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Complete ammonia oxidation: an important control on nitrification in engineered ecosystems?

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Nitrification has long been considered to be mediated by two distinct microbial guilds, the ammonia-oxidizing bacteria and archaea, and the nitrite-oxidizing bacteria. The process has been widely applied as an environmental biotechnology for ammonium removal during water and wastewater treatment. Recently, bacteria capable of complete nitrification of ammonia to nitrate (a process termed complete ammonia oxidation, or comammox) have been discovered. These novel nitrifiers have been identified in a range of engineered, natural freshwater and terrestrial ecosystems, challenging previously held knowledge on the key microorganisms and biochemical pathways controlling nitrification. This paper discusses the distribution of comammox bacteria with a focus on engineered ecosystems, as well as emerging insights from recent genomic and experimental studies on their ecophysiology.

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Introduction

Nitrification, the biological oxidation of ammonia (NH₃) via nitrite (NO₂⁻) to nitrate (NO₃⁻), has been widely applied in engineered ecosystems for ammonium (NH₄⁺) removal during drinking water and wastewater treatment. In drinking water systems, nitrification is employed to treat ground waters with elevated ammonium concentrations to produce biologically stable water for distribution [1]. Control of unwanted nitrification in water distribution systems has also been an engineering objective to avoid decay of chloramine disinfectants by nitrifying microorganisms [2]. In wastewater systems, nitrification is

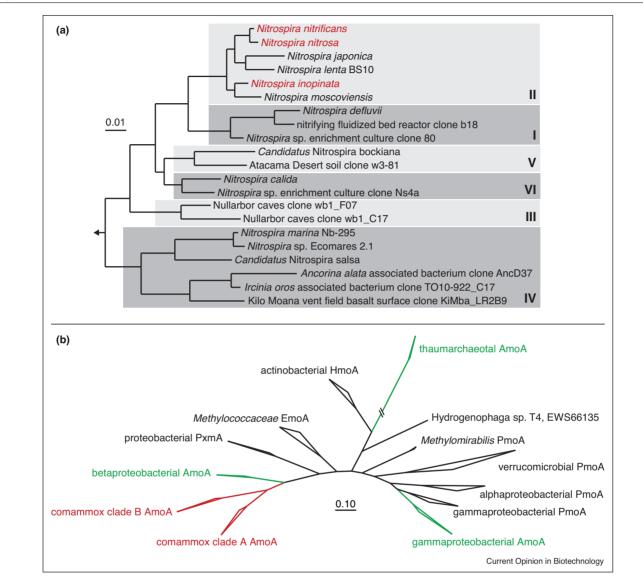
employed to prevent oxygen depletion and fish toxicity in receiving waters, and is often combined with denitrification (reduction of NO_3^-/NO_2^- to nitrogen gas, N_2) and more recently anaerobic ammonium oxidation (anammox; oxidation of NH_4^+ with NO_2^- to N_2) for complete nitrogen removal to prevent eutrophication [3,4]. Furthermore, nitrification is used to remove ammonium in recirculating aquaculture systems (RAS) and bioreactors treating landfill leachate [5,6].

Nitrification has traditionally been thought to occur as a two-step process, where ammonia-oxidizing bacteria and archaea (AOB and AOA) first oxidize ammonia to nitrite, which nitrite-oxidizing bacteria (NOB) subsequently convert to nitrate. However, this view has been radically altered recently when bacteria able to oxidize ammonia all the way to nitrate were identified [7^{••},8^{••}]. While the thermodynamic feasibility of this so-called comammox process (for complete ammonia oxidation) had been predicted [9^{••},10], it took more than 120 years from the first description of nitrifying bacteria [11] to its discovery [7^{••},8^{••}]. Since then, comammox organisms have been detected in a range of engineered and natural ecosystems, challenging previously held knowledge about the key microorganisms performing nitrification in them.

In this review, we summarize the identification and distribution of comammox *Nitrospira* in engineered ecosystems, highlight recent insights on their ecophysiology inferred from comparative genomic studies, and examine their interactions with other nitrogen-cycling microorganisms. We also discuss the importance of incorporating comammox bacteria into nitrification process control development and highlight future research directions.

Comammox in engineered ecosystems

All complete nitrifiers identified to date [7^{••},8^{••},12–15] belong to sublineage II of the genus *Nitrospira* (Figure 1a) [16,17]. This genus has been long known [18], but all members described were canonical NOB [17,19,20]. Consequently, despite several studies observing disproportionally high abundances of *Nitrospira* in response to ammonium amendment [21,22], their potential role in ammonia oxidation had previously been overlooked. Since their original discovery, comammox *Nitrospira* have been identified in a range of engineered systems, including aquaculture biofiltration units [8^{••},12], drinking water treatment [7^{••},13,14] and distribution systems [15], and wastewater treatment plants [7^{••},23,24[•]]. They usually co-occur with AOB and/or AOA, but can greatly



Phylogenetic analyses of comammox *Nitrospira*. (a) 16S rRNA-based phylogenetic tree of the genus *Nitrospira*. Comammox *Nitrospira* are depicted in red. *Nitrospira* sublineages are indicated by roman numbers. (b) Phylogenetic analysis of the ammonia/methane monooxygenase family. AmoA protein clusters of comammox *Nitrospira* are shown in red, AmoA sequences of canonical ammonia oxidizers in green. *Abbreviations*: Amo, ammonia monooxygenase; Emo, ethane monooxygenase; Hmo, hydrocarbon/butane monooxygenase; Pmo/Pxm, particulate methane monooxygenase.

outnumber other ammonia-oxidizing prokaryotes (AOP), highlighting their potential contribution to nitrification in these systems [13,15,24,25]. However, to date it is still unknown to which extend biogeography, process configuration and chemical composition of the treated (waste) water influences their distribution and abundance.

Identification of comammox

Nitrifying microorganisms can exhibit ecophysiological differences that can influence process performance and stability, and it thus is important to identify and monitor their abundance and activity in engineered ecosystems.

Initial identification of comammox *Nitrospira* resulted from screening of metagenomic datasets and subsequent assignment of all key genes required for ammonia oxidation (ammonia monooxygenase [AMO] and hydroxylamine oxidoreductase [HAO]), and nitrite oxidation (nitrite oxidoreductase [NXR]) to single *Nitrospira* genomes or population-level genomic bins [7^{••},8^{••},13–15]. These studies showed that the AMO encoded by comammox *Nitrospira* is phylogenetically distinct from the AMO forms of canonical AOB and AOA (Figure 1b) [7^{••},8^{••}]. Furthermore, it was observed that different comammox *Nitrospira* encode AMO orthologs that are as dissimilar to



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