Facilitation–Competition Tradeoffs Structure Microbial Niches and Nitrogen Cycling

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Abstract

The marine nitrogen cycle is regulated by ecological interactions among diverse microbial populations, especially in oxygen minimum zones where populations carrying out anaerobic metabolisms, mainly denitrification and anammox, drive fixed nitrogen loss. While competition for limiting resources is well studied, the combined effects of competition and facilitation, where a “feeder” population supplies a required resource to a “recipient”, remain poorly understood. Here we develop a trait-based consumer–resource framework to test how recipient populations reshape the ecological niches of their feeders and competitors. Invasion analysis shows that recipients expand either their feeder’s or the feeder’s competitor’s niche, depending on the populations' relative competitive abilities on limiting resources. In terms of biogeochemistry, ecological outcomes result in diverse N-loss pathways; specifically, when growth is limited by both organic matter and nitrate, we observe increased nitrous oxide

production. Additionally, the model suggests that anammox bacteria occupy a wider range of organic matter and nitrate supply regimes than denitrifying populations, consistent with their more frequent detection across diverse marine environments. The results link microbial interaction networks to biogeochemical fluxes relevant at global scales, and extend ecological theory to multi-resource systems with nested competitive and facilitative interactions.

1. Introduction

Microbial interactions regulate the transformation of energy and matter in ecosystems, from soils to oceans, and strongly influence global biogeochemical cycles (Falkowski *et al.* 2008; Bardgett & van der Putten 2014; Bertolet *et al.* 2024). In oxygen-deficient regions of the ocean, the nitrogen cycle is shaped by anaerobic microbes that transform reactive nitrogen into inert gases, driving ecosystem-scale nitrogen loss (Ward *et al.* 2009). Understanding these processes is essential for predicting how nitrogen loss will evolve, impacting primary productivity and the emission of the greenhouse gas nitrous oxide (N_2O).

Ecological theory has provided powerful tools for studying microbial coexistence (Tilman 1982; Chesson 2000; Chase & Leibold 2003), but most models reduce complexity by focusing on competition for a single resource, treating multiple resources as substitutable, or representing facilitation as symmetric mutualism, where both species derive benefit from the interaction (Bruno *et al.* 2003; Bulleri *et al.* 2016; Orr *et al.* 2025). However, in reality, facilitation often involves intricate, asymmetric interactions rather than simple bidirectional benefits. These simplifications cannot anticipate the ecological outcomes in systems where microbes are limited by multiple, non-substitutable resources, and where interactions are competitively and facilitatively nested. How such dependencies shape both community structure and ecosystem function remains poorly understood.

Oxygen minimum zones (OMZs) provide a natural laboratory for advancing microbial interaction theory. In these anoxic waters, two main functional groups

mediate most fixed nitrogen loss: heterotrophic denitrifying microorganisms (hereafter, "denitrifiers") and anaerobic ammonium-oxidizing (anammox) bacteria (Lam & Kuypers 2011). Denitrifiers use nitrate (NO_3^-) or nitrite (NO_2^-) as electron acceptors to oxidize organic matter, producing a stepwise cascade of intermediates—from nitrite and nitric oxide to nitrous oxide (N_2O) and ultimately dinitrogen gas (N_2). They are phylogenetically and functionally diverse, with different lineages performing different subsets of these steps (Sun & Ward 2021; Zhang *et al.* 2023). Some produce only intermediates (e.g., N_2O), while others carry reactions to completion (Fig. 1). In contrast, anammox bacteria are phylogenetically conserved autotrophs that fix carbon by oxidizing ammonium (NH_4^+) with nitrite, producing N_2 as their sole product. These functional groups are metabolically interconnected, with nitrite produced by some denitrifiers (the feeders) providing a key substrate for both other denitrifiers and anammox bacteria (the recipients). Consequently, shifts in the abundance or traits of one group, set by external forcings such as nutrient supply, can cascade through the community, restructuring coexistence and altering the magnitude and form of nitrogen loss.

In this study, we analyze a mechanistic consumer–resource model that links microbial traits to the supply and transformation of organic matter and nitrate. Microbial populations carry out diverse N-cycling metabolisms that are quantitatively distinguished from one another using the underlying redox chemical reaction (Sun et al. 2024). Using invasion analysis and graphical theory, we ask how the presence of recipient populations modifies the coexistence space of their feeders and competitors,

and how these changes propagate to ecosystem-scale nitrogen loss. Our results show that recipients can either contract or expand a feeder's niche depending on their resource use, and that the relative supply of organic matter and nitrate governs whether nitrogen is lost primarily as dinitrogen or as nitrous oxide. Our analysis extends beyond that of Sun et al. 2024 to consider the two-dimensionality of the gradients in organic matter and nitrate supply, which allows us to identify a region of co-limitation with a qualitatively different ecological outcome where only nitrous oxide is produced. We also more comprehensively consider the role of anammox as both a competitor and a recipient. By linking microbial ecology with biogeochemistry, our framework provides new insights into the mechanisms that regulate nitrogen cycling in the ocean. Such theoretical advances are critical for interpreting observed patterns of nitrogen loss and understanding how they change over time.

2. Methods

2.1. Functional Groups

We consider seven microbial functional groups that represent the major anaerobic nitrogen-cycling pathways in oxygen-deficient marine systems (Sun & Ward 2021; Zhang *et al.* 2023). These include the stepwise denitrifiers, anammox bacteria, and the complete denitrifier. Each group is defined by its essential resource requirements—typically organic matter (OM) as an electron donor and nitrate or nitrite as acceptors—and by the metabolic byproducts they release. These byproducts frequently serve as substrates for other groups, establishing a network of competitive and facilitative interactions. Presenting the functional types first provides the biological

context for how resources flow among populations and why dependencies arise among them (Fig. 1).

1. $NO_3^- \rightarrow NO_2^-$ denitrifiers (Group 1, B_1): Heterotrophic denitrifiers that use OM and nitrate (NO_3^-) to produce nitrite (NO_2^-).
2. $NO_3^- \rightarrow N_2O$ denitrifiers (Group 2, B_2): Heterotrophs that use OM and NO_3^- to produce nitrous oxide (N_2O).
3. $NO_2^- \rightarrow N_2$ denitrifiers (Group 3, B_3): Heterotrophs requiring OM and NO_2^-, producing dinitrogen gas (N_2).
4. $N_2O \rightarrow N_2$ denitrifiers (Group 4, B_4): Heterotrophs requiring OM and N_2O, producing N_2.
5. Anammox bacteria (Group 5, B_5): Autotrophs that oxidize ammonium (NH_4^+) with nitrite (NO_2^-), using the released energy to fix inorganic carbon, and producing N_2 as their sole product.
6. $NO_2^- \rightarrow N_2O$ denitrifiers (Group 6, B_6): Heterotrophs requiring OM and NO_2^-, producing N_2O.
7. Complete denitrifiers (Group 7, B_7): Heterotrophs that reduce nitrate (NO_3^-) all the way to N_2, using OM as the electron donor.

2.2. Model Framework

To formalize these interactions, we implement a virtual chemostat–based consumer–resource model that tracks both microbial biomasses and the concentrations

of OM, nitrate, nitrite, nitrous oxide, and ammonium. Growth follows Liebig's Law of the Minimum, reflecting the requirement that each functional group depends on two essential and non-substitutable resources. The model links the physiological traits of each group—maximum uptake rates, affinities, and biomass yields—to their realized growth rates and subsistence concentrations. This structure enables direct comparison of competitive abilities and allows facilitative links to emerge naturally from the excretion of metabolic byproducts defined in Section 2.1.

The dynamics are generally given by:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \mu_i - a \qquad 1$$

$$\frac{dR_j}{dt} = a\left(s_j - R_j\right) + \sum_{i=1}^{7} E_{ij}B_i - \sum_{i=1}^{7} V_{ij}^{r}B_i \qquad 2$$

where B_i is the biomass of group i, and a is the dilution rate. To compute growth and uptake under Liebig's Law, we proceed in two steps. The maximum specific uptake rate for each functional group i on resource j, V_{ij}^{m}, is specified a priori from the trait parameterization (Table 1). For each essential resource, we first calculate the potential growth rate it can support:

$$\mu_{ij} = A_{ij}\, y_{ij}\, V_{ij}^{m}\, \frac{R_j}{R_j + K_{ij}}, \qquad 3$$

where y_{ij} is the biomass yield, K_{ij} is the half-saturation constant, and R_j is the resource concentration. A_{ij} indicates whether group i uses resource j, given by

$$A_{ij} = \begin{array}{c} \begin{array}{ccccc} \mathrm{OM} & NO_3^- & NO_2^- & N_2O & NH_4^+ \end{array} \\ \begin{pmatrix} 1 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 \end{pmatrix} \end{array} \begin{array}{c} NO_3^- \rightarrow NO_2^- \\ NO_3^- \rightarrow N_2O \\ NO_2^- \rightarrow N_2O \rightarrow \mathrm{N}_2 \\ N_2O \rightarrow \mathrm{N}_2 \\ NO_2^- + NH_4^+ \rightarrow \mathrm{N}_2 \\ NO_2^- \rightarrow N_2O \\ NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow \mathrm{N}_2 \end{array} \quad 4$$

In classic resource competition theory (Tilman 1982), the subsistence concentration (R_{ij}^*) for each resource, defined as the minimum concentration at which the growth rate balances mortality, implies competitive ability to that resource:

$$R_{ij}^* = \frac{K_{ij} a}{y_{ij} V_{ij}^m - a}. \quad 5$$

Lower R_{ij}^* values indicate stronger competitive ability under the limitation of resource j (Table 1). The realized growth rate is then given by Liebig's Law as

$$\mu_i = \min_j(\mu_{ij}), \quad 6$$

corresponding to the most limiting essential resource.

Because the realized growth rate cannot exceed the rate supported by the limiting resource, uptake of all essential nutrients must be adjusted accordingly. The realized uptake rate on resource j is therefore

$$V_{ij}^r = \frac{\mu_i}{y_{ij}}. \quad 7$$

This formulation ensures that V_{ij}^m defines the potential maximum uptake, while the realized uptake V_{ij}^r remains consistent with the growth rate imposed by the limiting resource, as required in a Liebig-type consumer–resource model.

The model tracks the concentrations of OM, nitrate (NO_3^-), nitrite (NO_2^-), nitrous oxide (N_2O), and ammonium (NH_4^+), denoted by $R_1, \cdots, R_5$ respectively. External

supplies (s_1 and s_2) are provided for OM and NO_3^-. The excreted compounds of microbial metabolism are defined in an excretion matrix E_{ij}, given by

$$E_{ij} = \begin{array}{c} \begin{array}{ccccc} \text{OM} & NO_3^- & NO_2^- & N_2O & NH_4^+ \end{array} \\ \begin{pmatrix} 0 & 0 & \mu_1/y_{12} & 0 & e_{15} \\ 0 & 0 & 0 & \mu_2/y_{22} & e_{25} \\ 0 & 0 & 0 & 0 & e_{35} \\ 0 & 0 & 0 & 0 & e_{45} \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mu_6/y_{63} & e_{65} \\ 0 & 0 & 0 & 0 & e_{75} \end{pmatrix} \end{array} \begin{array}{c} NO_3^- \rightarrow NO_2^- \\ NO_3^- \rightarrow N_2O \\ NO_2^- \rightarrow N_2O \rightarrow \mathrm{N}_2 \\ N_2O \rightarrow \mathrm{N}_2 \\ NO_2^- + NH_4^+ \rightarrow \mathrm{N}_2 \\ NO_2^- \rightarrow N_2O \\ NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow \mathrm{N}_2 \end{array} \quad 8$$

For example, NO_2^- is produced by $NO_3^- \rightarrow NO_2^-$ denitrifiers, and N_2O is produced by $NO_3^- \rightarrow N_2O$ and $NO_2^- \rightarrow N_2O$ denitrifiers. Note that NH_4^+ arises internally as a byproduct of OM remineralization by heterotrophs, determined by the C:N of the OM and the electron-balanced budget for each metabolic functional type (Sun *et al.* 2024). Thus, we assume that $\sum_{i=1}^{7} e_{i5} B_i$ in the range of 70–86% of s_1 as a supply rate of NH_4^+.

Trait values were derived following the framework of Sun et al. (2024), which estimates the biomass yields from underlying redox chemistry and energetic constraints (Rittmann & McCarty 2012), and shows consistency with observations (Table 1).

2.3. Simulation Setup and Analysis

We focused on ecological equilibria—specifically, microbial survival, exclusion, and community composition—under a wide range of nutrient supply conditions. To explore how nutrient regimes shape coexistence, we systematically varied the supply rates of OM and NO_3^- across ecologically relevant ranges (Supplementary Material).

Invasion analysis was used to determine whether a group could increase from low abundance in a given resource environment. Graphical analyses of zero net growth

isoclines (ZNGIs) and consumption vectors were employed to visualize competitive outcomes and facilitative interactions among groups (Chase & Leibold 2003; Xu *et al.* 2025). The consumption vector characterizes the relative uptake of essential resources and delineates the regions of coexistence and dominance among groups (Tilman 1982; Chase & Leibold 2003; Xu *et al.* 2025). In our framework, it is defined as the ratio of yields on each of the two essential substrates for each functional type. For example, for the $NO_3^- \rightarrow NO_2^-$ denitrifiers that utilize OM and NO_3^- as essential substrates, the consumption vector is given by (see derivation of Eqn. S20 in the Supplementary Material):

$$c_1 = \frac{y_{1,OM}}{y_{1,NO_3^-}}. \quad 9$$

We then evaluate how the consumption vectors change when recipients from different feeder groups are introduced, to examine the resulting shifts in coexistence patterns.

We also examine how microbial interactions influence ecosystem-scale nitrogen cycling by determining the form of nitrogen loss at steady state. Nitrogen is considered lost when converted to gaseous products (N_2 or N_2O). Across most of the OM–NO_3^- supply domain, N_2O is produced and consumed internally at comparable rates, making it a transient intermediate rather than a true loss pathway. However, this cycling still identifies regions with high potential for N_2O emission: if an external process—such as physical mixing or transport—were to decouple N_2O production from its consumption, these regions could generate net N_2O release. By mapping N-loss outcomes across the two-dimensional supply space of OM and nitrate, we identified

threshold regimes, coexistence regions, and the dominant pathways under which either N_2 or N_2O (or a combination) is favored, including a distinct co-limitation zone where simultaneous OM and nitrate limitation results in net N_2O accumulation.

3. Results and Discussion

We analyze the resulting complex interactions among the seven microbial functional types by incrementally constructing the system from simpler subsystems, starting with only two microbial types, $NO_3^- \rightarrow NO_2^-$ denitrifiers (B_1) and $NO_3^- \rightarrow N_2O$ denitrifiers (B_2), as all other types depend on production from one of these two types (except for a third NO_3^- consumer, the complete denitrifier (B_7), discussed below). This stepwise approach allows us to disentangle the quantitative principles that govern microbial coexistence, exclusion, and resource partitioning. Furthermore, simplified microbial consortia are central to engineered ecosystems, such as wastewater treatment facilities, where specific functional groups—particularly denitrifiers and anammox bacteria—are selectively enriched to maximize nitrogen removal efficiency (Rittmann & McCarty 2012; Ali *et al.* 2020), and so understanding the interactions of these simplified consortia could be useful for these contexts (Baeten *et al.* 2019).

3.1. Baseline System: Two Nitrate-reducing Competitors

We begin by analyzing the baseline system, which includes two heterotrophic denitrifiers competing for OM and nitrate (NO_3^-): the $NO_3^- \rightarrow NO_2^-$ denitrifier (B_1) reducing NO_3^- to nitrite (NO_2^-) and the $NO_3^- \rightarrow N_2O$ denitrifier (B_2) reducing NO_3^- directly to nitrous oxide (N_2O). Trait-based parameterization reveals a trade-off in their resource requirements (Sun *et al.* 2024): the $NO_3^- \rightarrow NO_2^-$ reducer has a lower

subsistence requirement and a better competitor for OM ($R^*_{1,OM} < R^*_{2,OM}$) but a higher requirement and a weaker competitor for NO_3^- ($R^*_{1,NO_3^-} > R^*_{2,NO_3^-}$) compared to the $NO_3^- \rightarrow N_2O$ reducer (Table 1). Their consumption vectors ($c_1 = \frac{y_{1,OM}}{y_{1,NO_3^-}}$, $c_2 = \frac{y_{2,OM}}{y_{2,NO_3^-}}$) then form a coexistence region (Fig. 2a) (Tilman 1982; Chase & Leibold 2003; Xu *et al.* 2025). As a result, the OM: NO_3^- supply ratio determines competitive outcomes. When the OM: NO_3^- supply ratio is small , the $NO_3^- \rightarrow NO_2^-$ reducer dominates; while the OM: NO_3^- supply ratio is large, the $NO_3^- \rightarrow N_2O$ reducer prevails; and at intermediate supply ratios, both groups coexist (Fig. 2a).

In this subsystem, because only the $NO_3^- \rightarrow N_2O$ reducer directly produces N_2O, nitrogen loss occurrs only when OM supply is sufficiently high to sustain the $NO_3^- \rightarrow N_2O$ reducer's persistence (Fig. 3a).

A third denitrifier—the complete denitrifier, B_7—is a direct competitor with B_1 and B_2, using both OM and NO_3^-. However, it has a competitive advantage in utilizing NO_3^- (a lower R^*_{7,NO_3^-}), allowing it to outcompete B_1 and B_2 under more NO_3^- -limited conditions (Sun *et al.* 2024). Consequently, B_7 dominates the community when NO_3^- availability is low (Fig. 4a). Because its coexistence region lies largely outside the primary parameter space of the other groups, we do not further analyze this denitrifier in detail but include it in the full system for completeness.

3.2. Recipient Groups Restructure Competitive Outcomes

We next examine how introducing recipient functional groups alters these baseline dynamics. Recipients require substrates produced by feeders, creating facilitative links, but often also compete with feeders or feeders' competitors for OM.

These dual roles restructure coexistence outcomes in qualitatively different ways depending on resource overlap.

Adding Anammox: Neutral Recipient, Expanded Nitrogen Loss

We first introduce anammox bacteria, which rely on nitrite produced by the $NO_3^- \rightarrow NO_2^-$ denitrifier and on ammonium derived from OM remineralization (Eqn. 4).

Anammox bacteria can be theoretically limited by one or both of their essential substrates, nitrite and ammonium. When anammox is limited by nitrite, which is produced by the $NO_3^- \rightarrow NO_2^-$ denitrifier (B_1), its biomass scales with the density of B_1, with a minimum requirement for the density of B_1 to produce enough nitrite to sustain anammox. A general criteria for the minimum equilibrium density of a feeder type required to sustain a recipient type is given by (see the supplementary material for derivation, Eqn. S15):

$$\hat{B}_{Feeder} > \frac{a y_{Feeder,Converted\ resource}}{\mu_{Recipient}} \qquad 10$$

Thus, the equilibrium density of B_1 required for anammox to invade is $\hat{B}_1 > \frac{a y_{12}}{\mu_5}$ while y_{12} denotes the yield of the feeder B_1 by synthesizing nitrate (R_2), which is converted to nitrite (R_3). μ_5 is the realized growth rate of anammox (B_5) when limited by nitrite (R_3) produced by the feeder type. Eqn. 10 shows that with a constant dilution rate, the requirement of the biomass of the feeder type increases with the yield of the feeder on nitrate as more N is absorbed in B_1 biomass and decreases with the growth rate of anammox on nitriteanammox. This is reflected in the graphic analysis as the ZNGI of B_5 being above the ZNGI of B_1 (Fig. 2b), showing that anammox can only persist when the $NO_3^- \rightarrow NO_2^-$ denitrifier (B_1) establishes a sufficient biomass.

In contrast, if nitrite is sufficiently supplied, anammox can be limited by ammonium, supplied by the remineralization from OM from the heterotrophs. In either case, the dynamics of anammox are decoupled from the direct competition between nitrate reducers. Thus, anammox does not alter the competitive boundaries between the two nitrate reducers.

The presence of anammox expands the region of nitrogen loss by introducing a pathway for N_2 production in conditions where the baseline system conserves nitrogen (Fig. 3b). The N-loss via N_2 then happens in the region where anammox can persist. This case demonstrates that recipients can broaden the functional consequences of microbial communities without altering coexistence boundaries among their feeders and the feeders' competitor.

Adding $NO_2^- \rightarrow N_2$ Denitrifiers: Priority Effects via Intensified Competition

Introducing the $NO_2^- \rightarrow N_2$ denitrifiers (B_3) into the baseline system produces a distinct outcome. Similar to anammox, these denitrifiers depend on nitrite supplied by the $NO_3^- \rightarrow NO_2^-$ reducer. Accordingly, the establishment of B_3 requires a minimum threshold density of B_1, given by $\hat{B}_1 \geq \frac{ay_{12}}{\mu_3}$ (Eqn. 10). Unlike anammox, however, B_3 also consumes OM and exhibit the lowest subsistence requirement for OM among the three groups ($R^*_{3,OM} < R^*_{1,OM} < R^*_{2,OM}$) (Table 1). Consequently, the $NO_2^- \rightarrow N_2$ denitrifiers must remain limited by nitrite when coexisting with the $NO_3^- \rightarrow NO_2^-$ reducer; otherwise, they would exclude the latter under OM-limited conditions when NO_2^- is sufficiently supplied externally.

Once established, the feeder–recipient pair forms a tightly coupled consortium that depletes OM more strongly than the $NO_3^- \rightarrow NO_2^-$ reducer alone. This is reflected in the consortium's consumption vector (Eqn. S19)

$$c_{13} = \frac{c_1}{(1 + c_1/c_3)} \qquad 11$$

where $c_1 = \frac{y_{1,OM}}{y_{1,NO_3^-}}$, $c_3 = \frac{y_{3,OM}}{y_{3,NO_2^-}}$ and c_{13} is the consortium's consumption vector. Eqn. 11 shows that c_{13} is smaller than c_1, indicating a greater relative consumption of OM compared to the $NO_3^- \rightarrow N_2O$ denitrifiers. Consequently, the consortium exerts a stronger suppressive effect on $NO_3^- \rightarrow N_2O$ denitrifiers under OM-limited conditions, thereby narrowing their niche (Fig. 2ac).

Furthermore, the consortium's stronger resource consumption on OM can generate priority effects in cases where $NO_3^- \rightarrow N_2O$ and $NO_3^- \rightarrow NO_2^-$ coexist in the baseline system. In this case, the outcome depends on the order of establishment (Fig. 2c and Fig. S1, Eqn. S19-S20) (Chase & Leibold 2003; Fukami 2015; Xu *et al.* 2025). If the feeder–recipient pair becomes established first, they prevent invasion by the $NO_3^- \rightarrow N_2O$ reducer; if the $NO_3^- \rightarrow N_2O$ reducer arrives first, it can exclude the pair. Therefore, the niche space of the $NO_3^- \rightarrow N_2O$ denitrifiers is potentially narrowed (Fig. 2ac).

From a biogeochemical perspective, the presence of the $NO_2^- \rightarrow N_2$ recipient expands the region of nitrogen loss by enabling N_2 production under OM-sufficient conditions, similar to the subsystem containing anammox (Fig. 3ac). In regions governed by priority effects, the dominant form of nitrogen loss depends on the

community's assembly history—yielding either N_2 from the feeder–dependent pair or N_2O from the $NO_3^- \rightarrow N_2O$ denitrifiers.

Interactions Among the Two Recipients of the $NO_3^- \rightarrow NO_2^-$ Reducer

When both recipients of the $NO_3^- \rightarrow NO_2^-$ reducer—anammox and $NO_2^- \rightarrow N_2$ denitrifiers—were present, their coexistence outcomes depend on ammonium availability. Our study parameterizes anammox as a more efficient nitrite competitor than $NO_2^- \rightarrow N_2$ denitrifiers (Table 1), characterized by a lower minimum subsistence concentration ($R^*_{5,NO_2^-} < R^*_{3,NO_2^-}$). If not so (Fadum *et al.* 2025), anammox will be completely excluded by $NO_2^- \rightarrow N_2$ denitrifiers (Fig. S9). Therefore, in principle, under nitrite limitation, anammox bacteria completely exclude $NO_2^- \rightarrow N_2$ denitrifiers . In contrast, if anammox is limited by ammonium, both dependent groups can coexist. In this case, the $NO_2^- \rightarrow N_2$ denitrifiers remain limited by nitrite. In fact, for the range of the supply of ammonium considered in our model, anammox is always limited by ammonium. Thus, anammox and $NO_2^- \rightarrow N_2$ denitrifiers coexist as long as the nitrite production is sufficient for $NO_2^- \rightarrow N_2$ denitrifiers' persistence at high supply of OM and nitrate (Fig. S8).

Because $NO_2^- \rightarrow N_2$ denitrifiers assist their feeder in suppressing the niche of $NO_3^- \rightarrow N_2O$ denitrifiers, whereas anammox exerts no such effect, the presence of anammox—which suppresses $NO_2^- \rightarrow N_2$ denitrifiers—indirectly benefits the feeder's competitor ($NO_3^- \rightarrow N_2O$ denitrifiers), allowing them to expand their niche. Consequently, the coexistence space of $NO_3^- \rightarrow NO_2^-$ and $NO_3^- \rightarrow N_2O$ reducers

broadens (Fig. 2acd). This, in turn, leads to an expanded N-loss region characterized by mixed N_2 and N_2O production.

Adding $\boldsymbol{N_2O \rightarrow N_2}$ denitrifiers: New Recipients Erode Feeder Dominance

When adding $\boldsymbol{N_2O \rightarrow N_2}$ denitrifiers into the baseline system, the $N_2O \rightarrow N_2$ denitrifiers depend on N_2O produced by the $NO_3^- \rightarrow N_2O$ reducer. They also consume OM, but more efficiently than their feeder as indicated by their lower subsistence requirement ($R^*_{4,OM} < R^*_{2,OM}$). This is different from the previous subsystems, because the feeder, $NO_3^- \rightarrow N_2O$ is a weaker competitor for OM when coexisting with the $NO_3^- \rightarrow NO_2^-$ denitrifier. Consequently, introducing the $N_2O \rightarrow N_2$ denitrifiers further increases the overall OM demand beyond that of the feeder alone. The consumption vector of this consortium is given by (Eqn. S94)

$$c_{24} = \frac{c_2}{(1 + c_2/c_4)}. \qquad 12$$

Because c_{24} is smaller than c_2, the consortium has a stronger requirement for OM. This shift effectively reduces the competitive advantage of the feeder and expands the niche space of the $NO_3^- \rightarrow NO_2^-$ denitrifiers (Fig. 2e).

In biogeochemical terms, the $N_2O \rightarrow N_2$ denitrifiers convert N_2O to N_2. In the virtual chemostat, N_2O acts as an intermediate that is consumed by $N_2O \rightarrow N_2$ denitrifiers immediately as it is produced. Thus, nitrogen loss is primarily in the form of N_2 while still maintaining the potential for N_2O escape (Fig. 3e).

3.3. The Full Ecological System and Its Biogeochemical impact

Ecological Dynamics

The ecological result is a community structured by trade-offs, priority effects, and indirect facilitation, rather than stable coexistence of all possible functional types (Fig. 4a). When all seven functional groups are included, the system does not support coexistence of all types at steady state in the supply range of OM and nitrate considered in the model. Instead, in the regimes where most types (except B6 and B7) are likely sustained priority effects between functional consortiums determine the outcome. The $NO_2^- \rightarrow N_2$ denitrifiers typically exclude the other recipient-feeder pair ($NO_3^- \rightarrow N_2O$ and $N_2O \rightarrow N_2$ denitrifiers) by consuming OM more efficiently than the feeder ($NO_3^- \rightarrow N_2O$) ($R^*_{3,OM} < R^*_{1,OM} < R^*_{2,OM}$), thereby restricting coexistence. However, anammox bacteria mitigated this dominance by outcompeting the $NO_2^- \rightarrow N_2$ denitrifiers under nitrite limitation ($R^*_{5,NO_2^-} < R^*_{3,NO_2^-}$), benefiting the recipient-feeder pair ($NO_3^- \rightarrow N_2O$ and $N_2O \rightarrow N_2$ denitrifiers) and facilitating broader coexistence among denitrifiers. The extent of the benefit depends on the severity of ammonium limitation in anammox bacteria.

Complete denitrifiers (B_7) only persist with sufficient supply of OM and are consistently outcompeted by more specialized groups when the supply of nitrate increases because of inefficient consumption on OM ($R^*_{1,OM} < R^*_{2,OM} < R^*_{7,OM}$, Table 1). For the supply range of OM considered in our simulation, it can only coexist with the $NO_3^- \rightarrow N_2O$ denitrifiers (B_2).

The $NO_2^- \rightarrow N_2O$ denitrifiers (B_6) could not exist when nitrite reducers or anammox are present under NO_2^--limited condition. Because $NO_2^- \rightarrow N_2O$ denitrifiers are a weaker competitor for nitrite compared to the nitrite reducers and anammox

($R^*_{5,NO_2^-} < R^*_{3,NO_2^-} < R^*_{6,NO_2^-}$). Thus, the $NO_2^- \rightarrow N_2O$ denitrifiers are effectively excluded, reflecting their weaker competitive ability.

Biogeochemical Impact

We next analyze the N loss patterns and other results relevant for the biogeochemistry of the "full system," as described above, when all seven functional types are introduced into the virtual chemostat.

Sustaining any denitrifier population requires minimal supplies of both OM and nitrate (NO_3^-); below these thresholds, no denitrifiers considered can persist in our model and nitrogen is conserved. Otherwise, the OM: NO_3^- supply ratio strongly controls both the magnitude and form of nitrogen loss (Fig. 3b).

Net N_2O Production Under Co-Limitation

Our findings identify a potential N_2O accumulation regime. When both organic matter (OM) and nitrate (NO_3^-) supplies are critically low, denitrifiers persist at densities too low to support downstream reducers, resulting in the production of N_2O without subsequent consumption (Fig. 4b, lower-left corner). While previous studies suggest that increased OM availability generally promotes both N_2O production and consumption (Li *et al.* 2022; Rummel *et al.* 2025) , our results demonstrate that this relationship is also contingent upon NO_3^--availability. We show that when both electron donors and acceptors are scarce, the metabolic pools become jointly limiting, decoupling the production and consumption phases of the denitrification pathway. Under these conditions, the nitrogen flux proceeds only partially, accumulating N_2O

because the system lacks the reducing power or substrate flux necessary to sustain complete reduction to N_2. Consequently, low substrate availability disrupts the metabolic balance between producers and reducers, fundamentally altering the magnitude and direction of the net nitrogen flux.

A Broad Niche for Anammox

A striking outcome of our model is the disparity in niche breadth between anammox bacteria and NO_2^--reducing denitrifiers. Anammox occupy expansive nutrient supply regimes where NO_2^--reducers could persist, yet the reverse was not true. This asymmetry stems from our evidence-based assumption that anammox possesses a lower requirement for nitrite (a lower $R^*_{NO_2^-}$) than its denitrifying competitors (but see (Fadum *et al.* 2025)). Consequently, if this competitive advantage holds, anammox maintains a strictly broader nutrient niche.

This ecological framework provides a mechanistic explanation for why anammox is more frequently detected in Oxygen Minimum Zones (OMZs), even in regions where denitrification-driven N_2 production is prevalent (Dalsgaard *et al.* 2012; Babbin *et al.* 2014; Ward *et al.* 2019; Tracey *et al.* 2023). While denitrifiers are biogeochemically vital, their narrower niches likely render them less consistently detectable across varying environmental gradients.

More broadly, the two major N_2 production pathways, $NO_2^- \rightarrow N_2$ and anammox, have been observed to dominate different oceanic regions, leading to historical debate over their relative importance (Ward *et al.* 2009; Dalsgaard *et al.* 2012;

Babbin *et al.* 2014; Tracey *et al.* 2023). Recent theoretical and modeling studies reconcile these contrasting observations by estimating that anammox contributes approximately 30% of global marine N_2 production (Ward 2013; Babbin *et al.* 2014; Koeve *et al.* 2020; Zakem *et al.* 2020) , with this fraction varying systematically in response to nutrient supply regimes (Sun *et al.* 2024).

4. Synthesis and General Principles

Our results reveal a set of general principles for how recipient populations reshape microbial coexistence and ecosystem function. Recipients may enhance the ecological niche of their feeders and/or their feeders' competitor, or not, depending on the circumstances. The outcome depends on their competitive ability for limiting resources relative to both the feeder and its competitor as follows.

Reinforcement of feeder dominance occurs when recipients are specialized on resources that are not limiting to their feeders but limiting to the competitor of their feeders. In these cases, the feeder–recipient association intensifies competitive exclusion of the competitor (e.g., the group of B_1, B_2, and B_3). In contrast, erosion of feeder dominance, by expanding feeder's competitor niche, arises when recipients overlap strongly in resource use with their feeders but are more competitive for the limiting resource to their feeders. This reduces the feeder's advantage and expands the niche of its competitor (e.g., the group of B_1, B_2, and B_4). Finally, intuitively, no change in the dominance of the feeder occurs when recipients rely on resources unrelated to their feeder's limitation, leaving competitive boundaries unaffected (e.g., the group of B_1, B_2, and anammox B_5).

Together, these principles extend coexistence theory to multi-resource systems with dependencies. Results are relevant for complex microbial interaction networks beyond just that of the marine nitrogen cycle, providing a framework by which to untangle the complexities. Specifically, our results highlight that facilitation interacts with competition to determine both community assembly and ecosystem-scale biogeochemical function.

5. Conclusion

We show that under nitrite-limited, fully anoxic conditions, anammox bacteria occupy a broader nutrient niche than NO_2^--reducing denitrifiers due to a lower $R^*_{NO_2^-}$. As a result, anammox can persist across all nutrient supply regimes that support denitrifiers, whereas the reverse is not true. This asymmetry provides a simple mechanistic explanation for the frequent detection of anammox in anoxic marine environments, including Oxygen Minimum Zones, even when denitrification-derived N_2production is substantial.

Beyond niche structure, our results highlight how microbial interactions shape nitrogen loss pathways across nutrient regimes. Varying both OM and nitrate supply reveals richer coexistence patterns and biogeochemical outcomes than varying either resource alone, even when supply ratios are held constant. In this way, we extend (Sun *et al.* 2024) by demonstrating that increasing the OM: NO_3^- ratio drives transitions from complete denitrification to N_2 toward partial denitrification across distinct nitrate supply regimes. Notably, under OM– and nitrate–colimited conditions, complete denitrification is constrained, allowing N_2O to accumulate.

More broadly, our framework demonstrates how microbial traits and multi-resource supply jointly regulate ecosystem-scale nutrient transformations. Because recipient–feeder interactions are common across microbial systems, these insights extend beyond OMZs to diverse environments where coexistence governs the fate of energy and matter.

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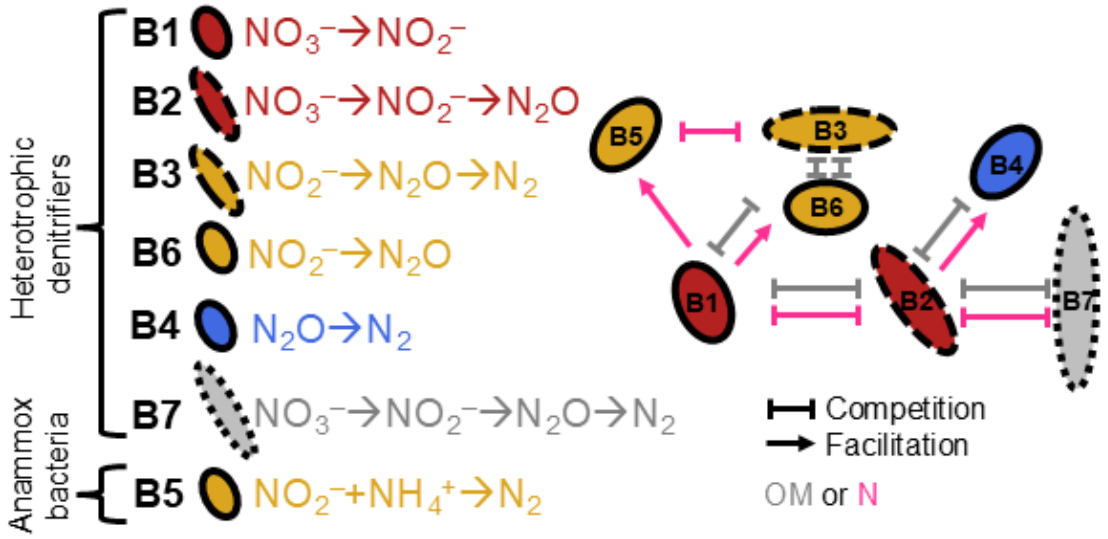


Figure 1. Microbial functional groups represented in the model and a schematic summary of their interactions.

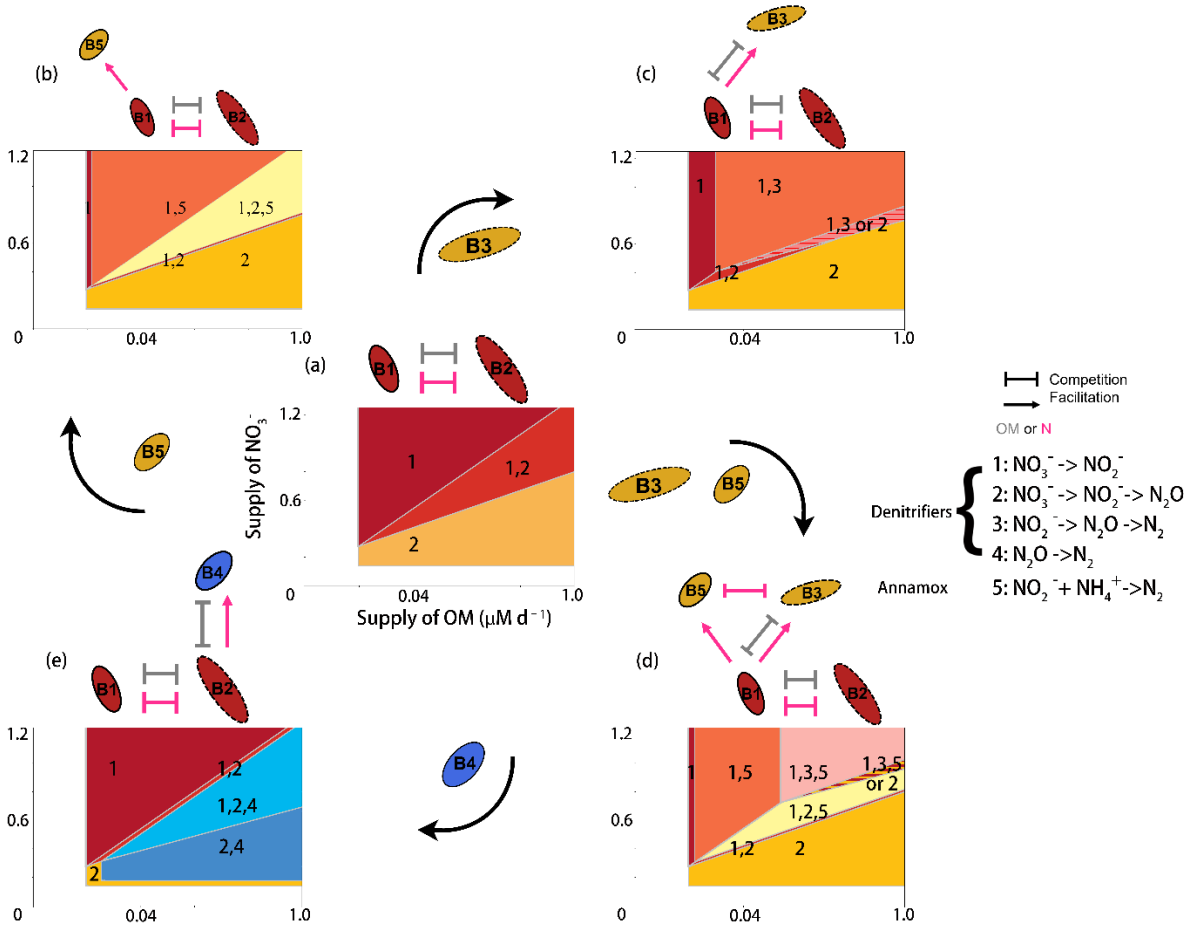


Figure 2. Competitive outcomes as a function of organic matter (OM) and NO_3^- supply rates across systems. Outcomes are shown in the OM–NO_3^- supply space for the baseline system (a, center panel) and for alternative subsystems (b–e, surrounding panels).

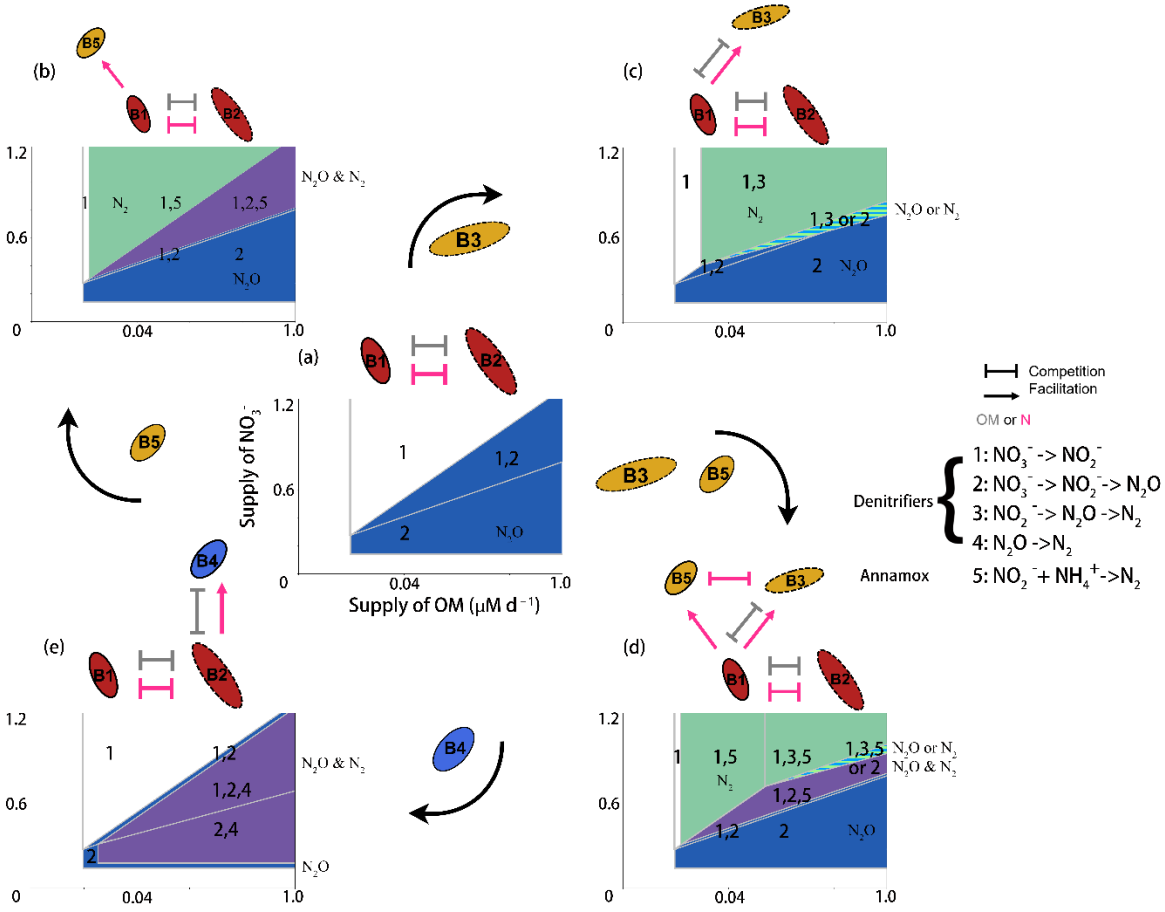
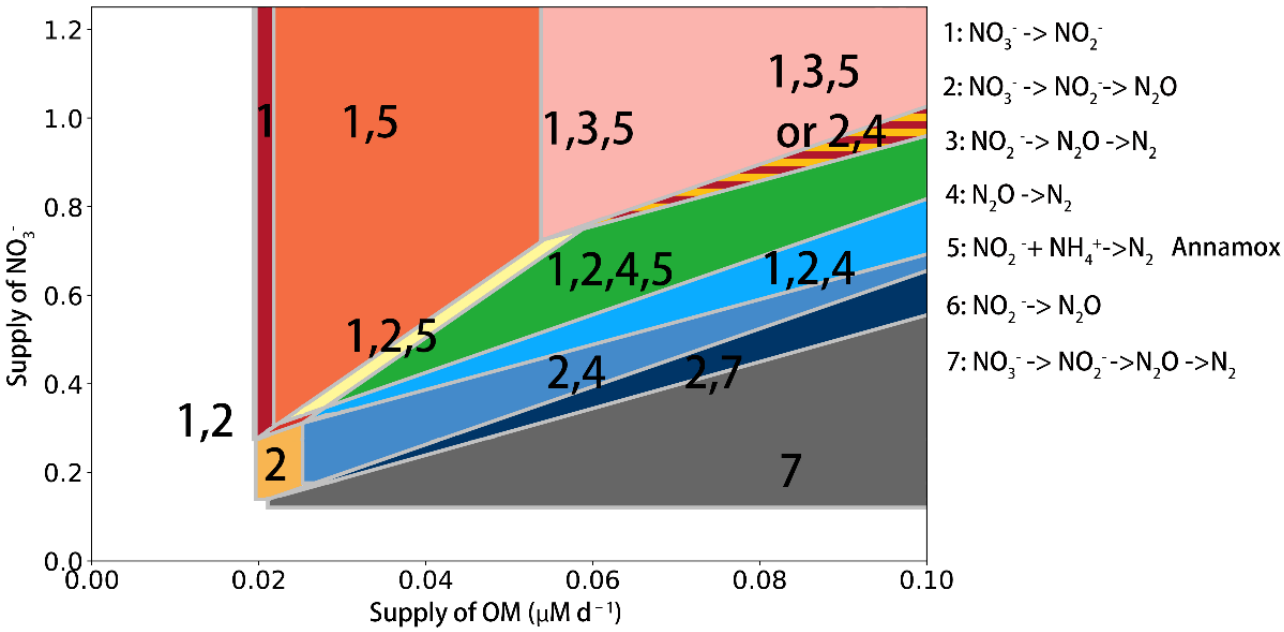


Figure 3. Nitrogen loss pathways as a function of organic matter (OM) and NO_3^- supply rates. Pathways are mapped in the OM–NO_3^- supply space for the baseline system (a, center panel) and for the corresponding subsystems (b–e, surrounding panels).

(a)



(b)

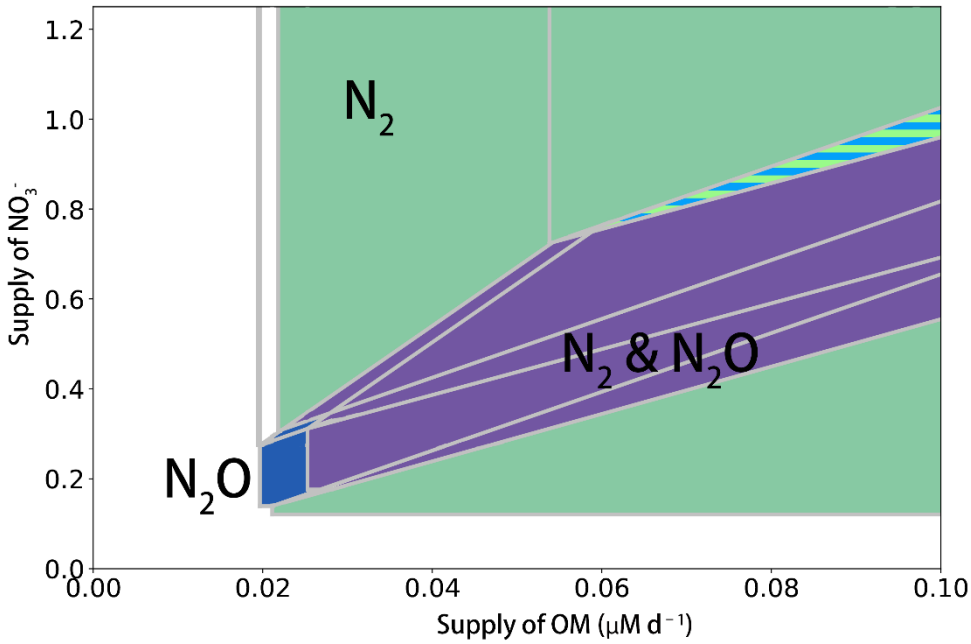


Figure 4. Graphical analysis of functional group coexistence (a) and nitrogen loss pathways (b) in the full system, together with the corresponding N-loss area. Nitrogen loss pathways denote the chemical

form in which nitrogen is removed—either as N_2 or N_2O. Regions showing both N_2 and N_2O correspond to steady states in which N_2O production is balanced by its consumption; in natural environments (e.g., the ocean), such conditions nonetheless create the potential for N_2O emission.

Microbes	Substrate	Max Uptake rate V_{ij}^{m} (MOL N d^{-1})	Yield y_{ij}	Half-saturation rate K_{ij} (μM N)	R_{ij}^{*}
$B_1: NO_3^- \rightarrow NO_2^-$	R_1: OM	1.377	0.15	0.1	0.024
$B_1: NO_3^- \rightarrow NO_2^-$	R_2: NO_3^-	50.8	0.011	4	0.295
$B_2: NO_3^- \rightarrow N_2O$	R_1: OM	1.377	0.148	0.1	0.0245
$B_2: NO_3^- \rightarrow N_2O$	R_2: NO_3^-	50.8	0.023	4	0.144
$B_3: NO_2^- \rightarrow N_2$	R_1: OM	1.377	0.197	0.1	0.0172
$B_3: NO_2^- \rightarrow N_2$	R_3: NO_2^-	50.8	0.024	4	0.138
$B_4: N_2O \rightarrow N_2$	R_1: OM	1.377	0.298	0.1	0.0108
$B_4: N_2O \rightarrow N_2$	R_4: N_2O	50.8	0.013	0.6	0.039
$B_5: ANAMMOX$	R_5: NH_4^+	50.8	0.013	0.45	0.028
$B_5: ANAMMOX$	R_3: NO_2^-	50.8	0.011	0.45	0.034
$B_6: NO_2^- \rightarrow N_2O$	R_1: OM	1.377	0.201	0.1	0.0169
$B_6: NO_2^- \rightarrow N_2O$	R_3: NO_2^-	50.8	0.016	4	0.2066
$B_7: NO_3^- \rightarrow N_2$	R_1: OM	1.377	0.138	0.1	0.0268
$B_7: NO_3^- \rightarrow N_2$	R_2: NO_3^-	50.8	0.026	4	0.124

Table 1: Physiological trait values are identical to those used in Sun *et al.* (2024).