



Redox controls on anaerobic ammonium oxidation coupled to reduction of natural organic matter in paddy ecosystems

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Abstract

Microbially mediated anaerobic ammonium oxidation can be coupled to the reduction of various terminal electron acceptors. Redox-active natural organic matter (NOM) can serve as an extracellular electron acceptor or donor in microbial redox reactions. The coupling of the anaerobic ammonium oxidation process to the reduction of NOM (herein termed NOM-ammox) is thermodynamically feasible and evidence has been provided demonstrating its environmental occurrence. Ecosystems with fluctuating redox conditions such as paddy fields are favorable for maintaining the redox reactivity of NOM, and thus may promote NOM-ammox. Here, we synthesize recent literature on NOM-ammox and discuss how redox conditions could control this process at different spatial scales in paddy ecosystems. We conclude that the inherent redox properties of NOM and environmental redox fluctuations are key for fueling and regulating NOM-ammox in paddy ecosystems.

Keywords Paddy soil · Nitrogen cycling · Geobattery · Redox potential · Electron transfer

Introduction

Biogeochemical nitrogen (N) cycling is a key component of Earth's elemental cycling and has been largely modified since the Anthropocene because of human perturbation such as intensified agriculture (Steffen et al. 2015; Waters et al. 2016). Rice paddies cover roughly 9% of the total cropland area worldwide, representing a prototypical artificial wetland characterized by frequent redox fluctuations. They feed over half of the global population and are increasingly reliant on

N fertilizer usage to meet the growing food demands driven by population growth (Zhu et al. 2016). The microbial N cycling in paddy soil is highly active and tightly linked to food productivity and security. Overuse of N fertilizer can decrease N use efficiency and increase N losses (Xing and Zhu 2000; Zhu et al. 2011). Microbial denitrification has long been thought to be the dominant pathway for N loss (with N₂ as the end product) in paddy ecosystems (Xing and Zhu 2000; Shan et al. 2016). It cannot explain all sources of the total N loss from paddy soil until the discovery of anaerobic oxidation of ammonium with nitrite as the electron acceptor (anammox) (Zhu et al. 2011; Yang et al. 2015). In natural settings, well-studied electron acceptors for anaerobic ammonium oxidation to produce N₂ include nitrite (Nie et al. 2019), sulfate (sulfammox) (Rios-Del Toro and Cervantes 2019), Fe(III) (Fe-ammox) (Tan et al. 2022), and Mn(IV) (Mn-ammox) (Desireddy and Pothanamkandathil Chacko 2021). Among them, anammox and Fe-ammox were shown to be important for N loss and indirect sinks of N₂O in paddy ecosystems (Reay et al. 2012; Ding et al. 2014; Yi et al. 2019). It was estimated that anammox contributed to 5–10% loss of fertilized N in agricultural soil including rice paddy globally (Nie et al. 2019). Fe-ammox in paddy soils can be facilitated during rice planting (Ding et al. 2014), and the resultant N loss accounted for 6.91% of the applied N fertilization in China (Li et al. 2019). These studies showed

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the occurrence of anaerobic ammonium oxidation in paddy ecosystems, but they also showed that the rates and extent of anaerobic ammonium oxidation coupled to different terminal electron acceptors differed.

Natural organic matter (NOM) is a predominant redox-active component in soil and sediment and is often associated with Fe(III) minerals (Tratnyek et al. 2011). The fraction of NOM with redox-active function, which also constitutes the majority of NOM, has historically been referred to as “humus” or “humic substances” (Martinez et al. 2013; Lehmann and Kleber 2015). Traditionally, humus is classified into humic acid, fulvic acid, and humin depending on their different solubilities under various pH ranges. NOM can serve as the terminal electron acceptor for microbial anaerobic ammonium oxidation (NOM-ammox) (Rios-Del Toro et al. 2018; Shaw et al. 2020). Additionally, it could act as an intermediary electron shuttle for Fe-ammox, which relies on NOM-ammox and abiotic Fe(III) reduction (Zhou et al. 2016). These mechanisms are analogous to those with other ecologically relevant molecules, such as methane and its anaerobic oxidation driven by NOM (Valenzuela and Cervantes 2021). As NOM comprises distinct types of redox-active functional groups with different contents, it exhibits a wide range of redox potentials. The redox potential of NOM, including the particulate fraction such as humin, mainly spans from -300 to $+300$ mV (vs. standard hydrogen electrode (SHE)) (Aeschbacher et al. 2011; Pavitt and Tratnyek 2019; Pham et al. 2021). Hence, NOM can be involved in various redox reactions by serving as an electron acceptor or donor (Martinez et al. 2013; Li et al. 2020). This enables NOM functioning as a sustainable (bio-)geobattery in many redox processes yet without being consumed (Peiffer et al. 2021; Li et al. 2022). The parameter describing the redox activity of a given NOM is the redox property, including electron-accepting (EAC) and electron-donating capacities (EDC) as well as the redox potential distribution (Tratnyek et al. 2011). The sum of EAC and EDC represents the redox capacity, and their ratios represent the redox state (Aeschbacher et al. 2010; Klüpfel et al. 2014). Over the past three decades, many studies have demonstrated that NOM can act as an extracellular electron acceptor in microbial respirations (Lovley et al. 1996; Keller et al. 2009; Bai et al. 2019; Valenzuela and Cervantes 2021; Peng et al. 2022), and recent studies have demonstrated some microbial enrichment cultures capable of NOM-reducing ammonium oxidation (Zhou et al. 2016; Rios-Del Toro et al. 2018; Shaw et al. 2020). For example, in a microbial consortium enriched from paddy soils, the Fe-ammox process can be significantly stimulated by the addition of AQDS (anthraquinone-2,6-disulfonic acid), a model compound for quinone moieties which are the major electron-accepting groups in NOM. AQDS can act as an electron shuttle between microbial cells and the Fe(III) oxyhydroxide mineral ferrihydrite (Zhou et al. 2016),

implying the important role of NOM in fueling anaerobic ammonium oxidation to N_2 . While anammox and Fe-ammox have been studied in paddy ecosystems (Zhu et al. 2011; Ding et al. 2014), the lack of definitive evidence on NOM-ammox necessitates further research, considering the ecological significance of NOM in these systems.

The redox conditions in paddy ecosystems undergo frequent fluctuations across various spatial scales (Kögel-Knabner et al. 2010). In anoxic paddy habitats that contain NOM and abundant ammonium (typically tens to hundreds of $mg\ kg^{-1}$ due to N fertilizer inputs) (Zhu et al. 2011; Yang et al. 2015; Zhu et al. 2015), which could be favorable for the occurrence of NOM-ammox, even subtle changes in redox potential at nano to micrometer scales could directly affect microbial electron transfer reactions. First, NOM molecules from different sources with varying amounts of different chemical components have distinct redox properties, including varying EAC values, so their ability to drive NOM-ammox may differ (Li et al. 2020). Second, for a given NOM molecule, as a (bio-)geobattery, it can be continuously reduced and oxidized in redox reactions occurring under anoxic conditions (Peiffer et al. 2021). Thus, the redox state of NOM is dynamic and its ability to drive NOM-reducing ammonium oxidation may vary (Li et al. 2022). In contrast, hydrological perturbations in paddy soil such as periodic dry-wet cycles can trigger more pronounced fluctuations in redox conditions at scales of centimeters to meters. This could activate and maintain the reactivity of the NOM geobattery in microbial redox processes (Peiffer et al. 2021) such as microbial anaerobic ammonium oxidation. Because environmental geobattery materials are often metastable and ripening increases its stability yet decrease its reactivity, striking redox oscillations can interrupt the ripening process and refresh the reactivity of geobattery (Peiffer et al. 2021). Together, changes in redox conditions, including redox properties of NOM at small scales (molecular level) and the overall average redox potential of paddy soil (habitat level) at large scales, may be key for the NOM-dependent anaerobic ammonium oxidation process in paddy ecosystems. This could lead to differences in kinetics of the NOM-ammox process. However, how this process responds to different redox conditions in paddy fields and the underlying mechanisms involved remain unclear.

In this perspective, we discuss the potential links between NOM-reducing ammonium oxidation and redox conditions in paddy fields. We emphasize the redox properties of NOM molecules and the overall redox potential of paddy habitats. For the molecular-level redox controls, due to the limited mechanistic studies, we mainly present research approaches to stimulate in-depth studies. For the habitat-level redox controls, we focus on synthesizing relevant research to exemplify our views. Last, we propose future research directions on studying NOM-ammox in paddy ecosystems.

Evidence of NOM-dependent anaerobic ammonium oxidation

NOM can serve as an extracellular electron acceptor in the anaerobic ammonium oxidation process and affect the rates and extent of this process, as illustrated below. Given the standard reduction potential of the N_2/NH_4^+ couple at pH 7, $E_h^0(\text{pH } 7) = -277 \text{ mV}$ (vs. SHE) (Li et al. 2020), is lower than most of the wide range of redox potentials of NOM (-300 to $+300 \text{ mV}$, vs. SHE), the NOM-ammo process is thermodynamically highly feasible. For example, the majority of reducing equivalents in standard humic acids ($E_h^0(\text{pH } 7)$, -300 to $+150 \text{ mV}$, vs. SHE) (Aeschbacher et al. 2011) are thermodynamically capable of routing electrons from anaerobic ammonium oxidation (Li et al. 2020). Paddy-derived NOM is also energetically favorable for serving as the electron acceptor in anaerobic ammonium oxidation. For example, the redox potentials reported for paddy humic acid (-0.12 V vs. SHE) (Tong et al. 2018) and several paddy humins (ranging from -300 to $+272 \text{ mV}$ vs. SHE) (Pham et al. 2021) can be generally higher than that of the N_2/NH_4^+ couple.

Anaerobic ammonium oxidation that relied on extracellular electron transfer has been recently verified in microbial electrolysis cells with carbon-based insoluble substances including graphene oxide or electrodes as electron acceptors (Shaw et al. 2020). This observation eloquently suggested that anaerobic oxidation of ammonium coupled to the reduction of natural extracellular electron acceptors such as NOM is feasible. There are some exemplifications. The addition of a quinone model compound (AQDS) stimulated the Fe-ammo process and increased N_2 emission of a microbial consortium enriched from paddy soils, probably by accelerating the microbial electron transfer to the poorly soluble Fe(III) minerals with AQDS as an electron shuttle (Zhou et al. 2016). In this scenario, anaerobic ammonium oxidation was coupled to microbial AQDS reduction; the reduced AQDS was then abiotically oxidized by Fe(III) minerals. High N removal efficiency via Fe-ammo was also detected after the addition of AQDS in a wastewater treatment reactor, resulting in the production of reduced AQDS (i.e., AH_2QDS) (Yang et al. 2019). Similarly, another quinone model compound, AQS (9,10-anthraquinone-2-sulfonate), has been shown to facilitate the Fe-ammo rate in mangrove sediments, possibly by serving as an electron shuttle (Guan et al., 2019). Although these studies did not explicitly examine the quinone-coupled anaerobic ammonium oxidation process as lacking either the Fe(III)-free control or the quinone model compound only treatment, the results nevertheless implied that the NOM analog could act as electron acceptor in this

process. Notably, the majority of reducing equivalents in NOM possess greater redox potentials for fueling the anaerobic ammonium oxidation process than AQDS ($E_h^0(\text{pH } 7) = -185 \text{ mV}$, vs. SHE) and AQS ($E_h^0(\text{pH } 7) = -225 \text{ mV}$, vs. SHE) (Clark 1960). Similar findings have been observed in marine sediments with clear evidence of NOM-ammo to N_2 . Rios-Del Toro et al. (2018) detected the metabolic activity of NOM-reducing ammonium oxidation in marine sediment, as evidenced by ^{15}N isotopic, stoichiometric, and spectroscopic analyses. Their findings suggested that the reduction of quinone-like functional groups of NOM, including both the externally added purified NOM and the intrinsic NOM of the sediment, could stimulate microbial anaerobic ammonium oxidation and N_2 production.

The redox capacity and redox state of NOM correlate with the structure and contents of redox-active functional groups, especially the changes in quinone and phenolic hydroxyl that can be detected by spectroscopic analyses (Chen and Yu 2021). Quinone groups are thought to be the main reducible functional groups in NOM, and the soil or sediment with high quinone content often exhibits high electron accepting capacity (Lovley et al. 1996; Scott et al. 1998), thus may be favorable for NOM-ammo. Indeed, NOM is ubiquitous and more abundant than NO_2^- in paddy soils, and NOM is a more preferential electron acceptor than Fe(III) in anaerobic microbial respiration (Jiang and Kappler 2008; Fan et al. 2020). Therefore, NOM-ammo could be a competitive pathway of N loss in paddy ecosystems compared to anammo and Fe-ammo, and being regulated by the different quinone compounds in NOM with different redox properties. Non-quinone redox functional groups are also thought to be significant reducing moieties in NOM (Hernández-Montoya et al. 2012; Yang et al. 2022). However, it remains unclear whether they can serve as electron sinks for anaerobic ammonium oxidation.

The genera *Candidatus Brocadia* and *Kuenenia* were found to be dominant groups catalyzing anaerobic ammonium oxidation in paddy soils (Nie et al. 2019). Intriguingly, the bacteria belonging to these genera have been shown to be electrochemically active and capable of reducing carbon-based extracellular electron acceptors coupled to anaerobic ammonium oxidation (Shaw et al. 2020). These genera may play a significant role in NOM-ammo processes in paddy ecosystems.

Linking the redox property of NOM to anaerobic ammonium oxidation

Owing to the complex structure and high heterogeneity of NOM, NOM molecules differed in source and their different components (e.g., dissolved or particulate NOM) could have

distinct redox properties. In addition, the redox properties of NOM can be modified by the adsorption and desorption onto mineral surfaces (Subdiaga et al. 2019). As a result, they could behave differently in driving biogeochemical redox processes (Klüpfel et al. 2014; Lau et al. 2015), potentially including microbial anaerobic ammonium oxidation in paddy ecosystems. Moreover, the redox state of a given NOM molecule is in dynamic change as it is cycled through redox reactions, which may affect its ability to drive anaerobic ammonium oxidation in paddy soils. Principally, only a small fraction of reducing equivalents in native NOM as well as highly reduced NOM molecules but prior to microbially and/or chemically re-oxidation, whose redox potentials are lower than that of the N_2/NH_4^+ couple, are unable to fuel anaerobic ammonium oxidation. As relevant mechanistic studies are rare, in this section we mainly discuss methodology including NOM separation and fractionation and its redox property measurement to pave the way for future research to address this gap.

To explicitly study the underlying mechanisms of NOM-ammox, non-destructive separation of the different components from NOM is required. The dissolved fractions of NOM (e.g., humic acid and fulvic acid), as well as the particulate fraction of NOM (e.g., humin), which is also microbially reducible, have been extracted from paddy soils and exhibit different redox properties (Qiao et al. 2019; Pham et al. 2021). Note that the traditional alkaline extraction method has commonly been employed to isolate NOM from natural environments (Lehmann and Kleber 2015). Nevertheless, recent studies found that using this extraction method could overestimate its electron transfer capacity by changing its structure and function (Kleber and Lehmann 2019; Bai et al. 2020b). Thus, more moderate extractants are required. Besides, NOM extracted under oxic conditions could overestimate its electron exchange capacity. Therefore, NOM extracted with water (pH 7.0) can be used to better reflect environmental NOM redox properties (Bai et al. 2020b). Since the composition and structure of NOM are complex, for brevity, many researchers have adopted model compound (e.g., AQDS) as an analogue/substitute of quinone moieties in NOM to simulate the redox activity of NOM in relevant studies (Lovley et al. 1996; Wolf et al. 2009; Bai et al. 2019). Recently, Bai et al. (2020a) proposed that agar-solidified AQDS, simulating poorly mobile particulate NOM, can facilitate the microbial Fe(III) reduction processes by electron hopping between redox-active particulate NOM structures. Additionally, Fe-NOM complexes could modify the rate of NOM-ammox, as Fe(III) can directly participate in Fe-ammox and affect the reduction of NOM (Kappler et al. 2021). When explicitly studying the electron transfer mechanisms of NOM-ammox in paddy fields, the removal of Fe from the mineral-NOM complex, which is ubiquitous in paddy soils (Kögel-Knabner et al. 2010), is also required. Decades ago,

dithionite-citrate-bicarbonate (DCB) extraction of Fe was proposed to study root Fe minerals or soil NOM (Taylor and Crowder 1983; Schulten and Leinweber 1995). Roden et al. (2010) proposed the DCB stripping method and applied it to study the mechanisms of extracellular electron transfer of particulate NOM. These studies provided applicable methods to study the role of different NOM components and relatively pure NOM in microbial redox processes and underpin future attempts to dig into the electron transfer mechanisms of NOM-ammox in paddy soils.

Advances in studying NOM-ammox largely depend on the development of methods to measure the redox properties of NOM. Mediated electrochemical analysis (MEA) is an excellent and now established tool for accurate and fast determination of the redox properties of NOM when compared to traditional chemical and non-mediated electrochemical approaches (Aeschbacher et al. 2010; Walpen et al. 2016). This electrochemical technique holds promise for tracking the flux of electrons transferring to (and from) NOM and unraveling the electron transfer mechanisms of NOM-ammox (Li et al. 2020). Traditional chemical methods require the addition of oxidants and reductants to determine the EDC and EAC, respectively (Aeschbacher et al. 2010; Li et al. 2020). However, this is time-consuming, and potentially involves many side reactions, and the results could differ significantly depending on the use of different chemical reagents. The non-mediated electrochemical method overcomes many disadvantages of the chemical method; however, electron transfer between NOM samples and electrodes is sluggish and difficult to attain equilibrium, which limits the application of the non-mediated electrochemical method (Sander et al. 2015; Li et al. 2020). In contrast, by introducing small soluble molecules with high redox activity as electron mediators, the emerging MEA greatly improves the rate of electron transfer between NOM samples and electrodes and enables a rapid establishment of redox equilibrium (Aeschbacher et al. 2010). Some studies have applied MEA to study microbial redox cycling processes of NOM (e.g., dissolved and particulate NOM) in pure cultures or environmental samples (Klüpfel et al. 2014; Lau et al. 2015). A full description of MEA is beyond the scope of this perspective. However, the strategies using MEA to uncover microbial NOM-N redox couplings have been recently reviewed in detail (Li et al. 2020). Nonetheless, so far, the MEA method has not been applied to investigate the NOM-ammox process and should be added into toolbox in future studies. The newly established spectrophotometric method for EAC determination, which has been validated for peat particulate NOM samples (Joshi et al. 2021), may be an additional tool to MEA for exploring anaerobic ammonium oxidation driven by particulate NOM in paddy soils.

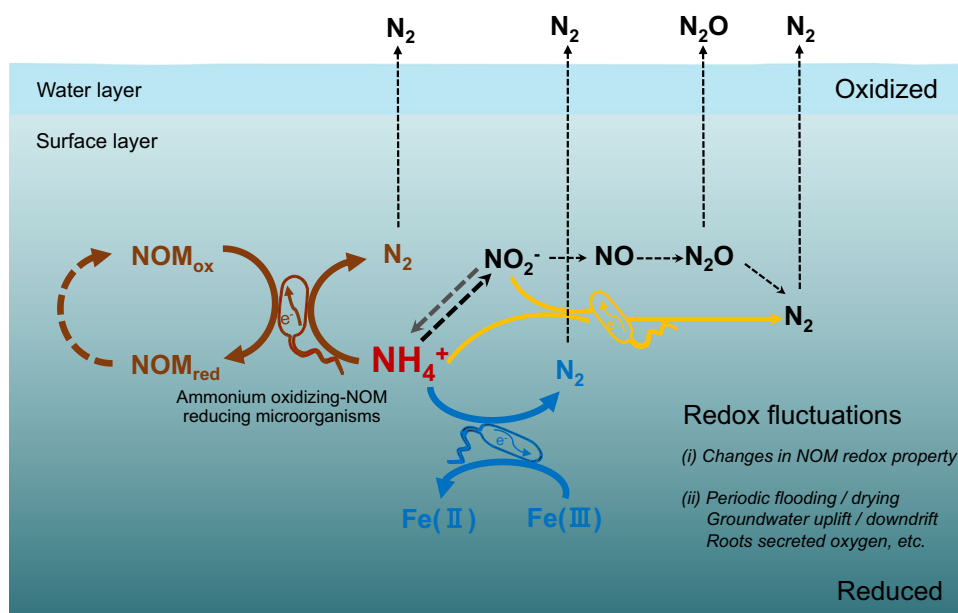
Controls of redox conditions of paddy habitats on NOM-dependent anaerobic ammonium oxidation

As outlined above, the redox conditions that vary at nano to micrometer scales, i.e., the redox properties of NOM molecules including their different components and redox-active functional groups, could impact NOM-ammo in paddy soils. Additionally, the overall redox potentials of paddy soil habitats vary at scales of centimeters to meters, and even hundreds of meters (Peiffer et al. 2021), potentially also representing a key factor affecting NOM-ammo. Changes in redox conditions can determine the energy available for microorganisms in catalyzing biochemical reactions and affect the rate and extents of microbial redox reactions as well as the cell growth (Levar et al. 2017; Zhao et al. 2020; Zhang and Furman 2021). We propose that under the significant and frequent alternation of redox conditions in paddy habitats, such as periodic flooding and drying, groundwater uplift and downdrift, and roots secreted oxygen, etc., the redox functioning of the NOM (bio-)geobattery could be activated and maintained (Peiffer et al. 2021) for better fueling anaerobic ammonium oxidation (Li et al. 2022). For instance, the oxidation-reduction cycles of NOM resulting from periodic oxygen inputs allow them to be a regenerable electron acceptor in microbial NOM reduction processes (Klüpfel et al. 2014; de Melo et al. 2016). Overall, redox fluctuations at large spatial scales (habitat level) are expected to play an important role in regulating NOM-ammo.

Growing evidence showed that terrestrial ecosystems (or niches) with redox oscillations, such as air-water or water-soil interfaces with rise and fall, rhizosphere vs. bulk soil, and intertidal wetlands, are hotspots for anaerobic

ammonium oxidation driven by nitrite and/or Fe(III) (Zhu et al. 2013; Li et al. 2015; Nie et al. 2015; Lansdown et al. 2016; Wang et al. 2020). In paddy soils, alternating redox conditions have a clear impact on the nitrite-driven anammox process, which is the most extensively studied form of microbial anaerobic ammonium oxidation. As an example, compared to sustained flooding, intermittent wetting and drying can enhance anammox activity and the abundance of anammox microbes in a paddy-wheat soil (Abbas et al. 2019). Anammox can also thrive in the oxic/anoxic interface of rice rhizosphere in fertilized paddy soil, causing 31–41% of N loss, 15 times more than non-rhizosphere. Anammox bacteria were twice as abundant in the rhizosphere compared to non-rhizosphere (Nie et al. 2015). These studies showed that the anammox process readily takes place in zones with redox gradients and fluctuations. However, in the NOM-ammo process under redox fluctuations, it remains unclear if and how microbial community composition and activity change. This is because the differences in the microbial community in these ecosystems were probably shaped by environmental redox gradients (Ramirez-Flandes et al. 2019; Cai et al. 2022; Dick and Meng 2023). In addition, the involvement of other microorganisms in NOM-ammo, alongside anaerobic ammonium oxidizers and/or electrogens (microbes that respire extracellular electron acceptors), and their specific roles remain unclear. Considering various redox fluctuations in natural settings such as alternative wetting and drying, oxic/anoxic interfaces, and rhizosphere/non-rhizosphere transition zones, which could be favorable for anaerobic ammonium oxidation depending on extracellular electron transfer, we propose the conceptual model of NOM-ammo in paddy soil (Fig. 1). The changes in redox property of NOM molecule are also highlighted, as discussed earlier.

Fig. 1 Conceptual model of natural organic matter (NOM) reduction coupled to anaerobic ammonium oxidation (brown) in paddy ecosystems, where nitrite- (yellow) and iron-driven (blue) anaerobic ammonium oxidation can also take place. NOM with reduced state can be re-oxidized abiotically by oxidants (such as oxygen or ferric iron) or biotically, for example, through coupling with microbial nitrate reduction (Li et al. 2022). Redox fluctuations can occur (i) at nano to micrometer scales and (ii) at scales ranging from centimeters to hundreds of meters. Ox, oxidized; Red, reduced



Conclusions and outlook

The redox alternation of paddy fields can strongly affect the biogeochemistry of nitrogen, specifically the turnover of ammonium, and may thus impact the fertility of paddy soils. Anaerobic ammonium oxidation could be coupled to the reduction of NOM which can serve as an extracellular electron shuttle or terminal electron acceptor. NOM is a (bio-)geobattery covering a wide range of redox potentials; the rates and extent of NOM-ammo are innately regulated by redox conditions. This is particularly the case in paddy ecosystems where redox fluctuations are significant and frequent. As highlighted in this perspective, how redox conditions control the process of NOM-ammo in rice paddies could be examined at different spatial scales. Suitable fractionation and extraction methods in combination with mediated electrochemical analysis can help quantify the true redox capacity of NOM and its changes in electron transfer reactions. However, the study of NOM-ammo is still in its infancy. Here, we propose several future research directions as below:

- (i) Future studies should explore more direct evidence of anaerobic ammonium oxidation driven by oxidized NOM as an electron acceptor in paddy ecosystems, particularly its contribution to N loss. Methods based on the ^{15}N isotope tracing technique to follow the fate of N, combined with measurements of the redox properties of redox state-preserved NOM samples, are required to decipher the reaction dynamics of NOM-ammo in paddy soils.
- (ii) We are far from understanding of the dominant microorganisms that are responsible for the NOM-ammo process. More research is warranted to unravel the genetic diversity and ecophysiology traits of anaerobic ammonium oxidizing microorganisms that are electroactive or require syntrophy with other microbial species for transferring electrons to NOM.
- (iii) Emphasizing the NOM-ammo process along different redox gradients or interfaces should be prioritized for next steps. By manipulating different redox conditions in field trials or laboratory microcosms, more studies can focus on alternative wetting and drying, partially hypoxic habitats caused by NOM decomposition, as well as rice rhizosphere/non-rhizosphere.
- (iv) The impact of diverse NOM molecules with different redox properties on the rates and extent of anaerobic ammonium oxidation is not yet comprehended. There is a complexity of NOM electron acceptors in paddy soil. The competition between different NOM for functioning as electron acceptors and the degree to which they are involved in anaerobic ammonium oxidation need more research.

- (v) Clarifying the influence of NOM adsorption and desorption to mineral surfaces on NOM-ammo is also crucial. The sorption of NOM to minerals is expected to alter the redox properties of NOM and thus may impact the dynamics of anaerobic ammonium oxidation in paddy soils. As such, more studies are warranted to elucidate the underlying regulatory mechanisms of this physicochemical process.
- (vi) By extension, Anthropocene events such as global warming and anthropogenic fertilization management may impact redox-driven NOM-ammo in paddy ecosystems. Rising temperatures could alter the redox property of soil NOM (Tan et al. 2017; LaCroix et al. 2020). The implementation of organic fertilizer materials (Yan et al. 2007; Li et al. 2010; Tian et al. 2015) could affect the formation and potentially alter the redox property of paddy NOM. Therefore, evaluating their effects on NOM-ammo in paddy soils is necessary within the context of global change.

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Declarations

Conflict of interest The authors declare no competing interests.

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