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ENVIRONMENTAL BIOTECHNOLOGY

Distribution of ammonia-oxidizing archaea and bacteria in plateau soils across different land use types

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Abstract Ammonia oxidation is known to be performed by both ammonia-oxidizing archaea (AOA) and bacteria (AOB), although their relative significance to nitrification process in soil ecosystems remains controversial. The distribution of AOA and AOB in plateau soils with different land use types and the influential factors remains unclear. The present study investigated the abundance and structure of AOA and AOB communities in upland soils adjacent to Erhai Lake in the Yunnan Plateau (China). Quantitative PCR assays indicated a large variation in the community size of AOA and AOB communities, with the numerical dominance of AOA over AOB in most of soils. Clone library analysis illustrated a marked shift in the structure of soil AOA and AOB communities. A high abundance of *Nitrososphaera*- and *Nitrosotalea*-like AOA was observed, while *Nitrosospira*-like species predominated in AOB. AOA and AOB abundance was positively influenced by total nitrogen and moisture content, respectively. Moreover, moisture content might be a key determinant of AOA community composition, while C/N and nitrate nitrogen played an important role in shaping AOB community composition. However, further efforts will be necessary in order to elucidate the links between soil AOA and AOB and land use.

Keywords Ammonia-oxidizing bacteria (AOB) · Ammonia-oxidizing archaea (AOA) · Riparian, agricultural soil · Grassland · Mountain

Introduction

Soil shelters a huge density and diversity of microbes, which are believed to participate in a variety of biogeochemical processes (Dey et al. 2012; Fahrenfeld et al. 2014; Stroobants et al. 2014). Nitrification process is of fundamental importance for nitrogen cycling in soil ecosystems. Ammonia oxidation, the first and rate-limiting step in the nitrification process, was traditionally assumed to be mainly performed by ammonia-oxidizing bacteria (AOB) that harbor ammonia monooxygenase a-subunit (*amoA*) gene. The cultivated soil AOB species are affiliated with genera *Nitrosomonas* and *Nitrosospira* within class *Betaproteobacteria* (Purkhold et al. 2000). However, the recent discovery of ammonia-oxidizing archaea (AOA) has put the sole role of AOB in ammonia oxidation into question (Könneke et al. 2005; Prosser and Nicol 2012). The coexistence of these two ammonia-oxidizing groups has been reported in various types of soil ecosystems (Li et al. 2012; Meyer et al. 2014; Wang et al. 2014a, b). Both of them might be mainly responsible for in the biotransformation of ammonia to nitrite (He et al. 2007; Paranychianakis et al. 2013; Wessen et al. 2010). The abundance and community structure of soil AOA and AOB have been found to be driven by various environmental factors,

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such as moisture (Vasileiadis et al. 2012), pH (Nicol et al. 2008), carbon- and nitrogen-related fertility (Wang et al. 2014c; Wessen et al. 2010; Wertz et al. 2012), climate (Yao et al. 2013), and pesticide (Wan et al. 2014a, b). Moreover, it has been well-documented that land use type can also affect the distribution of soil ammonia-oxidizing microorganisms (Li et al. 2012; Meyer et al. 2014; Qin et al. 2013; Wang et al. 2014a; Zhao et al. 2015). Multiple environmental factors may collectively regulate the distribution of AOA and AOB in soil ecosystems (Jiang et al. 2014; Yao et al. 2013), and no single factor can discriminate between AOA and AOB (Prosser and Nicol 2012). Therefore, the relative contribution of AOA and AOB to nitrification in soil ecosystems remains still in debate.

The Yunnan Plateau is located in southwestern China, and its average elevation is about 2000 m above sea level. It is located in the subtropical monsoon climate zone, with an annual mean temperature of about 15–18 °C and an annual mean precipitation of about 1000–1200 mm. A relatively strong ambient ultraviolet radiation might select for a distinctive plateau soil microbial community (Ding et al. 2014). However, little is known about the abundance and structure of soil AOA and AOB communities in the Yunnan Plateau (Ding et al. 2014; Yang et al. 2014), and the key drivers governing their distribution in plateau soils remain unclear. Moreover, there are about 40 natural freshwater lakes in the Yunnan Plateau. Lake riparian buffer zones play important roles in maintaining sustainability of water quality, reducing sediment accumulation and preventing erosion (Dindaroglu et al. 2015). So far, information on the abundance and structure of soil AOA and AOB in lake riparian zones is still lacking. Therefore, the main objective of the present study was to investigate the abundance and structure of AOA and AOB communities in lake riparian zones and other adjacent soils in the Yunnan Plateau.

Materials and methods

Site description and sampling

Erhai Lake, the second largest freshwater lake in the Yunnan Plateau, is located in Dali City. In this study, a total of ten surface upland soil samples (0–5 cm depth) adjacent to Erhai Lake (N1–N5 and S1–S5) in triplicate were collected in June 2014 (Fig. 1). These soil samples were obtained from bare lake riparian zones (S1 and N1), rice fields (S2 and N2), maize fields (S3 and N3), grasslands (S4 and N4), and tree-vegetated mountain fields (S5 and N5), respectively. These soil samples were homogenized and subsampled for further analysis. The geographic and physicochemical parameters of the soils are described in Table S1.

Molecular analyses

Soil DNA was extracted using the Powersoil DNA extraction kit (Mobio Laboratories, USA). The specific primer sets Arch-amoAF/Arch-amoAR and AmoA-1F/AmoA-2R were applied for quantitative PCR (qPCR) assay of the archaeal and bacterial *amoA* genes, and construction of AOA and AOB clone libraries, following the previously reported conditions (Liu et al. 2014; Wang et al. 2014a). One-way analysis of variance (ANOVA) followed by Student–Newman–Keuls test was used to check the quantitative differences ($P<0.05$) in the abundance of AOA or AOB *amoA* gene among different soils. Chimera-free *amoA* gene sequences were grouped into operational taxonomic units (OTUs) using a 97 % similarity as a cutoff, and the MOTHUR program was used to generate OTU-based Shannon diversity index and rarefaction curve (Schloss et al. 2009). In addition, microbial community difference was compared using phylogeny-based weighted UniFrac environmental clustering (Lozupone et al. 2006). Phylogenetic analysis of AOA or AOB community was performed using MEGA6 software with the neighbor-joining and maximum parsimony methods (Tamura et al. 2013). Moreover, Pearson's correlation analysis using SPSS 20.0 software was used to illustrate the links between microbial community with the determined environmental factors [moisture content, organic matter (OM), total nitrogen (TN), ratio of OM to TN (C/N), NH_4^+–N, NO_3^-–N, and total phosphorous (TP)]. The *amoA* gene sequences obtained in the current study were deposited in the GenBank database under accession numbers KM116728–KM117158 for AOA, and KM250523–KM250902 for AOB, respectively.

Results

Abundance of AOA and AOB communities

Figure 2 illustrates a large variation in the AOA community size in the ten studied plateau soils. The archaeal *amoA* gene copy numbers varied from 8.68×10^5 to 9.32×10^7 copies per gram dry soil. Soils N1, N2, N3, S2, and S4 ($>5\times10^7$archaeal *amoA* gene copies per gram dry soil) had much higher AOA abundance than other five soils ($P<0.05$). Significant difference in the AOA abundance was also observed in the two soils from riparian zones, rice fields, maize fields, or grasslands ($P<0.05$). A large shift was also found in the density of AOB community, ranging from below detection to 3.79×10^7 bacterial *amoA* gene copies per gram dry soil. Moreover, soils N2 and N3 ($>1\times10^7$ bacterial *amoA* gene copies per gram dry soil) had much higher AOB abundance than the other seven soils ($P<0.05$). The two soils from riparian zones,

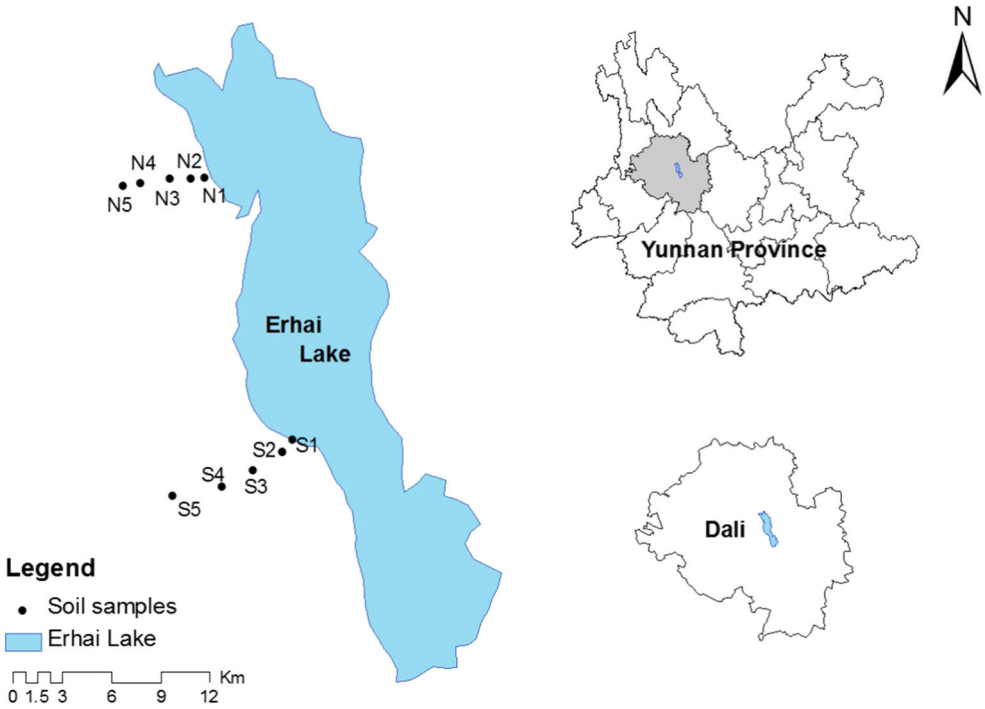


Fig. 1 Schematic representation of the different soil sampling sites

rice fields or maize fields, also showed significant difference in the AOB abundance ($P<0.05$). In addition, except for soils N4, N5, and S3, the studied plateau soils showed the numerical dominance of AOA over AOB.

Diversity of AOA and AOB communities

In this study, the AOB clone library with soil S5 was not successfully constructed, due to a very low abundance of bacterial *amoA* gene (below PCR detection). A total of 431 archaeal and 380 bacterial sequences were obtained from *amoA* gene clone libraries. The AOA and AOB clone libraries consisted of 3–13 and 8–18 OTUs, respectively (Table 1). A large variation in AOA and AOB community diversity was found among different soils, with the Shannon index of 0.49–2.17 and 1.33–2.58, respectively. Soils N1, N3, and N5 had the highest AOA diversity (Shannon index>2), while the lowest AOA diversity

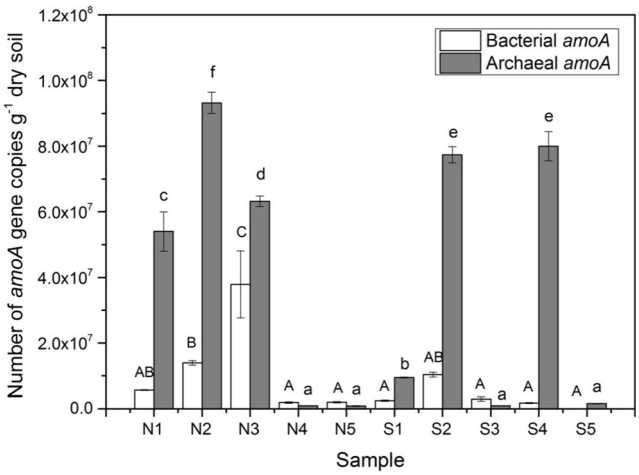


Fig. 2 Abundance of archaeal and bacterial *amoA* genes in different soils. *Different letters above the columns* indicate significant differences ($P<0.05$)

Table 1 Diversity of each soil AOA or AOB clone library

amoA gene	Soil	Number of clones	OTUs	Shannon index
AOA	N1	41	13	2.10
	N2	44	5	0.78
	N3	47	12	2.17
	N4	43	3	0.49
	N5	43	10	2.03
	S1	42	12	1.79
	S2	43	8	1.32
	S3	43	9	1.47
	S4	44	7	1.64
	S5	41	7	0.76
AOB	N1	42	13	1.74
	N2	42	10	1.50
	N3	42	16	2.12
	N4	39	13	1.95
	N5	36	9	1.54
	S1	44	9	1.37
	S2	42	8	1.33
	S3	46	18	2.58
	S4	47	12	1.80

(Shannon index<0.8) was found in soils N2, N4, and S5. Soils N3 and S3 illustrated the higher AOB diversity (Shannon index>2.1) than other soils. In addition, for most of the studied soils, a marked difference existed between AOA and AOB community Shannon diversity.

Comparison of AOA and AOB communities

Phylogeny-based weighted UniFrac environmental clustering analysis showed three distinctive AOA clades in ten plateau soils (Fig. 3a). Soils S4 and N5 were grouped together, but they were separated from other soils. Soils N1, N2, and S1 fell into a clade, while soils N3, N4, S2, S3, and S5 were clustered. These results indicated that soils with the same land use type could have much different AOA community composition. In addition, two distinctive AOB clades could be assigned (Fig. 3b). Soils N3 and N4 were clustered, while other soils fell into a large clade, suggesting that much different AOB composition could exist in soils with the same land use type.

Phylogeny of AOA and AOB

In this study, the representative *amoA* gene sequences for phylogenetic analysis were selected from the OTUs containing no less than two sequence members. All the AOA sequences from the ten studied soils could be grouped into three clusters (Fig. 4a). These soils differed remarkably in the composition of AOA clusters and their proportions, indicating a large variation in AOA community structure (Fig. 5a). Cluster-I-like AOA organisms predominated in soils N1, N2, and S1, while cluster-II-like AOA in soils N4 and S5. Soils N5 and S4 were mainly composed of cluster-III-like AOA species. Moreover, the AOA organisms affiliated with clusters I and II were dominant in soils N3, S2, and S3. These results further confirmed the occurrence of a much different AOA community composition in soils with the same land use type. Moreover, cluster I was the largest AOA group and contained 173 archaeal sequences that could be grouped with uncultured ones from a variety of ecosystems, such as river, estuary, cave, and lake sediments, agricultural and grassland soils, wastewater bioreactor, and river biofilm. Cluster II was composed of 134 archaeal *amoA* gene sequences. They were affiliated with a cultivated soil AOA species (*Nitrosotalea* sp. Nd2) (Lehtovirta-Morley et al. 2014). In addition, cluster III was the smallest AOA group including 85 members. The archaeal sequences in cluster III could also be affiliated with a cultivated soil AOA species (*Nitrososphaera viennensis* EN76) (Tourna et al. 2011).

All the bacterial *amoA* gene sequences from nine soils could be divided into four AOB clusters (Fig. 4b). These soils

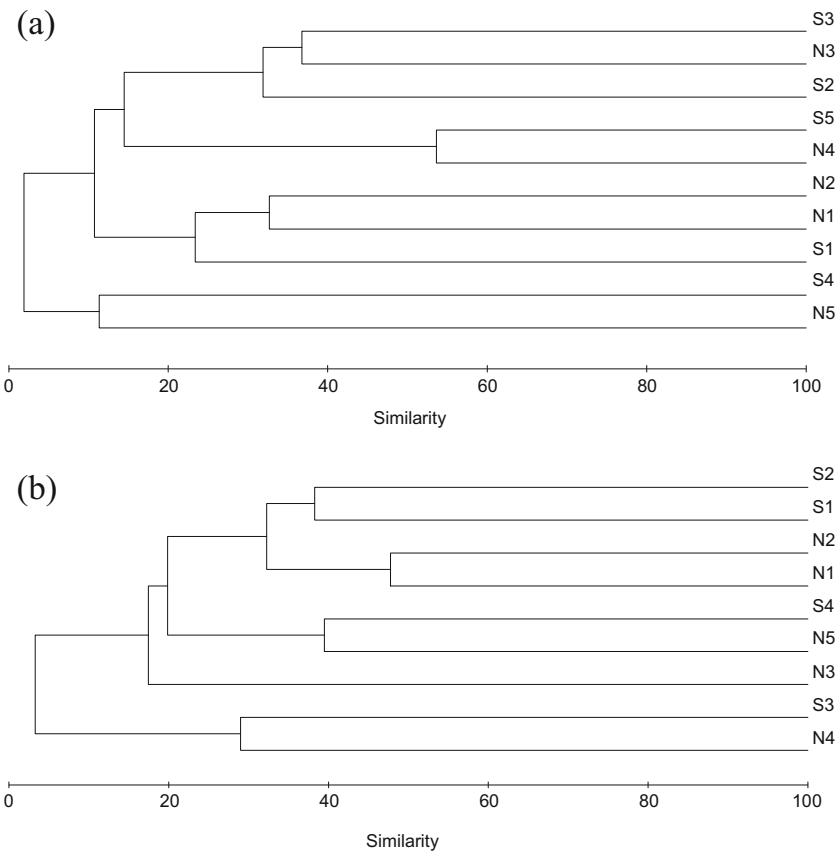


Fig. 3 Clustering of AOA (**a**) and AOB (**b**) clone libraries based on weighted UniFrac algorithm

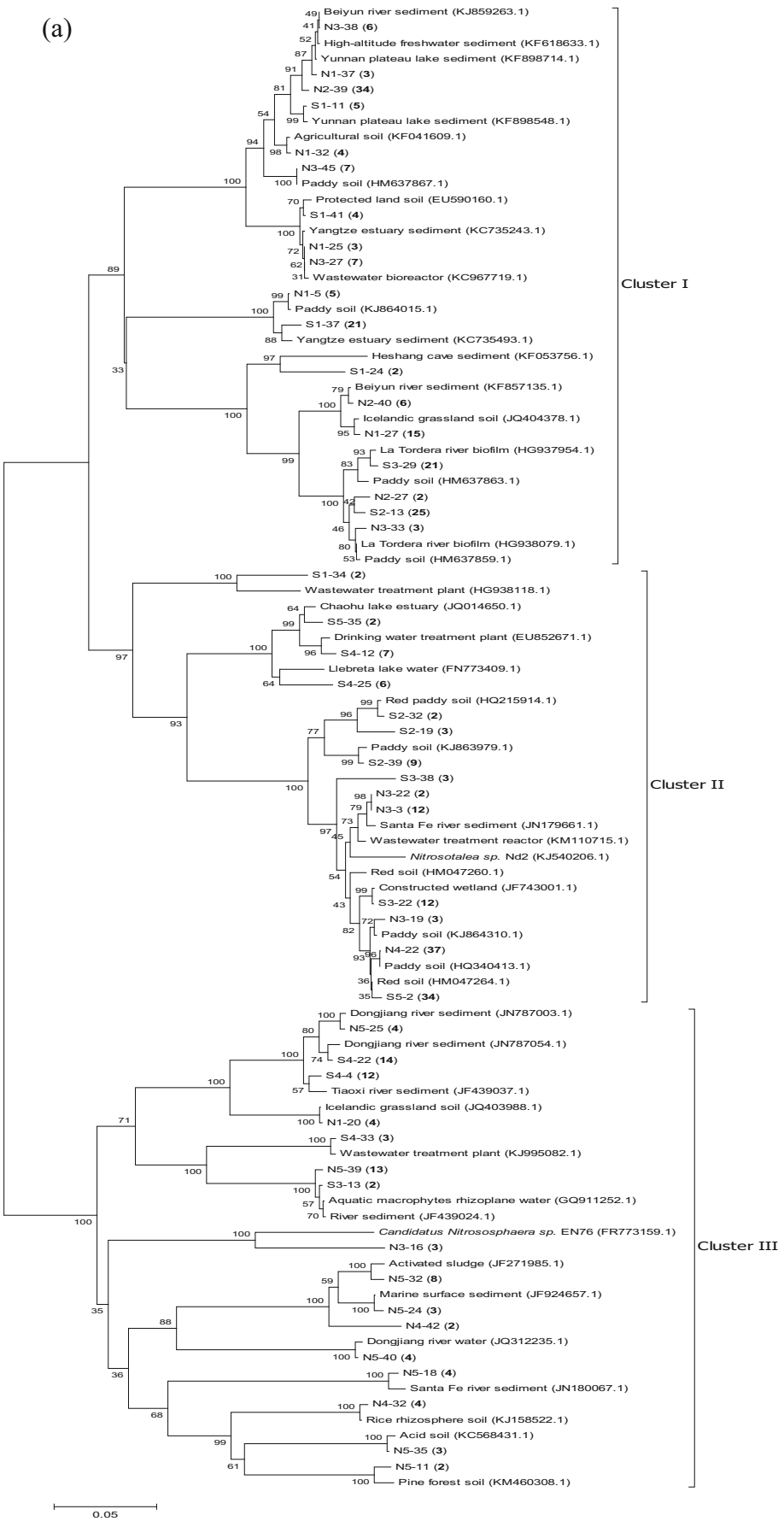
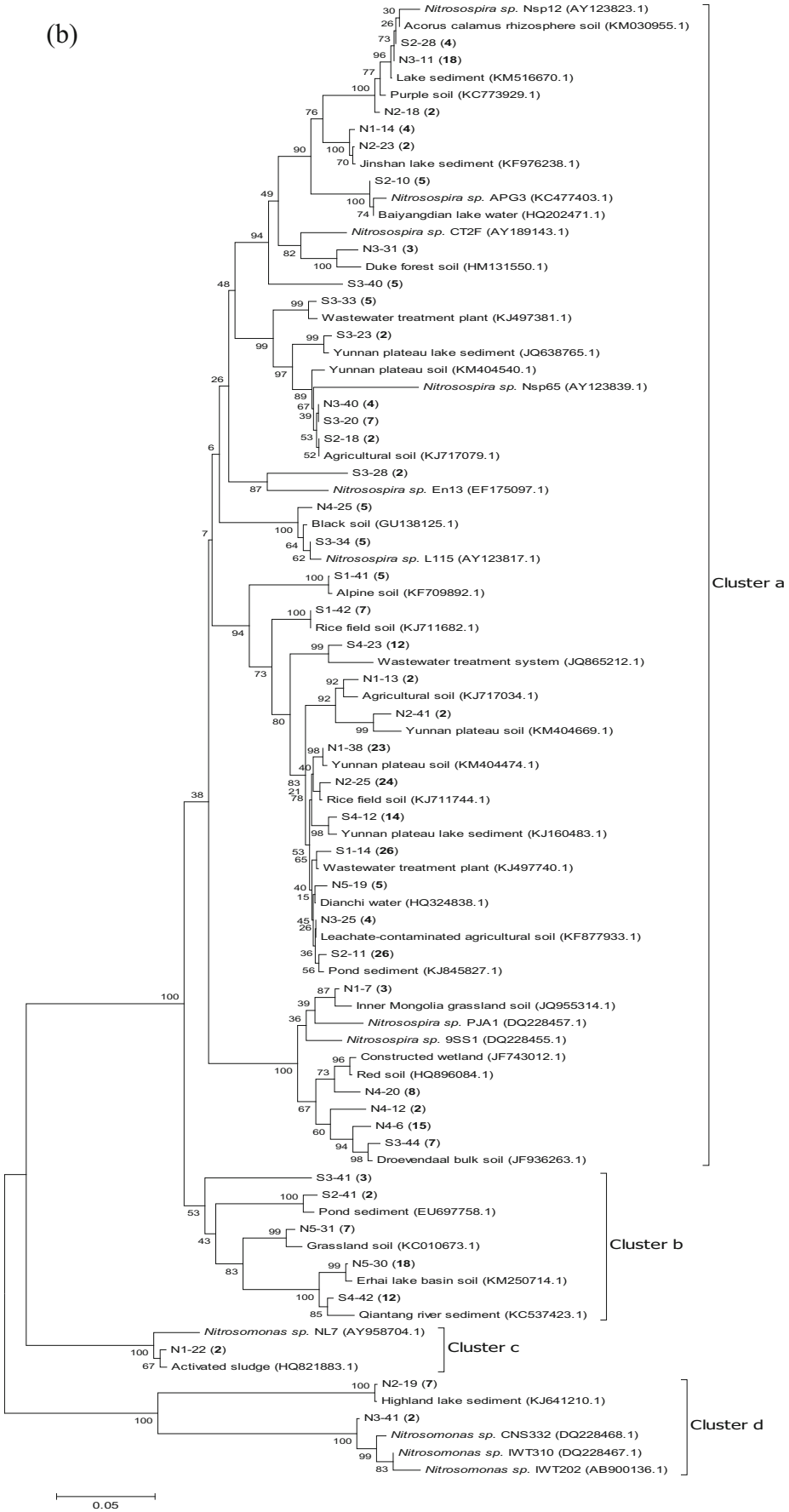


Fig. 4 Phylogenetic tree of representative archaeal (**a**) and bacterial (**b**) *amoA* sequences and reference sequences from GenBank. The obtained sequences beginning with "N1"–"N5" and "S1"–"S5" were referred to the sequences retrieved from soils N1–N5 and S1–S5, respectively. The *bold number in parentheses* represents the numbers of the sequences in the same OTU in a given clone library. *Numbers at the nodes* indicate the levels of bootstrap support based on neighbor-joining analysis of 1000 resampled datasets. The *bar* represents 5 % sequence divergence

Fig. 4 (continued)



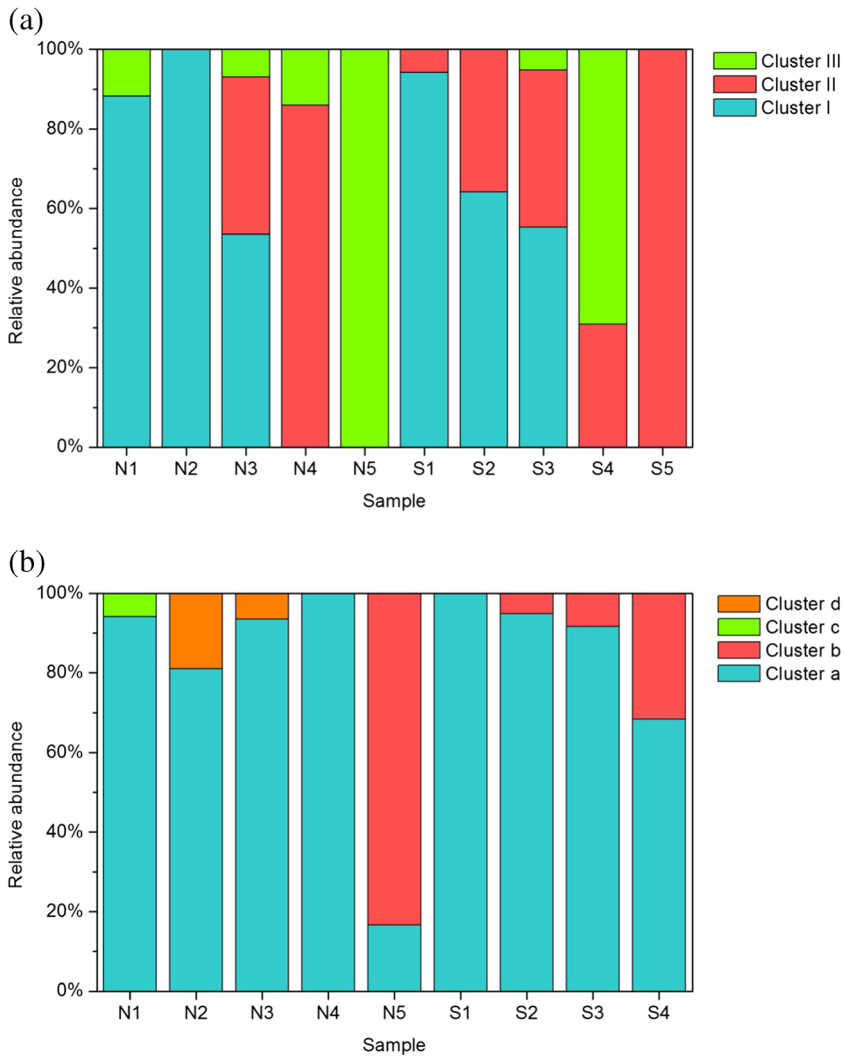


Fig. 5 Composition of AOA clusters (**a**) and AOB clusters (**b**) in each soil sample

showed the marked difference in the composition of AOB clusters and their proportions, indicating a large shift in the AOB community structure (Fig. 5b). Cluster-a-like AOB organisms predominated in most of soils (soils N1–N4 and S1–S4), but cluster-b-like AOB species in soil N5. Cluster-c-like AOB was a minor component in soil N1 and was not detected in other soils. Cluster-d-like AOB appeared with a low proportion in soils N2 and N3. Moreover, cluster a was the predominant AOB group containing 260 bacterial *amoA* gene sequences. These AOB sequences could be grouped with a number of cultivated *Nitrosospira* species (Nsp12, Nsp65, L115, APG3, CT2F, En13, PJA1, and 9SS1) (Mintie et al. 2003; Purkhold et al. 2003; Urakawa et al. 2015). Cluster b was the second largest AOB group and had 42 members. The AOB sequences in cluster b were close to some uncultured ones from various soil and sediment ecosystems. Cluster c only contained two bacterial sequences from soil N1. They could be affiliated with a cultivated *Nitrosomonas* species (NL7) (Park and Noguera 2007). In addition, cluster d was a nine-member AOB group. The bacterial *amoA* gene sequences in this cluster could be affiliated with two cultivated *Nitrosomonas* species (CNS332 and IWT310).

Influential factors regulating AOA and AOB communities

Pearson's correlation analysis indicated that AOA and AOB abundance were positively correlated with TN and moisture content, respectively ($P < 0.05$) (Table 2). However, no significant correlation was found between AOA and AOB Shannon diversity and the determined environmental factors ($P > 0.05$). The proportion of cluster-I-like AOA showed a highly significant positive correlation with moisture content ($P < 0.01$), while the proportion of cluster-III-like AOA showed significant positive correlations with C/N and nitrate nitrogen ($P < 0.05$ or 0.01). Moreover, soil C/N and nitrate nitrogen showed highly significant negative correlations with the proportion of cluster-a-like AOB, but positive with that of cluster-b-like AOB ($P < 0.01$). The proportion of cluster-d-like AOB was positively correlated with OM and TN ($P < 0.05$ or 0.01).

Table 2 Pearson's correlation analysis of AOA and AOB community with soil physicochemical properties

Parameter	OM	TN	C/N	NO_3^-–N	NH_4^+–N	TP	pH	Moisture content
AOA abundance	0.544	*0.733**	−0.186	−0.248	−0.438	−0.444	0.1	0.161
AOB abundance	0.182	0.518	−0.358	−0.331	0.310	−0.198	0.002	*0.655**
AOA Shannon diversity	−0.285	−0.410	0.230	0.363	−0.081	0.128	0.364	−0.105
AOB Shannon diversity	0.416	0.082	0.134	−0.187	−0.132	0.539	−0.517	−0.582
AOA cluster I	0.026	0.253	−0.454	−0.373	−0.445	−0.004	0.549	**0.811****
AOA cluster II	0.152	0.252	−0.201	−0.363	−0.084	−0.339	−0.57	−0.514
AOA cluster III	−0.186	−0.564	*0.755**	*0.822***	0.624	0.351	−0.081	−0.455
AOB cluster a	0.015	0.362	*−0.835***	*−0.937***	−0.492	−0.357	−0.184	0.314
AOB cluster b	−0.185	−0.522	*0.814***	*0.942***	0.505	0.329	0.112	−0.447
AOB cluster c	0.003	−0.158	0.061	−0.087	−0.249	0.196	−0.001	0.099
AOB cluster d	*0.741**	*0.816***	−0.099	−0.185	−0.081	−0.009	0.277	0.612

*Correlation is significant at the 0.05 level; **correlation is significant at the 0.01 level

Discussion

Soil AOA and AOB abundance

A few previous studies showed the numerical dominance of AOA over AOB in plateau grassland soils, agricultural soils, and forest soils (Chen et al. 2013; Ding et al. 2014; Wang et al. 2012; Yang et al. 2014; Zheng et al. 2014). In this study, AOA outnumbered AOB in most of the studied plateau soils, suggesting that AOA might play a more important role in ammonia oxidation. This was in agreement with the results reported in those previous studies. AOA can out-compete AOB in low-ammonium environments (Hofferle et al. 2010). The plateau soils with low levels of ammonia nitrogen (3.2–11.2 mg/kg) might account for the advantage of AOA over AOB. In addition, an increase in nitrogen content was usually found to increase the community size of soil AOB, instead of AOA (Chen et al. 2013; Glaser et al. 2010; Wertz et al. 2012). However, the result obtained in this study revealed that AOA abundance showed a positive correlation with TN, while no significant correlation was found between AOB abundance and nitrogen level.

So far, the impact of soil moisture on AOA and AOB abundance remains poorly understood. Di et al. (2014) indicated that an increase in soil moisture content increased the community size of both AOA and AOB. AOA abundance was found to be more responsive to the change in soil moisture (Thion and Prosser 2014; Szukics et al. 2012), while Vasileiadis et al. (2012) showed that moisture variation only had a strong impact on AOB abundance. In this study, moisture content was found to be an important driver of AOB abundance in different upland soils adjacent to Erhai Lake in the Yunnan Plateau.

Several previous studies indicated that soil AOA and AOB abundance could be influenced by land use type (Li et al. 2012; Qin et al. 2013; Wang et al. 2014a; Yang et al. 2014). However, in this study, the soils with the same land use type usually showed a large difference in the community size of AOA and AOB. This suggested that land use type might not play a crucial role in determining the abundance of AOA and AOB in upland soils adjacent to Erhai Lake.

Soil AOA and AOB community diversity and structure

A few recent studies showed a profound variation in the community diversity of AOA and AOB in different plateau soils (Ding et al. 2014; Yang et al. 2014; Zheng et al. 2014), while the driver of AOA and AOB diversity in plateau soils remains elusive. Ding et al. (2014) suggested that TN and OM content might be a key determinant of AOA community diversity in plateau soils. In the current study, the factor governing AOA and AOB Shannon diversity was not identified. Further efforts will be necessary in order to elucidate the links between plateau soil AOA and AOB diversity and environmental factors.

AOA organisms are able to adapt to a variety of habitats (Wang and Gu 2013; Liu et al. 2014, 2015). In this study, the obtained archaeal *amoA* gene sequences in AOA cluster I could be affiliated with those from various ecosystems, such as sediments, soils, wastewater bioreactor, and river biofilm, suggesting that AOA species of different evolutionary origins existed in soils in the Yunnan Plateau. Moreover, the result of Pearson's correlation analysis suggested that moisture content was likely a key driver of cluster-I-like AOA. Since cluster I was the largest AOA group, it could be assumed that moisture content might play an import role in shaping AOA communities in upland soils adjacent to Erhai Lake in the Yunnan Plateau.

A high proportion of *Nitrososphaera*-like microorganisms in AOA community existed in a variety of soil ecosystems (Ke and Lu 2012; Li et al. 2012), while *Nitrososphaera*-like AOA was found to be in low proportion or even was not detected in grassland and forest soils in the Tibetan Plateau (Wang et al.

2012; Zheng et al. 2014). Our previous study indicated that, in the Yunnan Plateau, *Nitrososphaera*-like species predominated in AOA community in garlic soil, but became a minor component in rice and cabbage soils (Yang et al. 2014). So far, the links between the abundance of *Nitrososphaera*-like AOA and environmental factors remains elusive. In this study, *Nitrososphaera*-like species predominated in one soil from mountain field (soil N5) and one soil from grassland (soil S4), but showed a low proportion or even none detection in other plateau soils. Moreover, AOA cluster-III-like organisms (affiliated with *Nitrososphaera*) were found to be positively influenced by C/N and nitrate nitrogen.

Several *Nitrosotalea* strains have been isolated from soil ecosystems (Lehtovirta-Morley et al. 2011, 2014). Some previous studies showed a high proportion of *Nitrosotalea*-like microorganisms in soil AOA communities (Long et al. 2012; Hu et al. 2012, 2014), while they were usually absent in other reported soil ecosystems (Ke and Lu 2012; Li et al. 2012; Xu et al. 2012; Wang et al. 2014a). *Nitrosotalea*-like AOA species were also not found in forest and grassland soils in the Tibetan Plateau (Wang et al. 2012; Zheng et al. 2014), and rice, cabbage, and garlic soils in the Yunnan Plateau (Yang et al. 2014). So far, little is known about the environmental factors regulating the distribution of *Nitrosotalea*-like AOA (Hu et al. 2014). In this study, *Nitrosotalea*-like organisms showed a high proportion or were even dominant in most of the studied plateau soils. However, other unknown factors might determine their distribution.

Due to the different of physiological traits, *Nitrosospira* favor low-ammonia environments, while *Nitrosomonas* favor polluted environments of high ammonia (Ke and Lu 2012; Wang and Gu 2013). *Nitrosospira* are usually the dominant AOB in soil environments (Ke and Lu 2012; Wang et al. 2014a). The dominance of *Nitrosospira* was also found in grassland soils in the Tibetan Plateau (Zheng et al. 2014) and agricultural soils in the Yunnan Plateau (Yang et al. 2014). However, the links between *Nitrosospira* species and environmental factors in plateau soils remains largely unclear. In this study, *Nitrosospira*-like species were found to predominate in upland soils adjacent to Erhai Lake in the Yunnan Plateau (except for one soil from mountain field). Moreover, the result of Pearson's correlation analysis suggested that soil C/N and nitrate nitrogen negatively affected the proportion of cluster a-like AOB (affiliated with *Nitrosospira*). Since cluster a was the predominant AOB group, it could be assumed that C/N and nitrate nitrogen were possibly the key determinants of AOB communities in plateau soils.

Wang et al. (2014a) revealed a marked difference in both AOA and AOB community composition in reed-planted riparian soil, bare riparian soil, and maize-planted agricultural soil. Yang et al. (2014) also showed a large shift in both AOA and AOB community composition in rice, cabbage, and garlic soils in the Yunnan Plateau. Moreover, Zhao et al. (2015) found that AOB community composition was more sensitive to the land use regimes than AOA, while Meyer et al. (2014) suggested that, compared with AOB, AOA community composition was responsive to land use intensity. In this study, although a large shift could be found in soils with different land use type, soils with the same land use type could have a much different AOA and AOB community composition. Therefore, the impact of land use type on plateau soils remains unclear. Land use type alone might not be able to discriminate AOA and AOB in upland soils adjacent to Erhai Lake in the Yunnan Plateau.

In conclusion, the abundance and structure of AOA and AOB communities illustrated a large shift in upland soils adjacent to Erhai Lake in the Yunnan Plateau. AOA usually outnumbered AOB in plateau soils. A significant proportion of AOA sequences affiliated with *Nitrososphaera* and *Nitrosotalea* were found, while *Nitrosospira*-like species were the predominant AOB. The distribution of AOA and AOB communities could be regulated by moisture and nitrogen content. Soils with the same land use type could have different AOA and AOB communities.

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Ethical statement No conflict of interest exits in the submission of this manuscript, and the manuscript is approved by all authors for publication. I would like to declare on behalf of my co-authors that the work described was an original research that has not been published previously, and not under consideration for publication elsewhere, in whole or in part.

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