Facilitation–competition tradeoffs structure microbial niches and nitrogen cycling

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Abstract

The marine nitrogen cycle is regulated by diverse microbial interactions, especially in oxygen minimum zones where denitrifiers and anammox bacteria drive fixed nitrogen loss. While competition for limiting resources is well studied, the combined effects of competition and facilitation remain poorly understood when microbes require multiple, non-substitutable resources such as carbon and nitrogen. Here we develop a trait-based consumer–resource framework to test how recipient populations—whose growth relies on the metabolic products of other groups—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 whether they are superior competitors for resources limiting the feeder's rivals or the feeder itself. These shifts alter biogeochemical outcomes: high organic matter to nitrate supply ratios favor nitrous oxide cycling over dinitrogen gas production. Moreover, anammox bacteria occupy a wider range of organic matter and nitrate supply regimes than nitrite-reducing denitrifiers, consistent with their more frequent detectability in diverse marine environments. Together, our results link microbial interaction networks to global biogeochemical fluxes, advancing trait-based ecological theory for multi-resource systems.

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 primary productivity and greenhouse gas emissions.

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 simple cross-feeding (Datta *et al.* 2016). These simplifications overlook the reality that many microbes require multiple, non-substitutable resources, and that interactions often combine competition and facilitation. 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 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 can cascade through the community, restructuring coexistence and altering the magnitude and form of nitrogen loss.

In this study, we develop a mechanistic consumer–resource model that links microbial traits to the supply and transformation of organic matter and nitrate. 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. By linking microbial ecology with nitrogen 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 anammox and denitrifier distributions in oxygen minimum zones.

2. Methods

2.1 Model framework

We developed a virtual chemostat-based consumer–resource model to investigate the interplay of competition and facilitation among microbial functional groups in anoxic ocean waters. The model explicitly links microbial physiological traits to the dynamics of both living (microbial biomass) and non-living (resource pools) components of the nitrogen cycle (Fig. 1). We assume a fully anoxic environment without oxygen intrusion, such that all relevant nitrogen transformations occur under anaerobic conditions.

Population dynamics follow standard chemostat equations, in which microbial growth depends on the minimum of two essential resources according to Liebig's law of the minimum. For a microbial group i and a substrate j, the dynamics are given by:

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

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

where B_i is the biomass of group i, $\mu_i = min\left(A_{ij}y_{ij}V_{ij}\frac{R_j}{R_j+K_{ij}}\right)$ for $j = 1, \cdots, 5$ is the growth rate of group i by taking up essential resources, and a is the mortality rate or the dilution rate. Growth on each resource depends on maximum uptake rates (V_{ij}), half-saturation constants (K_{ij}), and biomass yields (y_{ij}) (Table 1). A_{ij} is the uptake matrix, indicating which group is utilizing what resource, given by

$$A_{ij} = \begin{array}{c} \begin{array}{ccccc} \mathrm{OM} & NO_3^- & NO_2^- & N_2O & NH_4^+ \end{array} \\ \begin{pmatrix} 1 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 \end{pmatrix} \end{array} \begin{array}{c} NO_3^- \rightarrow NO_2^- \\ NO_3^- \rightarrow N_2O \\ NO_2^- \rightarrow N_2O \rightarrow \mathrm{N_2} \\ N_2O \rightarrow \mathrm{N_2} \\ NO_2^- + NH_4^+ \rightarrow \mathrm{N_2} \\ NO_2^- \rightarrow N_2O \\ NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow \mathrm{N_2} \end{array} \qquad 3$$

The model tracks the concentrations of organic matter (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^-, while NH_4^+ arises internally as a byproduct of OM remineralization by heterotrophs. Specifically, the effective ammonium supply rate is modeled as:

$$\left(1 - \frac{d_{OM}}{d_B}f\right) \times s_1 \qquad 4$$

where f is the fraction of the electrons originated from OM used in biomass synthesis, d_{OM} and d_B are denominators in the half reactions that normalize each half reaction to one electron (Sun *et al.* 2024).

The generation of byproducts of microbial metabolism are defined in an excretion matrix E_{ij}, given by

$$E_{ij} = \begin{array}{c} \begin{array}{ccccc} \mathrm{OM} & NO_3^- & NO_2^- & N_2O & NH_4^+ \end{array} \\ \begin{pmatrix} 0 & 0 & \mu_1/y_{12} & 0 & 0 \\ 0 & 0 & 0 & \mu_2/y_{22} & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \end{array} \begin{array}{c} NO_3^- \rightarrow NO_2^- \\ NO_3^- \rightarrow N_2O \\ NO_2^- \rightarrow N_2O \rightarrow \mathrm{N_2} \\ N_2O \rightarrow \mathrm{N_2} \\ NO_2^- + NH_4^+ \rightarrow \mathrm{N_2} \\ NO_2^- \rightarrow N_2O \\ NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow \mathrm{N_2} \end{array} \quad (5)$$

For example, NO_2^- is produced by $NO_3^- \rightarrow NO_2^-$ denitrifiers, and N_2O is produced by $NO_3^- \rightarrow N_2O$ denitrifiers. These byproducts provide essential substrates for other functional groups, establishing facilitative links.

2.2 Functional groups

The model includes seven microbial functional groups that collectively represent the main processes of the anoxic nitrogen cycle:

1. $NO_3^- \rightarrow NO_2^-$ denitrifiers (Group 1, B_1): Heterotrophic denitrifiers that use organic matter (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.

These functional groups encompass the diversity of denitrification and anammox metabolisms documented in oxygen minimum zones (Sun & Ward 2021; Zhang *et al.* 2023). Importantly, they differ in their resource requirements and byproducts, creating a network of both competition and facilitation.

2.3 Trait parameterization

Each microbial group is parameterized by key physiological traits: maximum specific uptake rate (V_i), half-saturation constant (K_{ij}), and biomass yield coefficient (y_{ij}). Together, these determine the realized growth rate (μ_i), given by

$$\mu_i = \min_j \left(A_{ij} y_{ij} V_{ij} \frac{R_j}{R_j + K_{ij}} \right) \tag{6}$$

and the subsistence concentration (R_{ij}^*) for each resource, defined as the minimum concentration at which the growth rate balances mortality,

$$R_{ij}^* = \frac{K_{ij} m}{y_{ij} V_{ij} - m}. \tag{7}$$

where R_{ij}^* is the subsistence concentration of resource j for group i. Lower R_{ij}^* values indicate stronger competitive ability under resource limitation (Table 1).

Another key metric is the consumption vector. The consumption vector characterizes the relative uptake of essential resources and delineates the regions of coexistence and dominance among groups (Chase & Leibold 2003; Xu *et al.* 2025). It is defined as the ratio of yield rates on the essential substrates. For example, for the $NO_3^- \rightarrow NO_2^-$ denitrifiers that utilize organic matter (OM) and NO_3^- as essential substrates, the consumption vector is given by (see derivation of Eqn. S20 in the Supplementary Material):

$$c_1 = \frac{y_{1,OM}}{y_{1,NO_3^-}}. \quad 8$$

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

Trait values were derived following the framework of Sun et al. (2024), which estimates microbial growth parameters from underlying redox chemistry and energetic constraints, and validates them with both metabolic modeling and empirical observations. This mechanistically grounded approach allows us to capture trade-offs between affinity (low K_{ij}) and maximum growth rate, which underpin coexistence patterns.

2.4 Simulation setup

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. We also varied the relative supply of NH_4^+ (70–86% of OM remineralization) suggested by Eqn. 4 to examine its role in sustaining anammox.

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).

2.5 Analysis of nitrogen loss

We explore the consequences of microbial interactions for ecosystem-scale nitrogen cycling by identifying the form of nitrogen loss at steady state. Nitrogen was considered lost when converted to gaseous forms (N_2 or N_2O). We mapped N-loss outcomes across supply planes of OM and NO_3^- to identify thresholds, coexistence regions, and shifts in dominant pathways.

3. Results and Discussion

In this section, we analyze the complex interactions among the seven microbial functional types by incrementally constructing the system from simpler subsystems, starting with only two microbial types (B_1 ($NO_3^- \rightarrow NO_2^-$ denitrifiers) and B_2 ($NO_3^- \rightarrow N_2O$ denitrifiers)) as all other types depend on production from these two types except a third complete denitrifier (B_7). 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, and so understanding the interactions of these simplified consortia could be useful for these contexts.

3.1 Baseline system: two nitrate-reducing competitors

We began by analyzing the baseline system, which includes two heterotrophic denitrifiers competing for organic matter (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 revealed a trade-off in their resource requirements: 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 strongly determined competitive outcomes. When the OM: NO_3^- supply ratio is small , the $NO_3^- \rightarrow NO_2^-$ reducer dominated; while the OM: NO_3^- supply ratio is large, the $NO_3^- \rightarrow N_2O$ reducer prevailed; and at intermediate supply ratios, both groups coexisted (Fig. 2a).

In this subsystem, because only the $NO_3^- \rightarrow N_2O$ reducer directly produces N_2O, nitrogen loss occurred only when OM supply was 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. Consequently, B_7 dominates the community when NO_3^- availability is low (corresponding to the lower-right triangular region in the resource plane, Fig. S7) (Fig. 4a). Because its coexistence region lies largely outside the primary parameter space of the other groups, we do not analyze this denitrifier in detail but include it in the full system for completeness.

3.2 Recipient groups restructure competitive outcomes

We next examined 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.

Anammox: neutral recipient, expanded nitrogen loss

We first introduced 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 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. 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):

$$\underbrace{\hat{B}_{\text{Feeder}}}_{\textbf{Min biomass}} > \frac{\overbrace{\hat{a}}^{\textbf{Dilution rate}} \quad \overbrace{y_{\text{Feeder,Converted resource}}}^{\textbf{Yield rate}}}{\underbrace{\mu_{\text{Recipient,Limiting resource}}}_{\textbf{Max growth rate}}} \tag{9}$$

Thus, the minimum equilibrium density of B_1 required for anammox to invade is $\hat{B}_1 > \frac{a y_{12}}{\mu_{53}}$ while y_{12} denotes the yield rate of the feeder B_1 by synthesizing nitrate (R_2), which is converted to nitrite (R_3). μ_{55} is the maximum growth rate of annamox (B_5) by taking up and also is limited by nitrite (R_3). Eqn. 9 shows that with 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 maximum growth rate of annamox on nitrite as nitrite limits the growth of annamox. This is reflected in the graphic analysis as the ZNGI of B_5 being above the ZNGI of B_1 (Fig. 2b), showing that annamox 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 is possible to be limited by ammonium due to lack of sufficient remineralization from OM. In either case, their dynamics were decoupled from the direct competition between nitrate reducers. Thus, annamox does not alter the competitive boundaries between the two nitrate reducers.

The presence of anammox expanded the region of nitrogen loss by introducing a pathway for N_2 production in conditions where the baseline system conserved nitrogen (Fig. 2b). The N-loss via N_2 then happens in the region where annamox 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.

$NO_2^- \rightarrow N_2$ denitrifiers: priority effects via intensified competition

Introducing the $NO_2^- \rightarrow N_2$ denitrifiers (B_3) into the baseline system produced 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 $\hat{B}_1 \geq \frac{ay_{12}}{\mu_{33}}$ according to Eqn. 9. 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.

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)

$$c_{13} = \frac{c_1}{(1 + c_1/c_3)}. \quad 10$$

where $c_1 = \frac{y_{1,OM}}{y_{1,NO_3^-}}$ and $c_3 = \frac{y_{3,OM}}{y_{3,NO_2^-}}$. Eqn. 10 shows that the consortium's consumption vector c_{13} is shallower than that of the $NO_3^- \rightarrow NO_2^-$ reducer alone, 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. a, c).

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 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. a, c).

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. Under

high ammonium supply, where anammox becomes limited by nitrite, anammox bacteria completely exclude $NO_2^- \rightarrow N_2$ denitrifiers by outcompeting them for nitrite, owing to their lower subsistence requirement ($R^*_{5,NO_2^-} < R^*_{3,NO_2^-}$). In contrast, when ammonium supply is low and constrains anammox activity, both dependent groups can coexist: anammox is then limited by ammonium, while the $NO_2^-(N_2)$ denitrifiers remain limited by nitrite.

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. 2a, c, d). This, in turn, leads to an expanded N-loss region characterized by mixed N_2 and N_2O production.

$N_2O \rightarrow N_2$ denitrifiers: recipients eroding feeder dominance

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, which is different from the previous subsystems, as indicated by their lower subsistence requirement ($R^*_{4,OM} < R^*_{2,OM}$). Notably, the feeder, $NO_3^- \rightarrow N_2O$ is OM-limited when coexisting with the $NO_3^- \rightarrow NO_2^-$ denitrifier. Consequently, when the $N_2O \rightarrow N_2$ denitrifiers are introduced into the baseline system, they further increase the overall OM demand beyond that of the feeder alone. The consumption vector of this consortium is given by (Eqn. S94)

$$c_{24} = \frac{c_2}{(1 + c_2/c_4)}. \qquad 11$$

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).

This case illustrates a general principle: recipients that do not share limiting resources with feeders (e.g., anammox) broaden nitrogen loss without shifting competition. Recipients that share limiting resources with its feeder's competitor and are competitively superior (e.g., $NO_2^- \rightarrow N_2$) reinforce feeder dominance, even generating priority effects. Recipients that have higher efficiency on substrates that their feeders are limited (e.g., $N_2O \rightarrow N_2$) expand feeder's competitor's niches, benefiting competitors. Thus, the direction of recipient effects depends on resource overlap and relative competitive ability.

In biogeochemical terms, the $N_2O \rightarrow N_2$ denitrifiers convert N_2O to N_2, enabling N-loss in a mixture of N_2 and N_2O, depending on resource supply levels (Fig. 3e).

Full system dynamics

When all seven functional groups were included, the system did not support coexistence of all types at steady state. Instead, priority effects between functional consortiums determined the outcome. The $NO_2^- \rightarrow N_2$ denitrifiers typically excluded 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.

Complete denitrifiers (B_7) only persisted with sufficient supply of OM and were 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.

The result is a community structured by trade-offs, priority effects, and indirect facilitation, rather than stable coexistence of all possible functional types (Fig. 4a).

3.3 Biogeochemical impact

Nitrogen loss thresholds and forms

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

Nitrogen could be lost as N_2, N_2O, or a mixture, depending on which denitrifiers can persist. Priority effects determined whether N_2 (from N_2O reducers) or N_2O (from nitrate reducers) dominated, while the $N_2O \rightarrow N_2$ recipient shifted loss composition by channeling intermediate N_2O into N_2. At extremely low OM supply, however, only the $NO_3^- \rightarrow NO_2^-$ denitrifier persisted at low density, insufficient to support $N_2O \rightarrow N_2$ reducers. As a result, N_2O was produced but not consumed. Together, these results show that both nutrient supply ratios and

community composition determine not only whether nitrogen is lost, but also the chemical form in which loss occurs.

These results align with previous studies, suggesting that increased OM availability promotes both the production and consumption of N_2O (Li *et al.* 2022; Rummel *et al.* 2025). However, our results advance this understanding by showing that the higher OM availability must be interpreted in the context of NO_3^- availability. Specifically, when both organic matter and nitrate are scarce but are sufficient to sustain $NO_2^- \rightarrow N_2O$ denitrifiers, the electron donor and acceptor pools become jointly limiting, leading to a decoupling between N_2O production and consumption. Under such conditions, denitrification may proceed only partially, accumulating N_2O without sufficient reducing power or nitrate flux to sustain its complete reduction to N_2. Thus, low substrate availability constrains the metabolic balance between N_2O-producing and N_2O-reducing processes, altering the overall direction and magnitude of net N_2O flux.

Niche breadth and detectability

A striking outcome was the difference in niche breadth between anammox bacteria and NO_2^--reducing denitrifiers. Anammox occupied large nutrient supply regimes where NO_2^- reducers could persist, but the reverse was not true. Because anammox has a lower requirement on nitrite compared to NO_2^- reducers. Thus, anammox had a strictly broader nutrient niche. This provides an ecological explanation for their frequent detectability in OMZs, even in regions where denitrification-derived N_2 production is known to occur (Ward et al. 2009; Babbin et al. 2014; Tracey et al. 2023). Narrower niches likely render denitrifiers less consistently detectable, despite their biogeochemical importance.

Synthesis and General Principles

Our results reveal a set of general principles for how recipient populations reshape microbial coexistence and ecosystem function. Recipients can enhance, or have neutral effects on the ecological niche of their feeders and/or their feeders' competitor, and the outcome depends on their competitive ability for limiting resources relative to both the feeder and its competitor.

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).

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).

Neutral effects occur 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 annamox B_5).

The ecological consequences of these dynamics map directly onto biogeochemical outcomes. Nitrogen loss requires minimal supplies of both OM and NO_3^-, but the ratio of OM to NO_3^-, supply governs whether nitrogen is lost primarily as N_2, N_2O, or not at all. Furthermore, the broader nutrient niche of anammox bacteria relative to nitrite-reducing denitrifiers provides a mechanistic explanation for their frequent detectability in oxygen minimum zones, even when denitrification also occurs but is less consistently observed.

Together, these principles extend coexistence theory to multi-resource systems with dependencies, highlighting how facilitation interacts with competition to determine both community assembly and ecosystem-scale biogeochemical function.

4. Conclusion

The two major N_2 production pathways, $NO_2^- \rightarrow N_2$ and anammox, have been observed to dominate different oceanic regions (Ward *et al.* 2009; Dalsgaard *et al.* 2012; Babbin *et al.* 2014; Tracey *et al.* 2023). Theoretical and modeling analyses reconcile these seemingly conflicting observations by estimating ~30% N_2 from anammox (Ward 2013; Babbin *et al.* 2014; Koeve *et al.* 2020; Zakem *et al.* 2020), and show that this fraction varies with changes in nutrient supply (Sun *et al.* 2024). Here, we show that regardless of the relative contribution of anammox to total N_2 production, anammox bacteria occupy a broader nutrient niche under nitrite limited conditions in anoxic systems than $NO_2^- \rightarrow N_2$ denitrifiers because of a lower $R^*_{NO_2^-}$. In other words, anammox bacteria can persist in all tested nutrient niches where $NO_2^- \rightarrow N_2$ denitrifiers are viable, but not vice versa (Fig. 4a). Our analysis shows that when OM and NO_3^- are sufficiently supplied such that nitrite is sufficiently produced to potentially sustain $NO_2^- \rightarrow N_2$ denitrifiers and annamox is limited by NH_4^+, $NO_2^- \rightarrow N_2$ denitrifiers are able to persist. This broader niche may explain why anammox is sometimes the only detectable N_2 production process in certain anoxic marine regions, even if denitrification-derived N_2 production also occurs but escapes detection due to narrower environmental constraints. The niche spaces of $NO_2^- \rightarrow N_2$ denitrifiers and annamox at the oxic-anoxic interface of OMZs, where oxygen supply is present, are influenced by their competition with another nitrite consumer, aerobic nitrite-oxidizing bacteria (NOB). Here, however, we focus on fully anoxic conditions, under which aerobic NOB cannot persist.

Our findings also reveal important biogeochemical consequences of microbial interactions across nutrient regimes. Specifically, we show that more diverse coexistence patterns and nitrogen loss pathways emerge when both OM and NO_3^- are varied simultaneously, compared to when

OM alone is altered. This is so even when the overall OM to NO_3^- supply ratio remains constant but the magnitude changes. Notably, sustaining active N_2O cycling requires a higher OM:NO_3^- ratio than that supporting complete denitrification to N_2, indicating that carbon-rich conditions favor partial denitrification..

Our framework links microbial interactions to nitrogen cycling in OMZs, but its insights are general. Many microbial systems involve multiple essential resources and recipient–feeder relationships, from soil carbon cycling to wastewater treatment. In all such systems, recipients may either amplify or diminish their feeder's niche depending on resource overlap, with consequences for community assembly and ecosystem function. By explicitly connecting microbial traits, resource supply ratios, and interaction networks, this work demonstrates that the fate of nutrients in ecosystems is inseparable from the rules governing coexistence. Applying this framework more broadly may help explain and predict how microbial communities regulate the transformation of energy and matter across diverse environments.

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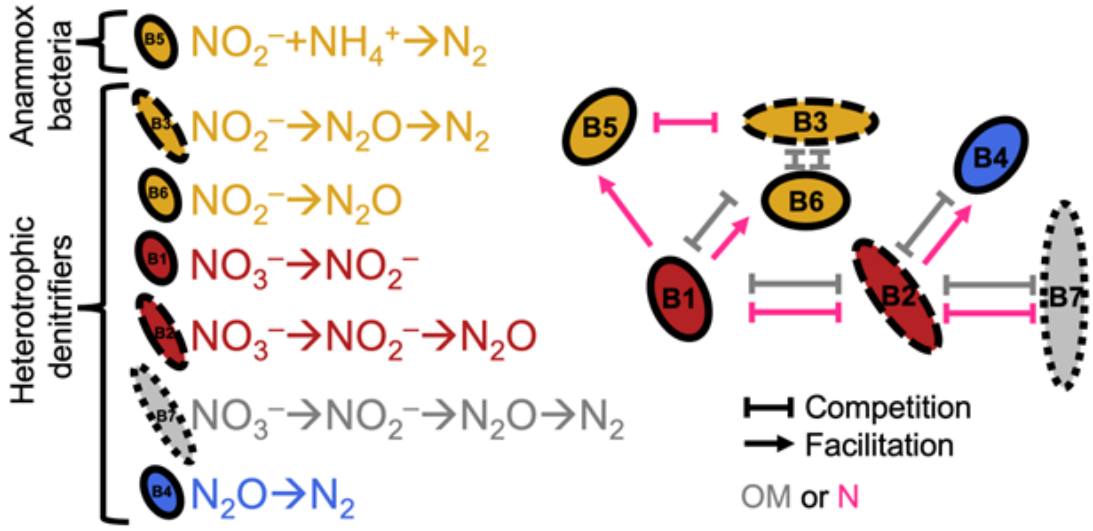


Figure 1. Microbial functional groups labels in the model and their interactions.

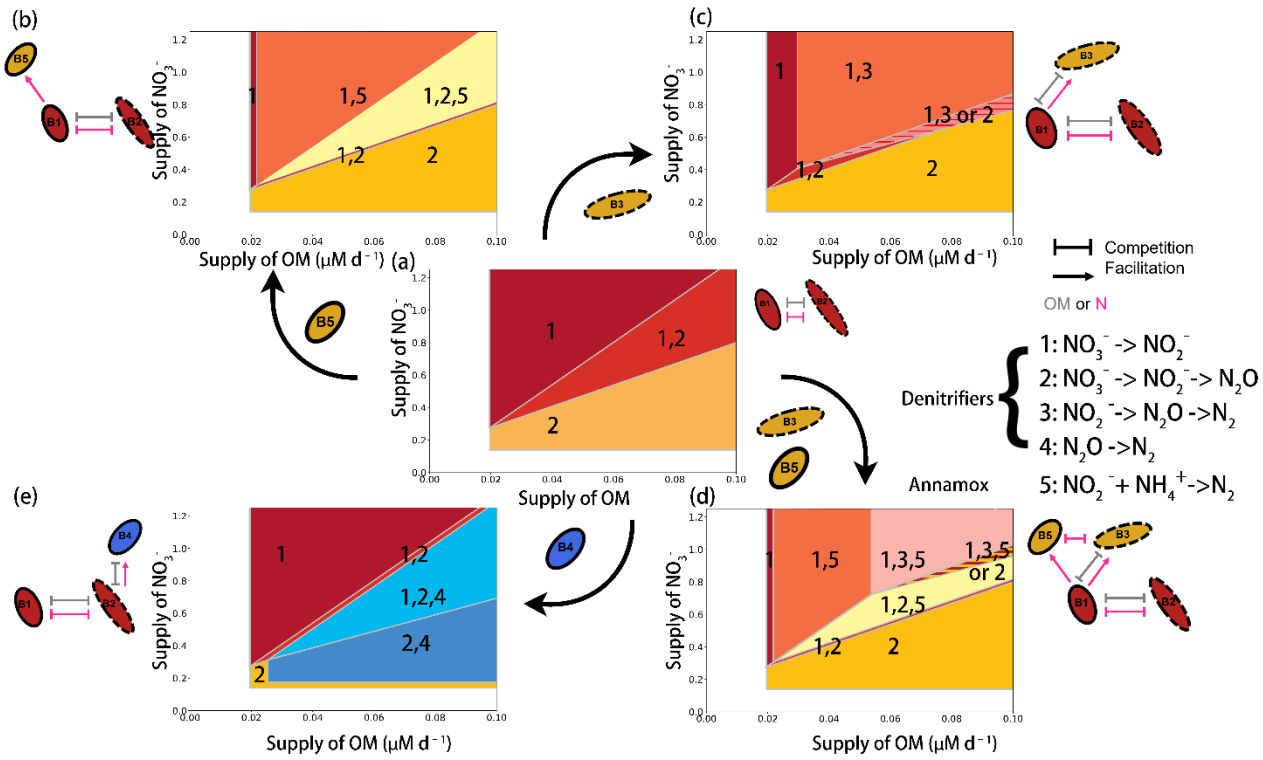


Figure 2. The competitive outcome is determined by the supply rates of OM and NO_3^- in the supply space of the baseline system (a, the center plot) and other subsystems (b-e, the surrounding plots).

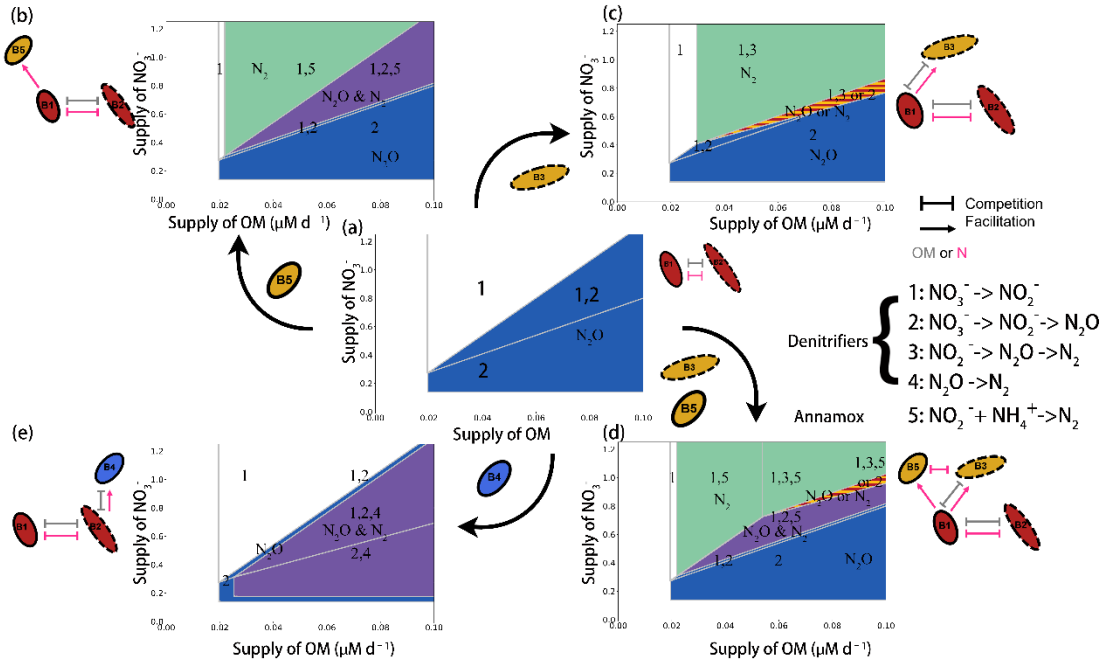
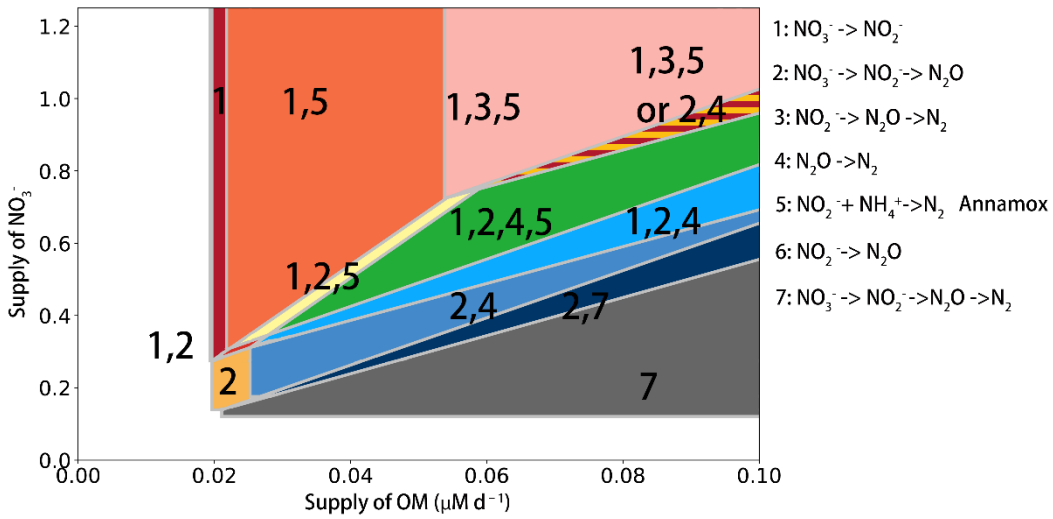


Figure 3. N-loss pathways are determined by the supply rates of OM and NO_3^- in the supply space of the baseline system (a, the center plot) and other subsystems (b-e, the surrounding plots).

(a)



(b)

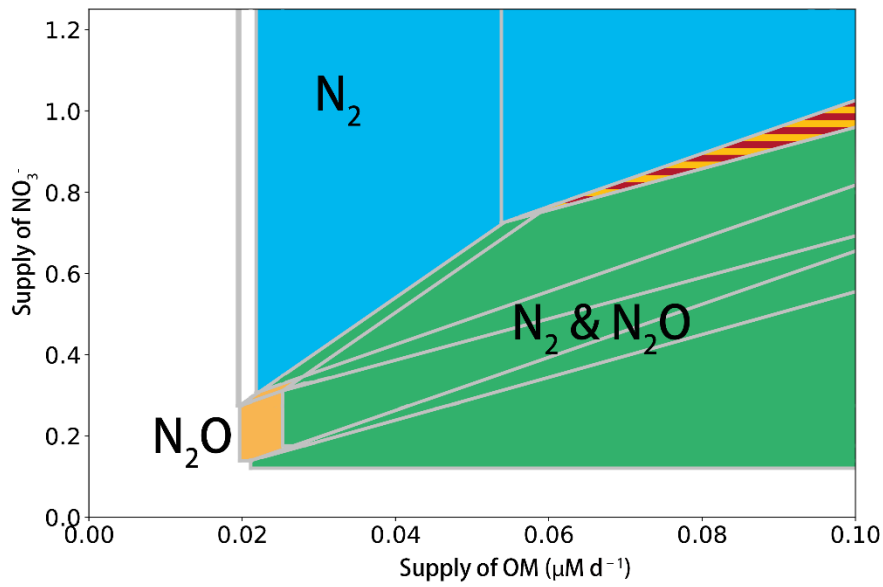


Figure 4. Graphic analysis of functional group coexistence patterns (a) and N-loss pathways (b) in the full system, along with the corresponding N-loss area. The N-loss pathways indicate the form of nitrogen removed from the system: either as N_2 or N_2O. When both N_2 and N_2O are present, this reflects a steady state in which N_2O is consumed as rapidly as it is produced, though in natural environments such as the ocean, this creates

an opportunity for N_2O emission.

Microbes	Substrate	Uptake rate V_m (MOL N d^{-1})	Yield rate y_{ij}	Half-saturation rate K_{ij} (μM N)	Max growth rate μ_{ij} (d^{-1})	R^*_{ij}
$B_1: NO_3^- \rightarrow NO_2^-$	R_1: OM	1.377	0.15	0.1	0.206	0.024
$B_1: NO_3^- \rightarrow NO_2^-$	R_2: NO_3^-	50.8	0.011	4	0.582	0.295
$B_2: NO_3^- \rightarrow N_2O$	R_1: OM	1.377	0.148	0.1	0.203	0.0245
$B_2: NO_3^- \rightarrow N_2O$	R_2: NO_3^-	50.8	0.023	4	1.148	0.144
$B_3: NO_2^- \rightarrow N_2$	R_1: OM	1.377	0.197	0.1	0.272	0.0172
$B_3: NO_2^- \rightarrow N_2$	R_3: NO_2^-	50.8	0.024	4	1.196	0.138
$B_4: N_2O \rightarrow N_2$	R_1: OM	1.377	0.298	0.1	0.41	0.0108
$B_4: N_2O \rightarrow N_2$	R_4: N_2O	50.8	0.013	0.6	0.653	0.039
$B_5: ANAMMOX$	R_5: NH_4^+	50.8	0.013	0.45	0.677	0.028
$B_5: ANAMMOX$	R_3: NO_2^-	50.8	0.011	0.45	0.571	0.034
$B_6: NO_2^- \rightarrow N_2O$	R_1: OM	1.377	0.201	0.1	0.277	0.0169
$B_6: NO_2^- \rightarrow N_2O$	R_3: NO_2^-	50.8	0.016	4	0.815	0.2066
$B_7: NO_3^- \rightarrow N_2$	R_1: OM	1.377	0.138	0.1	0.189	0.0268
$B_7: NO_3^- \rightarrow N_2$	R_2: NO_3^-	50.8	0.026	4	1.326	0.124

Table 1: Physiology traits values used in the model.