com/science/article/pii/S0925857417303944.
Uroz, S., Buée, M., Murat, C., Frey-Klett, P., Martin, F., 2010. Pyrosequencing reveals a contrasted bacterial diversity between oak rhizosphere and surrounding soil. Environ. Microbiol. Rep. 2, 281–288.
Vajrala, N., Martens-Habbena, W., Sayavedra-Soto, L.A., Schauer, A., Bottomley, P.J., Stahl, D.A., Arp, D.J., 2013. Hydroxylamine as an intermediate in ammonia oxidation by globally abundant marine archaea. Proc. Natl. Acad. Sci. U. S. A. 110, 1006–1011.
Verhamme, D.T., Prosser, J.I., Nicol, G.W., 2011. Ammonia concentration determines differential growth of ammonia-oxidising archaea and bacteria in soil microcosms. ISME J. 5, 1067–1071.
Villa, J.A., Mitsch, W.J., 2014. Methane emissions from five wetland plant communities with different hydroperiods in the Big Cypress Swamp region of Florida Everglades. Ecohydrol. Hydrobiol. 14, 253–266.
Vymazal, J., Richardson, C.J., 1995. species composition, biomass, and nutrient content of periphyton in the Florida Everglades 1. J. Phycol. 31, 343–354.

Vymazal, J., 2007. Removal of nutrients in various types of constructed wetlands. Sci. Total Environ. 380, 48–65, http://dx.doi.org/10.1016/j.scitotenv.2006.1009.1014.

Waite, D.W., Vanwonterghem, I., Rinke, C., Parks, D.H., Zhang, Y., Takai, K., Sievert, S.M., Simon, J., Campbell, B.J., Hanson, T.E., Woyke, T., 2017. Comparative genomic analysis of the class Epsilonproteobacteria and proposed reclassification to Epsilonbacteraeota (phyl. nov.). Front. Microbiol. 8, 682.

Walker, C.B., de la Torre, J.R., Klotz, M.G., Urakawa, H., Pinel, N., Arp, D.J., Brochier-Armanet, C., Chain, P.S., Chan, P.P., Gollabgir, A., Hemp, J., Hugler, M., Karr, E.A., Könneke, M., Shin, M., Lawton, T.J., Lowe, T., Martens-Habbena, W., Sayavedra-Soto, L.A., Lang, D., Sievert, S.M., Rosenzweig, A.C., Manning, G., Stahl, D.A., 2010. Nitrosopumilus maritimus genome reveals unique mechanisms for nitrification and autotrophy in globally distributed marine crenarchaea. Proc. Natl. Acad. Sci. U. S. A. 107, 8818–8823.

Walter, K.M., Zimov, S.A., Chanton, J.P., Verbyla, D., Chapin, F.S., 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. Nature 443, 71–75.

Wang, Y., Sheng, H.-F., He, Y., Wu, J.-Y., Jiang, Y.-X., Tam, N.F.-Y., Zhou, H.-W., 2012. Comparison of the levels of bacterial diversity in freshwater, intertidal wetland, and marine sediments by using millions of illumina tags. Appl. Environ. Microbiol. 78, 8264–8271.

Wang, Y.-F., Feng, Y.-Y., Ma, X., Gu, J.-D., 2013. Seasonal dynamics of ammonia/ammonium-oxidizing prokaryotes in oxic and anoxic wetland sediments of subtropical coastal mangrove. Appl. Microbiol. Biotechnol. 97, 7919–7934.

Warnecke, F., Sommaruga, R., Sekar, R., Hofer, J.S., Pernthaler, J., 2005. Abundances, identity, and growth state of Actinobacteria in mountain lakes of different UV transparency. Appl. Environ. Microbiol. 71, 5551–5559.

Wei, B., Yu, X., Zhang, S., Gu, L., 2011. Comparison of the community structures of ammonia-oxidizing bacteria and archaea in rhizoplanes of floating aquatic macrophytes. Microbiol. Res. 166, 468–474.

Weinbauer, M.G., Beckmann, C., Höfle, M.G., 1998. Utility of green fluorescent nucleic acid dyes and aluminum oxide membrane filters for rapid epifluorescence enumeration of soil and sediment bacteria. Appl. Environ. Microbiol. 64, 5000–5003.

Weng, B., Xie, X., Yang, J., Liu, J., Lu, H., Yan, C., 2013. Research on the nitrogen cycle in rhizosphere of Kandelia obovata under ammonium and nitrate addition. Mar. Pollut. Bull. 76, 227–240.

Werker, A.G., Dougherty, J.M., McHenry, J.L., Van Loon, W.A., 2002. Treatment variability for wetland wastewater treatment design in cold climates. Ecol. Eng. 19, 1–11.

Whiting, G.J., Gandy, E.L., Yoch, D.C., 1986. Tight coupling of root-associated nitrogen fixation and plant photosynthesis in the salt marsh grass Spartina alterniflora and carbon dioxide enhancement of nitrogenase activity. Appl. Environ. Microbiol. 52, 108–113.

Williams, K.P., Kelly, D.P., 2013. Proposal for a new class within the phylum Proteobacteria, Acidithiobacillia classis nov., with the type order Acidithiobacillales, and emended description of the class Gammaproteobacteria. Int. J. Syst. Evol. Microbiol. 63, 2901–2906.

Wright, A.L., Reddy, K.R., 2001. Heterotrophic microbial activity in northern Everglades wetland soils. Soil Sci. Soc. Am. J. 65, 1856–1864.

Wright, A.L., Ramesh Reddy, K., Newman, S., 2009. Microbial indicators of eutrophication in Everglades wetlands. Soil Sci. Soc. Am. J. 73, 1597–1603.

Wu, Y., Kerr, P.G., Hu, Z., Yang, L., 2010. Removal of cyanobacterial bloom from a biopond-wetland system and the associated response of zoobenthic diversity. Bioresour. Technol. 101, 3903–3908.

Zamyadi, A., McQuaid, N., Dorner, S., Bird, D.F., Burch, M., Baker, P., Hobson, P., Prevost, M., 2012. Cyanobacterial detection using in vivo fluorescence probes: managing interferences for improved decision-making. J.: Am. Water Works Assoc. 104, pE466–E479.

Zehr, J.P., Mellon, M.T., Hiorns, W.D., 1997. Phylogeny of cyanobacterial *nifH* genes: evolutionary implications and potential applications to natural assemblages. Microbiology 143, 1443–1450.

Zehr, J.P., Jenkins, B.D., Short, S.M., Steward, G.F., 2003. Nitrogenase gene diversity and microbial community structure: a crossâ€?system comparison. Environ. Microbiol. 5, 539–554.

Zhang, L.-M., Wang, M., Prosser, J.I., Zheng, Y.-M., He, J.-Z., 2009. Altitude ammonia-oxidizing bacteria and archaea in soils of Mount Everest. FEMS Microbiol. Ecol. 70, 208–217.

Zhang, W., Wu, X., Liu, G., Chen, T., Zhang, G., Dong, Z., Yang, X., Hu, P., 2013. Pyrosequencing reveals bacterial diversity in the rhizosphere of three *Phragmites australis* ecotypes. Geomicrobiol. J. 30, 593–599.

Zhao, D., Luo, J., Wang, J., Huang, R., Guo, K., Li, Y., Wu, Q.L., 2015. The influence of land use on the abundance and diversity of ammonia oxidizers. Curr. Microbiol. 70, 282–289.

Zhen-Yu, W., Yuan-Zheng, X.I.N., Dong-Mei, G.A.O., Feng-Min, L.I., Morgan, J., Bao-Shan, X., 2010. Microbial community characteristics in a degraded wetland of the Yellow River Delta. Pedosphere 20, 466–478.

Zhong, F., Gao, Y., Yu, T., Zhang, Y., Xu, D., Xiao, E., He, F., Zhou, Q., Wu, Z., 2011. The management of undesirable cyanobacteria blooms in channel catfish ponds using a constructed wetland: contribution to the control of off-flavor occurrences. Water Res. 45, 6479–6488.

Zhou, X., Li, Y., Zhang, J., Liu, B., Wang, M., Zhou, Y., Lin, Z., He, Z., 2016. Diversity, abundance and community structure of ammonia-oxidizing archaea and bacteria in riparian sediment of Zhenjiang ancient canal. Ecol. Eng. 90, 447–458.

de la Torre, J.R., Walker, C.B., Ingalls, A.E., Könneke, M., Stahl, D.A., 2008. Cultivation of a thermophilic ammonia oxidizing archaeon synthesizing crenarchaeol. Environ. Microbiol. 10, 810–818.

el Zahar Haichar, F., Marol, C., Berge, O., Rangel-Castro, J.I., Prosser, J.I., Balesdent, J., Heulin, T., Achouak, W., 2008. Plant host habitat and root exudates shape soil bacterial community structure. ISME J. 2, 1221–1230.

el Zahar Haichar, F., Santaella, C., Heulin, T., Achouak, W., 2014. Root exudates mediated interactions belowground. Soil Biol. Biochem. 77, 69–80.

op den Camp, H.J.M., Islam, T., Stott, M.B., Harhangi, H.R., Hynes, A., Schouten, S., Jetten, M.S.M., r. Birkeland, N.K., Pol, A., Dunfield, P.F., 2009. Environmental, genomic and taxonomic perspectives on methanotrophic Verrucomicrobia. Environ. Microbiol. Rep. 1, 293–306.

van Kessel, M.A.H.J., Speth, D.R., Albertsen, M., Nielsen, P.H., den Camp, H.J.M.O., Kartal, B., Jetten, M.S.M., Lücker, S., 2015. Complete nitrification by a single microorganism. Nature 528, 555–559.

Zwart, G., Crump, B.C., Kamst-van Agterveld, M.P., Hagen, F., Han, S.-K., 2002. Typical freshwater bacteria: an analysis of available 16S rRNA gene sequences from plankton of lakes and rivers. Aquat. Microb. Ecol. 28, 141–155.