RESEARCH ARTICLE

Potential correlated environmental factors leading to the niche segregation of ammonia-oxidizing archaea and ammonia-oxidizing bacteria: A review

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Abstract: Ammonia oxidation is an important step of the nitrogen cycle and was considered to be conducted only by ammonia-oxidizing bacteria (AOB) for a long time. The discovery of ammonia-oxidizing archaea (AOA) caused consideration of the relative contributions of these two functional groups in different niches and factors resulting in their niche segregation. Previous studies showed that some environmental factors may correlate to the abundance and distribution of AOA and AOB, including ammonia/ammonium concentration, pH, organic matters, oxygen concentration, temperature, salinity, sulfide concentration, phosphate concentration, soil moisture and so on. Despite extensive studies conducted on ecology of AOA and AOB to find key environmental factors dominating niche segregation between AOA and AOB, few studies were conducted to explore the interrelationship among environmental factors. In this review, five main environmental factors which may be related to each other were selectively reviewed independently, including ammonia concentration, pH, temperature, oxygen concentration and organic matters. Furthermore, potential interrelationship among environmental factors was proposed.

Keywords: ammonia concentration, pH, temperature, oxygen concentration, organic matters

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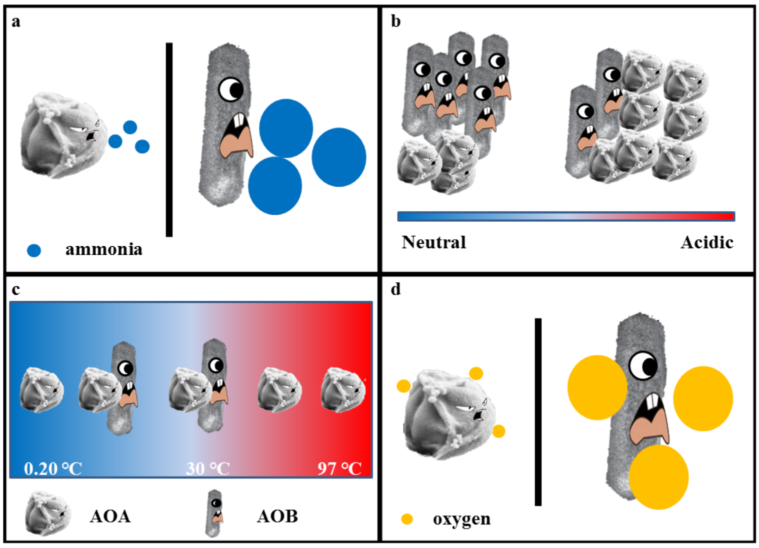
1. Introduction

Nitrification, the oxidation of ammonia to nitrite and nitrate, has long been considered a central biological process in the global nitrogen cycle (Monteiro et al., 2014). Ammonia oxidation was considered to be performed only by microbes from bacteria domain for more than 100 years. This traditional viewpoint was thoroughly challenged and changed on the basis of the discovery of AOA. So far, more than 10 strains of AOA were already isolated, and more than 10 enrichments have been cultivated (Blainey et al., 2011; De La Torre et al., 2008; Elling et al., 2015; Hallam et al., 2006; Hatzenpichler et al., 2008; Jung et al., 2011; Jung et al., 2014; Kim et al., 2012; Kim et al., 2016; Könneke et al., 2005; Lehtovirta-Morley et al., 2011; Lehtovirta-Morley et al., 2016a; Mosier et al., 2012; Qin et al., 2014; Sauder et al., 2017). Yet more than 80% of the AOA were still undiscovered so far (Biller et al., 2012). According to the dissimilarities of the *amoA* genes, AOA was divided into four clusters (1.1a, 1.1b, 1.1a-associated and ThAOA). Corresponding to the diversity of AOA, different ecotypes of AOA distribute widely in both marine (Wuchter et al., 2006) and terrestrial ecosystems (Leininger et al., 2006) and often outnumber AOB. A series of environmental factors appears to influence the niche segregation of AOA and AOB, including ammonia concentration (Verhamme et al., 2011), pH (Gubry-Rangin et al., 2011), organic matters (Qin et al., 2014), DO (dissolved oxygen) levels (Santoro et al., 2008), and temperature (De La Torre et al., 2008). In the previously published review articles, environmental factors were collected and independently discussed within some parts of physiological mechanisms, microcosm experiments and ecological researches (Hatzenpichler, 2012; Stahl and De La Torre, 2012). Here, this review provides a synopsis of the effects of the most important factors list above on the niche segregation of AOA and AOB in nature and microcosm experiments, and discusses the mechanisms from the physical point of cultivated ammonia-oxidizing microorganism-



Note: a: the difference of ammonia affinity between AOA and AOB. The blue discs represent ammonia, with larger area representing higher concentration. b: AOA adapt better to acidic environments than AOB. c: AOA have wider living temperatures than AOB. d: the difference of oxygen affinity between AOA and AOB. The yellow discs represent dissolved oxygen, with larger area representing higher concentration.

Figure 1. Schematic diagrams showing differences between AOA and AOB.

s. Furthermore, this review proposes potential interrelationship among environmental factors, which might help people analyze the complex process of ammonia oxidation.

2. Ammonia Concentration Leading to the Niche Segregation of AOA and AOB

Ammonia is one of key environmental factors leading to the niche segregation of AOA and AOB. Ammonia, as the electron donor shared by both AOA and AOB, its concentrations would influence the relative abundance of the two functional groups of microbes, afterwards, leading to a niche segregation of AOA and AOB. It has been widely accepted that AOA maintained a higher affinity for substrate than AOB and were more likely to survive under oligotrophic conditions (Figure 1a).

Studies specified on the growth kinetics related to isolated strains and enrichment cultures had examined and testified the standpoints above. The half-saturation constant (K_m) for substrate of the *Nitrosopumilus maritimus* SCM1 isolated from the ocean was 132 nM (NH_3+NH_4^+-N) and over 200 times lower than the K_m of the known AOB (>30 μM) (Martens-Habbena et al., 2009). Correspondingly, the affinity for substrate of *Nitrosopumilus maritimus* SCM1 was higher than AOB by two or three orders of magnitude (Martens-Habbena et al., 2009). However, a higher affinity for substrate implied lower substrate inhibition concentrations. Normally, the growth of *Nitrosopumilus maritimus* SCM1 would be inhibited when substrate concentration (NH_3+NH_4^+-N) increased to 2-3 mM (Könneke et al., 2005). Compared with *Nitrosopumilus maritimus* SCM1, other AOA isolates or enrichment cultures displayed relative lower affinities for substrate and higher substrate inhibition concentrations.*Candidatus* Nitrososphaera gargensis derived from thermal springs maintained its highest growth rate at the substrate (NH_3+NH_4^+-N) concentration of 0.14-0.79 mM, and its growth inhibition was detected at the substrate (NH_3+NH_4^+-N) concentration of 3.08 mM (Hatzenpichler et al., 2008). It is noteworthy that AOA isolated or enriched from soils maintained higher tolerance to the substrate. The complete substrate (NH_3+NH_4^+-N, inhibition concentration was around 20 mM for *Nitrososphaera viennensis* EN76 (Tourna et al., 2011), *Candidatus* Nitrosoarchaeum koreensis MY1 (Jung et al., 2011) and *Candidatus* Nitrososphaera sp. JG1 (Lehtovirta-Morley et al., 2016a). The substrate inhibiting concentration of AOA appeared lower than that of AOB (ranged from 22 to 1000 mM) (NH_3+NH_4^+-N) (Suwa et al., 1994; Koops et al., 2003). For this reason, growth of AOA tended to be inhibited prior to AOB in conditions with high substrate concentrations. For ammonia-oxidizing microorganisms in soil, the K_m for activity of soil AOA ranged from 3.60×10^{-3} to 1.90×10^{-2} μM NH_3 and were lower than that of soil AOB (6-11 μM) (Prosser and Nicol, 2012). All these indicated in essence that a large group of AOA was inhibited at ammonia concentrations that appropriate for the growth of AOB, and the ammonia concentrations at which AOA would grow well might not support the growth and metabolism of AOB.

A series of ecological researches verified that AOA were more suitable to live with low substrate concentrations in different habitat types. In an agricultural soil whose nitrification rate was dominated by AOA out of low ammonium availability, ammonium fertilizers stimulated AOB activity and community more strongly than AOA (Ouyang et al., 2016). In a temperate forest soil where AOA significantly contribute to ammonia oxidation, substrate availability limits nitrification by AOB. However, addition of high levels of substrate inhibited the growth of AOA, but stimulated nitrification by AOB (Norman and Barrett, 2014). In temperate grasslands in Inner Mongolia, before exceeding 224 kg N/ha/yr, N additions had the effect that decreasing the *amoA* gene copy ratios of AOA to AOB (Zhang et al., 2016). In oligotrophic marine surface sediments, the relative abundance of archaeal and bacterial *amoA* decreased when ammonium concentrations increased (Lagostina et al., 2015). In a simulated creek ecosystem, incubating from 50 or 20 μM NH_4^+ to 350 μM NH_4^+ established AOB predominance more rapidly. Biofilm-associated potential nitrification activity was positively correlated with AOB rather than AOA (Herrmann et al., 2011). In two freshwater lakes at different trophic states on the Yunnan Plateau, sediment AOB usually outnumbered AOA in hypertrophic Dianchi Lake, while sediment AOA showed the dominance in mesotrophic Erhai Lake (Yang et al., 2016). In wastewater treatment plants, it was also true that AOA favors niches with relative lower concentration of substrate. In rotating biological oxidizing process, the abundance of the *amoA* gene and 16S rRNA gene of AOA increased with the ammonia concentration decreased, which implied a propensity of lower ammonia concentration by AOA (Sauder et al., 2012).

3. pH Leading to the Niche Segregation of AOA and AOB

pH is another key environmental factor leading to the niche segregation of AOA and AOB. In the environment, decrease of pH values leads to ammonia protonation, which lessens bio-availability of ammonia oxidizing substrate (ammonia) and enforces energy selection pressure. Niches with low pH are fit for the growth of AOA from the view of the substrate utilization since AOA preferred oligotrophic conditions (Figure 1b).

Physiological and genomic researches showed that AOA adapt to lower pH than AOB. So far, none of the known AOB strains had the ability to survive autotrophically by utilizing ammonia as their nitrogen source in the conditions with pH below 6.50 (Burton and Prosser, 2001). An interpretation, perhaps, lied on that the substrate of bacterial ammonia oxidation was ammonia (NH_3) (von Uexküll and Mutert, 1995). In addition, concentrations of the non-protonated ammonia (NH_3) would be reduced by one order of magnitude when pH values decreased by one unit in the environments. So, AOB could not live in acid conditions due to the lack of substrate of ammonia oxidation. Soil investigation showed that acid soils (pH<5.50) took up 30% of soils all around the world (von Uexküll and Mutert, 1995). A paradox between ammonia oxidizing activity in acid soil and feeble acid-resistant characteristic of AOB had long confused us on the ammonia oxidation in acid soils. The discovery of *Candidatus* Nitrosotalea devanaterra provided concrete evidence for the ammonia oxidation in acid environments, as *Candidatus* Nitrosotalea devanaterra was able to catalyze ammonia oxidation in the conditions with pH values of 4.0-5.5 (Lehtovirta-Morley et al., 2011). The latest discovery of the AOA strain PS0 could perform ammonia oxidation at a pH level of 5.90 (Qin et al., 2014). Survival of *Candidatus* Nitrosotalea devanaterra at an extreme low substrate level (0.18 nM) indicated a novel ammonia oxidizing mechanism applied in AOA in the acid environments (Lehtovirta-Morley et al., 2011). Apart from the high affinity for substrate, decomposition of urea in the environment into ammonia probably accounted for another acid-resistant mechanism of AOA. Previous study had certified this through isotopic labelling and found that urea addition promoted AOA growth in acid environments (Lu and Jia, 2013). Identifying considerable amount of urease-coding genes in AOA genomes suggested the likehood of a metabolic pathway utilizing urea (Hallam et al., 2006). In addition, the third latent acid-resistant mechanism was that AOA could utilize ammonium as the substrate for ammonia oxidation (Stahl and De La Torre, 2012). A more recently study by analysis of the sequenced genome, transcriptional activity and lipid content of '*Ca.* N. devanaterra' revealed that a predicted high affinity substrate acquisition system and potential pH homeostasis mechanisms is essential for archaeal ammonia oxidation in acidic environments (Lehtovirta-Morley et al., 2016b). Three possible or feasible acid-resistant mechanisms mentioned above facilitated AOA to attain certain competitive advantages over AOB in acid environments.

Microcosm and ecological researches also showed that archaea dominated the ammonia oxidation in acid soils. It was found that in the acid soil the copy numbers and transcriptional abundance of AOA *amoA* genes increased as the pH value reduced. AOB, however, exhibited the opposite and the copy numbers and transcriptional abundance of AOB *amoA* genes were less than that of AOA by two orders of magnitudes (Nicol et al., 2008). In most acid soils, the abundance of AOA was more than that of AOB, suggesting a greater adaptability of AOA to live in the acid environment (Gan et al., 2016; He et al., 2007; Hu et al., 2014; Leininger et al., 2006; Norman and Barrett, 2016; Stempfhuber et al., 2015). In a peaty soil with a pH value of 4.1, the abundance of AOB *amoA* genes was below the detection limit while the abundance of AOA increased as the incubation went on. Also, the net ammonia oxidation rate of the peaty soils appeared high, indicating that AOA was the main catalyzer performing ammonia oxidation in the acid soil (Stopnišek et al., 2010). Other researchers also found that in acid soils, the ratio of AOA/AOB increased as the pH of soils decreased (Yao et al., 2011; Zhou et al., 2015). In a continuously acidifying soil caused by over-fertilization with nitrogen, AOB was dominant in nitrification when soil pH ranged from 5.6 to 7.0, but was inhibited when soil pH was below 5.0 (Song et al., 2016).

4. Temperature Leading to the Niche Segregation of AOA and AOB

In moderate environments, AOA and AOB showed differences in response to temperature. For example, soil nitrification potential of eight soils from four different sites in Oregon were evaluated across a temperature gradient (4-42°C), showing the optimal temperatures for AOA 12°C greater than that for AOB (Taylor et al., 2016).

However, in some extreme niches, AOA often dominated the ammonia oxidation (Figure 1c). Most of the AOB strains discovered so far were categorized into the mesophilic bacteria whose optimal living temperatures were around 30°C. However, the optimal growth temperatures of AOA varied greatly. For example, AOA strains *Nitrosopumilus maritimus* HCA1 and PS0 have the highest growth rates at 25°C and 26°C, respectively (Qin et al., 2014); the optimal growth temperature of *Candidatus* Nitrososphaera sp. JG1 ranged from 35 to 40°C (Kim et al., 2012); a thermophilic AOA *Candidatu*s Nitrosocaldus yellowstonii conducted ammonia oxidation under 60-74°C (De La Torre et al., 2008). Ammonia oxidation activity and archaeal *amoA* genes were both detected at high temperatures of 84-85°C (Reigstad et al., 2008). The glycerol dialkylglycerol tetraethers in the cell membrane of AOA contributed to their tolerance for a wide range of temperatures (Reigstad et al., 2008) and facilitated AOA with competitive advantages over AOB and other microbes in some extreme high or low temperatures.

5. Oxygen Concentration Leading to the Niche Segregation of AOA and AOB

Different oxygen affinity and response to oxygen toxicity of AOA and AOB make oxygen another nonnegligible environmental factor. The niche segregation was mainly resulted from the differences for oxygen affinity of the two ammonia-oxidizing groups (Figure 1d). To be more specific, relative higher affinity for oxygen made AOA more competitive than AOB in the environment with low oxygen concentration. Kinetics studies found that the K_m for oxygen of *Nitrosopumilus maritimus* SCM1, *Candidatus* Nitrososphaera sp. JG1, *Candidatus* Nitrosoarchaeum koreensis MY1 were 3.90 μM, 4.67 μM, 10.38 μM, respectively (Jung et al., 2011; Kim et al., 2012; Martens-Habbena et al., 2009). The K_m for oxygen of AOA enrichment cultures from marine sediment was 2.01 μM (Park et al., 2010). Besides, the *in-situ* K_m for oxygen of AOA in the oxygen minimum zones (OMZs) in eastern pacific was 330 nM (Dalsgaard et al., 2013). However, the K_m for oxygen of AOB such as *Nitrosomonas oligotropha* NL7 and Nitrosomonas europaea C-31, whose K_m values were 76.3 μM and 183.3 μM respectively (Park and Noguera, 2007; Park et al., 2010), were higher than that of AOA's. A recent study showed that relatively high H_2O_2 concentration may toxify the cells of AOA (Kim et al., 2016), which may explain the real function of oxygen on ammonia-oxidizing microorganisms. Microcosm tests indicated that AOA were more suitable than AOB for growth in the environment with low oxygen concentrations. When the oxygen concentration decreased from 75% to 5%, the transcriptional abundance of AOA *amoA* genes increased rapidly, while transcription activity of AOB *amoA* genes reduced by an order of magnitude (Abell et al., 2011).

A series of ecological evidence showed that AOA were more adaptable to low oxygen habitat than AOB. In the agricultural soil around Europe, it was reported that with the increased soil depth, the oxygen concentration decreased and the ratio of AOA/AOB increased. In the soil with depth from 0 to 30 cm, the ratio of AOA/AOB tended to be less than 1000; in the soil with depth ranging from 30 to 40 cm, the ratio exceeded 3000 (Leininger et al., 2006). In rice field soil, the abundance and activity of AOB rather than AOA were increased by high oxygen concentration, indicating that AOB were more sensitive to oxygen availability than AOA (Ke and Conrad, 2015). In a freshwater aquaculture pond, AOA dominated in the surface sediment as they were more adaptive to low levels of dissolved oxygen than AOB (Lu et al., 2016). Similar patterns were also found in the marine ecosystem. In OMZs of the eastern Pacific Ocean near Peru and Chile, the copy numbers of AOA *amoA* genes ranged from 10^2-10^5 copies/mL while the AOB *amoA* genes were under the detection limit (Molina et al., 2010). It was also found that AOA would live better in conditions with low oxygen concentration in freshwater sediments. In an oligotrophic lake in Switzerland, the ratio of AOA/AOB abundance increased along with the increased water depth (Vissers et al., 2013). In oxygenated/hypoxic alternant conditions, AOA outnumber AOB significantly (Liu et al., 2015).

6. Organic Matters Leading to the Niche Segregation of AOA and AOB

The different responses to organic matters of AOA and AOB may also lead to their niche segregation in the environments. So far, the role of organic matters on ammonia-oxidizing microorganisms had not yet been conclusive.

The addition of organic matters was likely to stimulate the growth of AOB, yet it was still uncertain that whether AOA grew strictly autotrophically or mixotrophically. As chemolithoautotrophic organisms, some AOA tend to be inhibited by organic matters (Jung et al., 2016; Kim et al., 2016; Könneke et al., 2005; Lehtovirta-Morley et al., 2014). For example, the very little dose of organic matters like 0.20 mg/L of yeast extract or 2 mM acetate inhibited the growth of *Nitrosocaldus yellowstonii* (De La Torre et al., 2008). Despite facts above, organic matters could sometimes stimulate the growth of AOA (Bayer et al., 2016; Kim et al., 2016; Lehtovirta-Morley et al., 2014; Sauder et al., 2017). The phenomenon that the growth rate of *Nitrososphaera viennensis* increased significantly and its cell generation got shortened by 11.5 times when 0.10 mM pyruvate was added, was misinterpreted as mixtrophy (Tourna et al., 2011), and was recently explained as a hydrogen peroxide detoxification mechanism (Kim et al., 2016). Possible interpretation was that AOA were lack of several key metabolic enzymes in their metabolic pathway and organic matters could complement the pathways of AOA and help them to perform a normal metabolism (Kim et al., 2016; Qin et al., 2014). Here, organic matters were more like a catalyst. However, studies using stable isotope probing (SIP) supported that AOA potentially utilized organic matters for their heterotrophic growth as well. It was found that marine archaea were able to take use of amino acids for its heterotrophic growth (Ouverney and Fuhrman, 2000). In the bottom of the North Atlantic, some AOA evolved a heterotrophic metabolism system utilizing organic matters to maintain the cell growth due to survival pressure caused by an energy deficit (Agogué et al., 2008).

Metagenomics researches further supported that some AOA could grow autotrophically by fixing and absorbing inorganic carbon source (Berg et al., 2010; Martin-Cuadrado et al., 2008). Genome analysis of *Nitrosopumilus maritimus* SCM1 and *Candidatus* hydroxypropionic Nitrosoarchaeum koreensis MY1 also led to the same conclusion that AOA took advantage of 3- acid /4-hydroxybutanoic acid metabolic pathway, absorbing and assimilating inorganic carbon source (Kim et al., 2012; Walker et al., 2010). Meanwhile, it was also found that AOA got the ability/potential to grow heterotrophically. *Cenarchaeum symbiosum* A and *Nitrosopumilus maritimus* SCM1 genome contained some coding genes related to the transport of amino acid, oligopeptide and glycerol, pointing out that AOA latently used TCA cycle for metabolizing organic carbon despite imperfection of the TCA cycle (Hallam et al., 2006; Walker et al., 2010).

7. Potential Interrelationship among Environmental Factors

Extensive studies were conducted on ecology of AOA and AOB, such as dominant environmental factors influencing abundance, diversity, ammonia-oxidizing activity of AOA and AOB. Some environmental factors have been gradually accepted as potential key environmental factors, such as ammonia concentration (Verhamme et al., 2011), pH (Gubry-Rangin et al., 2011), organic matters (Qin et al., 2014), DO (dissolved oxygen) levels (Santoro et al., 2008), and temperature (De La Torre et al., 2008), supported by ecology results or physiological experiments. Here comes a question: Are those environmental factors regarded independent when different ecotypes of AOA and AOB select their habitats?

Some evidences showed that those environmental factors might have interrelationship (Figure 2). Strong ecological coherence was reflected between phylogeny and pH, or phylogeny and organic matter content for terrestrial *Thaumarchaeota* (Oton et al., 2016). This implied that pH and organic matter content might have some internal direct or indirect connection. The interrelationship among environmental factors was important to understand the complex process of ammonia oxidation under various environments. Obviously, the change of pH inevitably can influence the availability of ammonia nitrogen, and pH could also have consequences for temperature optima of AOA for growth and activity in the environment (Gubry-Rangin et al., 2017). In most acidic soils detected, AOA *amoA* gene abundance and yield were greater at 20°C than 30°C. With the increase of temperature, oxygen availability will inevitably decrease for ammonia-oxidizing organisms. Organic matters such as pyruvate could potentially detoxify hydrogen peroxide caused by ammonia oxidation or oxygen (Kim et al., 2016). So when pH changed, ammonia availability was directly influenced; temperature optima of AOA, oxygen concentration and organic matter content (or might be replaced by heterotrophic bacteria) also indirectly selected for specific group AOA.

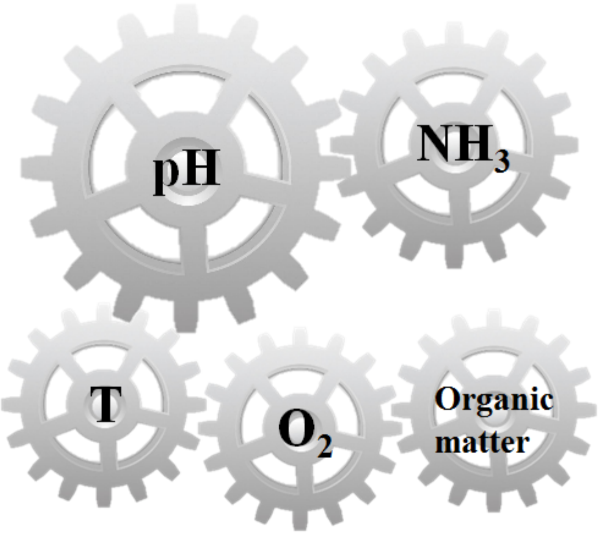


Figure 2. Schematic diagram showing the potential interrelation among environmental factors.

8. Conclusion

In this mini-review, we provided some evidences derived from physiological analysis, microcosm experiments, ecological researches and metagenomic approaches that how the environmental factors affect the niche segregation of AOA and AOB. To our knowledge, AOA might dominant ammonia oxidation in the niches with relative low ammonia concentration or low pH or low oxygen concentration or extreme temperatures. The conclusions were temporary and dubious since more than 80% of the AOA in nature were undiscovered (Biller et al., 2012). In the future, on the one hand, we propose joint study of multi-factors in ecological studies, by regarding different factors as dependent variables. On the other hand, finding distinctive pathways from genomes or metagenomes may help explain the intricate results dominated by key environmental factors. Furthermore, if the recently discovered ammonia-oxidizing organisms comammox were verified to exist ubiquitous in nature such as soils, marine sediments or water columns, rivers and lakes, they should be considered into niche segregation of ammonia-oxidizing organisms, too (Daims et al., 2015; van Kessel et al., 2015).

Author Contributions

Shuai Liu drafted the manuscript; Jia-Jie Hu, Guang-Ming Tian, Ping Zheng, Li-Ping Lou and Fang Ma revised the manuscript; Jia-Xian Shen wrote the part of “Influence of pH values on ammonia-oxidizing microbes”; Shu Chen wrote the part of “Influence of Oxygen concentration on ammonia-oxidizing microbes”; Bao-Lan Hu did the final approval of the version.

Conflict of Interest Statement

No conflict of interest was reported by all authors.

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