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Review 综述

好氧氨氧化微生物类群及其介导的氧化亚氮产生机制综述

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摘　要：近年来，随着氧化亚氮(nitrous oxide, N_2O)在大气中浓度的逐年上升，微生物介导的 N_2O 产生机制日益引起学界的关注。近期研究表明，好氧氨氧化微生物(aerobic ammonia oxidizing microorganisms, AOMs)参与的氨氧化过程是全球 N_2O 的主要来源之一。本文从 AOMs 的种群分类、各类群的生态分布特点及影响其分布的环境因素、AOMs 介导 N_2O 产生的热点地区、AOMs 产生 N_2O 的途径及其影响因素进行归纳总结，并对未来的研究方向进行了展望。本综述有助于进一步理解 AOMs 类群及其产 N_2O 机制。

关键词：好氧氨氧化微生物；N_2O 产生；影响因素；热区

Aerobic ammonia-oxidizing microorganisms and the mechanisms of nitrous oxide production: a review

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Abstract: The rising level of atmospheric nitrous oxide (N_2O) has garnered the attention of researchers to microorganism-mediated N_2O synthesis in recent years. According to the recent studies, one of the main sources of N_2O in the world is the nitrification process carried out by

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aerobic aerobic ammonia oxidizing microorganisms (AOMs). We summarized the taxa of AOMs, the ecological distribution of AOMs, the environmental factors influencing the distribution, and the hotspots, pathways, and influencing factors of AOM-mediated N_2O production. Finally, we prospected the future research directions in this field. This review improves our understanding of AOMs and their mechanisms of N_2O production.

Keywords: aerobic ammonia oxidizing microorganisms; nitrous oxide production; influencing factors; hotspots

好氧氨氧化是在好氧条件下将铵盐转化为亚硝酸盐或硝酸盐的过程，是氮循环的基本过程之一，对大多数陆地、海洋以及淡水生态系统的元素循环至关重要[1]。好氧氨氧化过程主要由好氧氨氧化微生物(aerobic ammonia oxidizing microorganisms, AOMs)介导，它们是一类化能自养细菌，能够通过氨或铵根的氧化获取能量[2]。AOMs 可分为氨氧化细菌(ammonia oxidizing bacteria, AOB)、氨氧化古菌(ammonia oxidizing archaea, AOA)和全程氨氧化菌(complete ammonia oxidizers, Comammox)[3]。由于 AOMs 在各种生态系统中普遍存在，了解其多样性、环境分布特征及其影响因素具有重要意义。

N_2O 是除二氧化碳和甲烷外最受关注的温室气体之一。自 1750 年以来，大气中的 N_2O 浓度增长了近 23%[4]。最近的研究表明，AOMs 是全球 N_2O 产生的主要贡献者之一[5]。随着对 AOMs 研究的不断深入，仍有许多尚未发现的 AOMs 介导 N_2O 产生的途径。因此，研究不同生境下 AOMs 介导 N_2O 产生的机制具有重要的生态学意义。

1 好氧氨氧化微生物类群

1.1 好氧氨氧化微生物的种群分类

Winogradsky 是最早从环境中分离出氨氧化细菌的学者，他于 1892 年发布了亚硝化单胞菌(*Nitrosomonas*)和亚硝化球菌(*Nitrosococcus*) 2 个新属，分别属于 β 变形菌纲(*Betaproteobacteria*)和 γ 变形菌纲(*Gammaproteobacteria*)；1933 年，Winogradsky 又发布了亚硝化螺菌(*Nitrosospira*)这一新属，其也属于 β 变形菌纲。为研究 AOB 的生物多样性并对新分离的未知 AOB 菌株进行分类鉴定，Head 等发布了第一个基于 16S rRNA 基因序列的 AOB 类群系统发育树，此后还有学者利用 AOB 的其他功能基因进行建树[6-8]。随着基因组测序技术的革新，Chain 等发布了第一个 AOB 的全基因组序列，此后陆续有许多 AOB 新物种的全基因组序列经测序获得[9-14]。现有可纯培养的 AOB 菌株均属于假单胞菌门(*Pseudomonadota*)下的 β-变形菌纲(*Betaproteobacteria*)和 γ-变形菌纲(*Gammaproteobacteria*)，包含亚硝化单胞菌(*Nitrosomonas*)、亚硝化螺菌(*Nitrosospira*)、亚硝化球菌(*Nitrosococcus*) 3 个属。

与 AOB 相比，学者们对 AOA 种群的认识相对有限。2005 年，第一株 AOA 从海洋中分离出来，当时被归类于泉古菌门(*Crenarchaeota*)，并被证实具有氨氧化作用，此后 AOA 的相关研究也备受学者关注[15]。例如，Stieglmeier 等于 2014 年发布了一株分离自土壤的新 AOA 类群，命名为亚硝化球形菌(*Nitrososphaera*) EN76，其曾属于奇古菌门(*Thaumarchaeota*)，但在最新的国际原核生物系统学委员会(International Committee on Systematics of Prokaryotes, ICSP)公布的名单中，奇古菌门(*Thaumarchaeota*)被重新归类命名[16-17]。目前可获得纯培养的 AOA 均属

于嗜热多形菌门(*Thermoproteota*)下的亚硝化球形菌纲(*Nitrososphaeria*)，包含亚硝化球形菌(*Nitrososphaera*)、亚硝化古菌(*Nitrosarchaeum*)、亚硝化侏儒菌(*Nitrosopumilus*) 3 个属。

学界一般认为硝化过程的两步反应分别由氨氧化微生物和亚硝酸盐氧化微生物(nitrite-oxidizing microbes, NOM)催化。然而，2015 年，Daims 等[18]和 Van Kessel 等[19]通过宏基因组测序，从不同的氨氧化富集产物中建立了 3 个全基因组草图，分别命名为 *Candidatus* Nitrospira inopinata、*Candidatus* Nitrospira nitrosa、*Candidatus* Nitrospira nitrificans，这些微生物均包含编码氨单加氧酶(ammonia monooxygenase, AMO)、羟胺氧化还原酶(hydroxylamine oxidoreductase, HAO)以及亚硝酸盐氧化还原酶(nitrite oxidoreductase, NXR)的基因。由于硝化过程的两步反应可以在单一细胞中实现，因此将这些 AOMs 统称为 Comammox[20]。2021 年，Sakoula 等[21]从富集实验中发现了一种新的 Comammox，命名为 *Candidatus* Nitrospira kreftii。然而，截至目前，只有 *Nitrospira inopinata* 这一株 Comammox 被成功分离纯化[22]。

1.2 好氧氨氧化微生物的分布特征

本文选取了 29 条分离自各种不同生境的 AOMs 的 16S rRNA 基因进行分子系统学分析(图 1)，并标记了其生境。其中，AOB 的 3 个属在自然界中分别具有各自的生态分布特征。*Nitrosococcus* 更偏好于含盐水体环境，例如，许多海洋亚硝化球菌(*Nitrosococcus oceani*)的菌株被发现在各大洋中分布[23-24]，而 *Nitrosococcus wardiae* D1FHS 则从中国胶州湾分离得到[25]。大部分 *Nitrosospira* 分布在土壤或沉积物中，例如，第一株从土壤分离出的 *Nitrosospira* 被命名为 *Nitrosovibrio tenuis*，其具有与以往 AOB 不同的膜系统[26]；全基因组分析发现，白里亚硝化螺菌(*Nitrosospira briensis*) C-128 具备一套可以让其在酸性农业土壤中生长的基因[9]；同样分布在土壤中的多形亚硝化螺菌(*Nitrosospira multiformis*) ATCC 25196 具有抵抗土壤复杂环境毒性、适应环境中铵含量变化以及在营养限制期间对底物储存的适应机制[11]；Urakawa 等[27]从沙质湖泊沉积物中分离出一株可以在低至 4 ℃的环境中生长的 AOB，命名为沙湖亚硝化螺菌(*Nitrosospira lacus*) APG3。*Nitrosomonas* 则广泛分布于土壤、畜禽粪污和淡水等各种环境，如模式种欧洲亚硝化单胞菌(*Nitrosomonas europaea*)是 Winogradsky 从土壤中分离而来的[28]；Nakagawa 等[29]从牛粪堆肥中分离到一株名为粪便亚硝化单胞菌(*Nitrosomonas stercoris*) KYUHI-S(T)的 AOB，其可以在高达 1 mol/L 的铵浓度下生长；*Nitrosomonas supralitoralis* APG5 是从沙滩中分离出的可以在淡水中生长的 AOB[30]。

AOA 的生态分布规律与 AOB 不同。例如，维也纳亚硝化球形菌(*Nitrososphaera viennensis*) EN76 分离自花园土壤，*Nitrosarchaeum koreense* MY1 分离自农业土壤，*Nitrosopumilus zosterae* NM25 分离自海岸带沉积物；同样分离自土壤的 *Nitrososphaera viennensis* 具有三者中最高的最适温度(42 ℃)，*Nitrosarchaeum koreense* 具有高达 10 mmol/L 的铵耐受能力，*Nitrosopumilus zosterae* 则有着最宽泛的盐度耐受能力[16,31-32]。AOA 同样也分布在海洋中，例如，分离自热带海洋鱼缸的海亚硝化侏儒菌(*Nitrosopumilus maritimus*) SCM1 在氧气耗尽后可以产生少量氧气用于进一步氨氧化[33-34]；亚德里亚亚硝化侏儒菌(*Nitrosopumilus adriaticus*) NF5 和皮兰亚硝化侏儒菌(*Nitrosopumilus piranensis*) D3C 均分离自沿海表层水域，其中

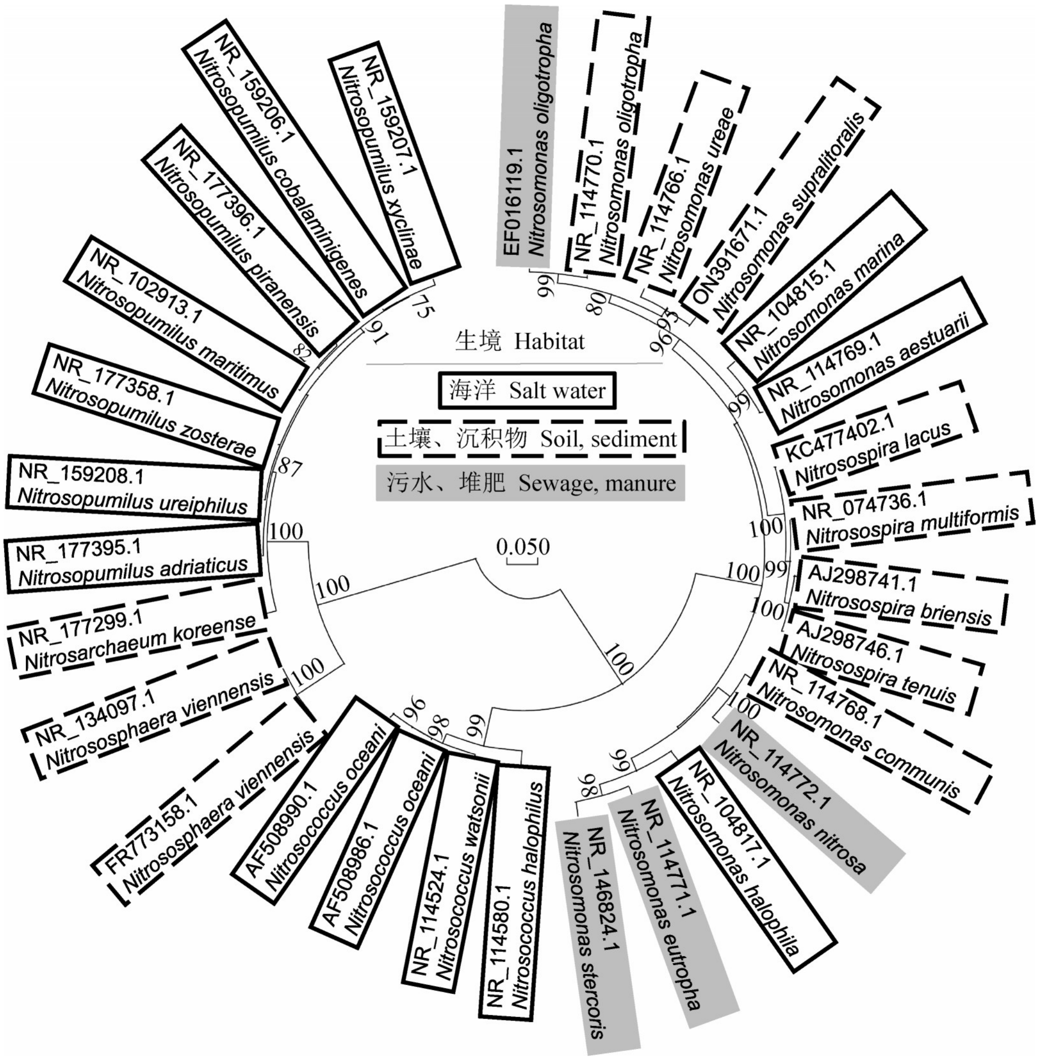

图1　好氧氨氧化菌基于16S rRNA基因序列的系统发育树

Figure 1　Phylogenetic evolutionary tree based on 16S rRNA gene sequences of aerobic ammonia oxidizing microorganisms

Nitrosopumilus piranensis 可以利用尿素中的氮作为氨的来源[35]。

上述AOA与AOB的生态分布特征主要基于其分离环境进行总结归纳。尽管目前Comammox的纯培养物还很有限，但宏基因组测序技术以及Comammox所携带的标记基因PCR使其在各种环境中的检测成为可能[36]。Comammox广泛分布于各种陆地生境，包括污水处理系统[37]、饮水系统[38]、河流[39]、河口[40]、海岸[41]、城市地下水[42]、热泉[43]、农业土壤[44]、湖泊与湿地沉积物[45-46]等，目前尚未有分布于海洋的Comammox被报道。

1.3　影响好氧氨氧化微生物分布的环境因素

影响AOMs分布的环境因素众多，主要包括溶解氧(dissolved oxygen, DO)、pH值、微量元素、铵浓度与水文异质性、氨亲和力等。

一般认为AOA比AOB更适应缺氧生态位。

例如，在一项对热带东北太平洋氧限制区(DO<2 μmol/L)的调查研究中，发现主要的氨氧化类群是 AOA 而非 AOB[47]。在另一项对沿海潮间带沉积物(氧化还原电位在 75−150 mV)中 AOMs 的调查中，发现氨氧化过程主要由 AOA 类群中的 *Nitrosopumilus* 主导[48]。

大部分 AOMs 是嗜中性微生物，但学者对一些酸性环境(包括农业土壤、森林土壤、火山土壤等)和碱性环境(包括盐碱地、碱性湖泊等)的调查发现，仍有可以生存于酸性或碱性环境的 AOMs[49]。例如，在酸性环境中分离的古菌 *Candidatus* Nitrosotalea，其最适 pH 范围为 4.0−5.5[50]；而从酸性环境中分离出的 2 株细菌均属于 γ 变形菌，它们的最适 pH 值为 6.0，但在 pH 值低至 2.5 时仍具有硝化功能[51-52]。*Nitrosomonas halophila* Ans5 是已知最嗜碱的 AOB，它可以在 pH 为 11.3 时维持生长，分离自蒙古国东北部草原的苏打湖[53]。在一项最新研究中还发现了可以在碱性环境中进行硝化作用的氨氧化古菌中的 *Nitrososphaerales* 类群[54]。

AOMs 在大洋中的分布还会受到游离的铁离子和铜离子的影响。游离的铁离子可能使 AOB 分布在较浅层的透光水域，那里铵供应较高，但也存在对铁离子的竞争；而 AOA 则对海洋中游离的铜离子有更强的亲和力和更高的耐受性[55]。

铵浓度与水文异质性同样影响着 AOMs 的分布。在一项对地下含水层的调查中，发现以 *Nitrosopumilus* 主导的 AOA 类群分布在地下水补给区(0.1 mg/L NH_4^+-N)，而以 *Nitrosospira* 主导的 AOB 则分布在地下水排泄区(3.8 mg/L NH_4^+-N)[56-58]。

在最近一项对 4 组 AOA 类群的氨亲和力进行定量的研究中发现，AOA 对氨的亲和力比之前学界所认为的更宽泛，甚至在某些情况下与非寡营养 AOB 的氨亲和力重叠，这可能会改变原有 AOMs 生态位分化的认知[59]。

2 好氧氨氧化微生物介导 N_2O 的产生

2.1 产生 N_2O 的热点区域

随着大气中 N_2O 浓度的逐年上升，不少 N_2O 产生的热点区域被发现，这些热点区域包括各种类型的土壤[60-63]、海洋[64-65]、各类淡水系统[66-69]以及各类沉积物[70-72]。表 1 总结了有 AOMs 参与的各类 N_2O 释放热点地区的通量。

2.2 产生 N_2O 的途径

目前发现 AOB 产生 N_2O 的途径主要有 2 类(图 2A)。(1) AOB 首先通过氨单加氧酶将氨转化为羟胺(NH_2OH)，当羟胺未完全氧化时，会在羟胺氧化还原酶(hydroxylamine oxidoreductase, HAO)作用下先转化为一氧化氮(NO)，随后一氧化氮还原酶(nitric oxide reductase, NOR)将 NO 转化为 N_2O；或者在缺氧条件下，羟胺在细胞色素 P460 的作用下直接转化为 N_2O[73-74]。(2) 在硝化反硝化过程中，整条途径包括氨氧化为羟胺；羟胺在好氧条件下被完全氧化为亚硝酸盐；在氧受限或低氧条件下，积累的亚硝酸盐作为底物还原为 NO；NO 在还原酶作用下转化为 N_2O[2,75]。

有学者认为 AOB 可以进行硝化反硝化，是因为其具有与经典反硝化菌同源的 2 种酶：一是含铜亚硝酸盐还原酶(nitrite reductase, NIR)，二是一氧化氮还原酶(NOR)。其中，NOR 被认为在 NO 还原为 N_2O 过程中是必需的，而 NIR 被认为可能参与了羟胺的氧化而非亚硝酸盐还原，因为有研究证明在缺乏 NIR 的 AOB 中仍能检测到 N_2O 的产生[76-78]。因此，仍有学者对催化亚硝酸根还原为 NO 这一步的酶进行研究。其中之一是亚硝基蓝蛋白酶(nitrosocyanin, NcyA)，

表1 典型N_2O释放热点区域及其通量

Table 1 Summary of typical hotspots and flux of N_2O

Hotspots	Samplinng environments	N_2O flux or concentration	Reference
Various types of soil	Alkaline, neutral purple soil	103.71 ng/(g·d)	[63]
	Oil palm soil	408.57 ng/(g·h)	[60]
	Forest soil	18.86 ng/(g·h)	[61]
	Agricultural soil	226.60 μg/(m^2·h)	[62]
Marine	The eastern tropical south Pacific	13.73 ng/(L·d)	[65]
	The eastern tropical north Pacific	13.20 ng/d	[64]
Various freshwater systems	River	580.80 μg/(m^2·d)	[68]
	Stream	264.00 μg/(m^2·h)	[69]
	Lake	69.41 g/(m^2·y)	[67]
	Sewage treatment system	7.00 μg/(g·min)	[66]
Various types of sediments	Plateau wetland sediment	50.29 ng/(g·d)	[71]
	Thawing Yedoma permafrost	1.72 mg/(m^2·d)	[72]
	Estuarine sediment	9.24 ng/(g·h)	[70]

该酶最初在 *Nitrosomonas europaea* 中被发现，后来在其他 AOB 中也发现了其编码基因，该基因在氧受限条件下能够表达，但目前尚未有直接证据证明它参与了 AOB 硝化反硝化过程中亚硝酸盐的还原[78-79]；另一个是多铜蓝蛋白酶(multicopper blue protein, MCBP)，其在 *Nitrosomonas europaea* 中被鉴定出，后来发现它是由 *nirK* 基因簇的 *ncgA* 基因编码，可以使 *Nitrosomonas europaea* 耐受亚硝酸根，并将其还原[80-81]。

与 AOB 类似，AOA 的第一步反应也是铵根或氨在氨单加氧酶的作用下发生转化，但是中间产物可能发生变化，证据有：(1) 在 AOA 的基因组中缺乏可以直接催化羟胺发生反应的酶的基因；(2) 在海洋 AOA 极其活跃的区域，有大量的 N_2O 产生；(3) 有研究检测到了 AOA 的中间产物包括 NO[82-84]。基于此，学者们对 AOA 产生 N_2O 的途径作出了 2 个假设(图 2B)：(1) AOA 利用 AMO 将氨氧化为羟胺，羟胺被铜羟胺氧化还原酶(copper hydroxylamine oxidoreductase, Cu-HAO)一步氧化成亚硝酸根，亚硝酸根再通过亚硝酸盐铜还原酶(copper nitrite reductase, Cu-NirK)还原为 NO，NO 通过非生物作用产生 N_2O；(2) AOA 利用 AMO 将氨氧化为硝基(nitroxyl, HNO)，硝基被硝基氧化还原酶(nitroxyl oxidoreductase, NXOR)一步氧化成亚硝酸根，亚硝酸根再通过亚硝酸盐铜还原酶(copper nitrite reductase, Cu-NirK)还原为 NO，NO 继续通过非生物作用产生 N_2O[82,85]。综上所述，对于 AOA 来说其 N_2O 产生途径是由生物和非生物作用相结合的。

在对农业溪流以及碱性耕地 N_2O 产生的主要贡献者的野外调查中，Tan[86]和 Wang 等[87]发现 Comammox 对 N_2O 产生的贡献显著低于 AOA 和 AOB 的总和。在实验室内对比 *Nitrospira inopinata* 与其他传统氨氧化微生物 N_2O 产量的研究中，Han 等[88]也发现 Comammox 的 N_2O 产量会显著低于 AOB，但却与某些 AOA 相当。由于 Comammox 的基因组中缺乏编码 NOR 的基因，其 N_2O 产生途径主要是羟胺的非生物反应[89]。

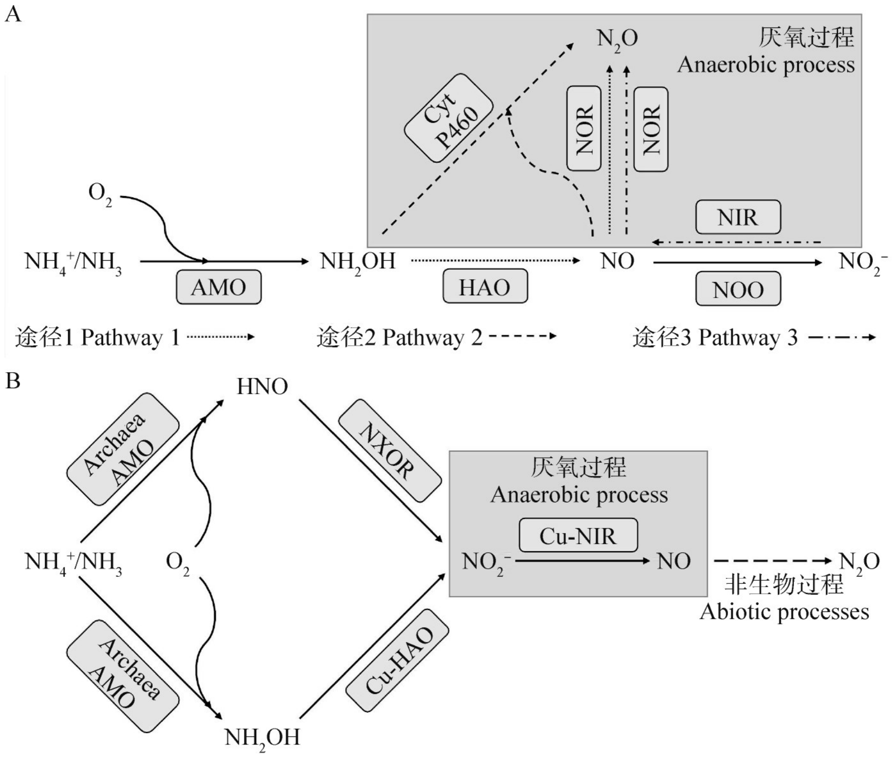

图2　好氧氨氧化菌N_2O产生途径示意图

Figure 2　Schematic diagram of N_2O production pathway of aerobic ammonia oxidizing microorganisms. A: Three pathways of AOB-mediated N_2O production; B: Two hypotheses for AOA-mediated N_2O production. AMO: Ammonia monooxygenase; HAO: Hydroxylamine oxidoreductase; NOO: Nitric oxide oxidase; NIR: Nitrite reductase; NOR: Nitric oxide reductase; Cyt P460: Cytochrome P460; NXOR: Nitroxyl oxidoreductase; Cu-HAO: Copper hydroxylamine oxidoreductase; Cu-NIR: Copper nitrite reductase.

2.3　影响产生 N_2O 的因素

随着从野外调查到室内研究的不断深入，众多因素被发现可以影响 AOMs 的 N_2O 产生，主要包括溶解氧、酸碱度、温度和底物浓度。

溶解氧、酸碱度和底物浓度均可通过控制代谢途径或影响某一途径的酶活性来改变 AOMs 产生 N_2O 的量。在多项溶解氧对 N_2O 产生影响的研究中发现，低氧或氧限制条件(DO< 1 mg/L)会使 AOMs 通过硝化反硝化途径产生 N_2O 的量增加，但随着 DO 的增加(DO> 2 mg/L)，AOMs 通过羟胺氧化途径产生 N_2O 的比例也会增加[90-92]。在对海洋缺氧区的调查研究中也发现，低氧条件下 AOMs 的硝化反硝化成为 N_2O 的主要来源[93-94]。在几项研究 pH 对 N_2O 产生影响的研究中发现，弱酸性环境主要促进 AOMs 硝化反硝化途径上酶的表达，而弱碱性环境则主要促进 AOMs 羟胺氧化途径上酶的表达[95-99]。当人为或自然活动导致环境中硝酸盐和亚硝酸盐积累时，过量的 NO_2^-和 NO_3^-会提高 NIRK 酶活性并抑制 N_2OR 酶活性，从而使 N_2O 排放量大于消耗量[100-101]。在一定温度和 pH 条件下，部分 NO_2^-会转化为 FNA，较高浓度的 FNA 会促进 AOMs 氧化亚氮的产生并抑制其消耗[102-103]。

同时，溶解氧、酸碱度和温度还可以通过改变体系的群落结构，进而影响 AOMs 对 N_2O

的产生。在高铵废水和硝化活性污泥的研究中分别发现，高氧条件[DO=(3.75±0.49) mg/L]会使 *Nitrosomonas* 这一类群占比增加 33.43%，导致亚硝酸盐累积，为 N_2O 产生创造了前体物质[104]；而长期低氧处理会使硝化活性污泥群落结构中的 AOB 丰度降低 28%，从而减少 N_2O 产生[105]。水稻田土壤酸化(pH<5.0)会直接导致 AOMs 的丰度降低，从而减少 N_2O 减排[106]；而在人工干预下，水稻田土壤 pH 升高(pH 约为 7.0)会富集含有 *nosZ* 基因的微生物类群，这类微生物可以通过还原 N_2O 来降低 N_2O 净通量[107]。在一项人工湿地微生物修复的研究中发现，AOA 类群比 AOB 更容易占据低温生态位，从而导致 N_2O 释放降低[108]。

3 研究不足与展望

近年来，关于 AOMs 类群及其 N_2O 产生机制的研究，学界已取得诸多重要进展。然而，随着科学技术的不断革新，更多机遇和挑战主要体现在以下几个方面。

目前，基于高通量测序技术从更多生境中挖掘出了 AOMs，但由于 AOMs 培养的难度，被纯培养的物种还很有限，亟待加强对 AOMs 菌株的分离、培养及其功能验证。将流式细胞仪[109]等先进细胞分选技术应用到 AOMs 的分离纯化中，可有助于获得更多纯培养物。与此同时，一些不依赖纯培养的单细胞技术的应用，如纳米二次离子质谱(nano secondary ion mass spectroscopy, NanoSIMS)[110]、单细胞拉曼光谱[111]等，可以在一定程度上避免无法获得纯培养的困境。

随着科学技术的发展，将(宏)基因组、(宏)转录组、(宏)蛋白组、代谢组等多组学技术与稳定同位素核酸探针技术(DNA-based stable isotope probing, DNA-SIP)[112]、稳定同位素示踪技术[113]相结合，用于挖掘和表征更多未知 AOMs 种群以及更多未知 N_2O 产生途径，将是今后研究的一个重要方向。

厘清不同生境下各种因素对 AOMs 类群产生 N_2O 的影响，并准确评估其贡献度，可以为农业生产、生活污水处理、畜禽养殖废水处理等与人类生产生活息息相关的行业，提供温室气体减排以及微生物调控技术更加科学和有效的指导。

作者贡献声明

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作者利益冲突公开声明

作者声明绝无任何可能会影响本文所报告工作的已知经济利益或个人关系。

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