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# Ideas and perspectives: Nitrite turnover controls nitrogen fate across redox gradients

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## Abstract

Reactive nitrogen fate in natural systems remains difficult to predict because pathway partitioning occurs at the stage of nitrite turnover, where rapid and tightly coupled production and consumption processes obscure the underlying fluxes. Concentration-based assessments emphasize the dominant pools — nitrate and ammonium — and pathway divergence is determined at the stage of nitrite turnover, independently of pool size. Nitrite is the only inorganic nitrogen species produced under both oxidative and reductive regimes and the obligatory precursor to all downstream dissolved and gaseous products. Because nitrite rarely accumulates, it has often been treated as a transient intermediate of limited interpretive value. This apparent invisibility reflects rapid, tightly coupled turnover and does not indicate functional insignificance. Nitrogen retention, recycling and atmospheric loss are resolved at the stage of nitrite turnover, where competing pathways partition fluxes under kinetic and environmental constraints.

Observed concentrations integrate formation and consumption into a net signal that masks opposing fluxes when internal cycling is rapid. Coupled $\delta^{15}N$–$\delta^{18}O$ measurements of nitrite constrain simultaneous production and consumption and differentiate biological from abiotic pathways. Partial oxygen isotope exchange with water increases the diagnostic primacy of $\delta^{15}N$ in resolving hidden turnover. Centering nitrogen-cycle interpretation on nitrite dynamics and isotopic expression across redox gradients from oxic soils to oxygen minimum zones, provides a mechanistic basis for predicting nitrogen budgets, $N_2O$ emissions, and ecosystem sensitivity to increasing redox variability under climate change and land-use intensification.

## Introduction

The nitrogen cycle regulates ecosystem productivity, water quality and climate. Anthropogenic perturbations have profoundly altered nitrogen fluxes across terrestrial and aquatic systems, leading to nitrate ($NO_3^-$) contamination, eutrophication, and enhanced emissions of nitrous oxide ($N_2O$), a potent greenhouse gas and ozone-depleting substance (Vitousek et al., 1997; Galloway et al., 2004; Gruber & Galloway, 2008). Uncertainty persists regarding the mechanisms that determine whether reactive nitrogen is retained within ecosystems or transferred to the atmosphere.

Conceptual representations of the nitrogen cycle have traditionally emphasized stable pools — ammonium ($NH_4^+$) and nitrate ($NO_3^-$) — providing a coherent basis for large-scale budget analyses (Canfield et al., 2010). However, the location within the reaction sequence at which pathway divergence is determined remains unresolved.

In reaction networks governed by rapid kinetics and tight coupling, the apparent invisibility of intermediates reflects rapid turnover rather than limited functional relevance. Nitrite ($NO_2^-$) exemplifies this conceptual blind spot. Described as an ephemeral intermediate that does not accumulate under steady-state conditions (Heil et al., 2016; Wrage et al., 2001), it is often omitted from conceptual frameworks or treated implicitly. This assumption is not consistent with the structure of the nitrogen cycle reaction network.

Nitrite is the only inorganic nitrogen species produced by both oxidative and reductive processes, and the obligatory substrate for all downstream transformations: denitrification, dissimilatory nitrate reduction to ammonium (DNRA), nitrifier-denitrification, anammox and chemodenitrification (Burgin & Hamilton, 2007; Lam & Kuypers, 2011; Kraft et al., 2014). No other inorganic nitrogen compound combines this dual role of convergence and divergence.

The fate of nitrogen at this junction is governed by the balance between nitrite-producing and nitrite-consuming processes under specific redox, kinetic and environmental constraints (Firestone & Davidson, 1989).

Current diagnostics rely on concentration measurements of nitrate, ammonium and gaseous products. These metrics integrate multiple processes, masking mechanistic controls on pathway partitioning: similar nitrate concentrations can arise from fundamentally different combinations of nitrification, denitrification and DNRA, leading to divergent outcomes in nitrogen retention and $N_2O$ emissions. A framework centered on nitrite would target the step at which these pathways converge and diverge.

Stable isotope measurements provide direct constraints on these hidden dynamics. Nitrite integrates oxidative and reductive fluxes; its isotopic composition records concurrent production and consumption even when net concentrations remain unchanged. Recent methodological advances permit direct determination of natural-abundance $\delta^{15}N$ and $\delta^{18}O$ in nitrite (McIlvin & Altabet, 2005; Sebilo et al., 2019). Oxygen isotopes are partially modified by exchange with water, increasing the diagnostic importance of δ¹⁵N.

Resolving nitrogen fate requires shifting analytical focus from accumulated pools to the intermediate at which pathway divergence is decided. The reaction network structure, kinetics of nitrite turnover, and stable isotope constraints together provide a mechanistic basis for predicting nitrogen budgets and $N_2O$ emissions, a basis accessible only when nitrite is treated as a control point rather than a transient residual.

## Nitrite as the structural branching node

The central role of nitrite emerges directly from the reaction network architecture (Fig. 1). Nitrite does not constitute a regulatory control point in a biochemical sense, but rather the reaction network node at which pathway partitioning is resolved. Under oxic conditions, nitrite is produced during ammonium oxidation by ammonia-oxidizing bacteria and archaea and subsequently oxidized to nitrate, or diverted into alternative pathways depending on oxygen availability and enzyme kinetics (Casciotti, 2016). In comammox organisms, both oxidation steps occur within a single metabolic framework (Daims et al., 2015; van Kessel et al., 2015), further constraining accumulation while maintaining high gross turnover.

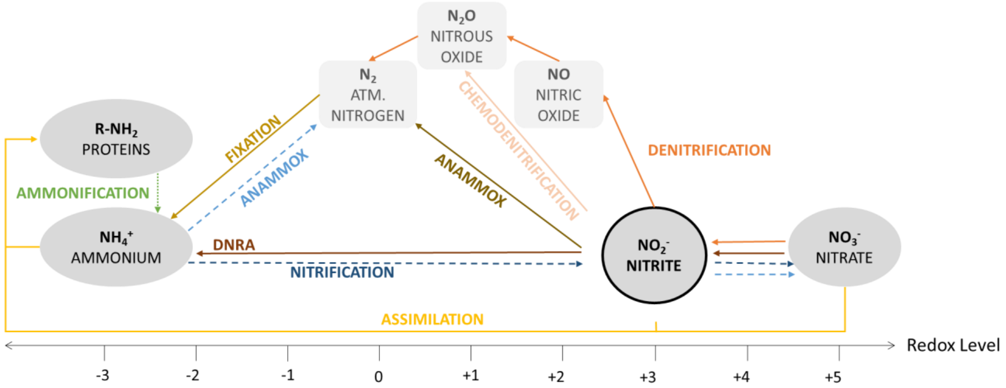

**Figure 1. Nitrite-based nitrogen cycling reactions across redox gradients.**

Under oxygen-limited or anoxic conditions, nitrite is produced during nitrate reduction and partitioned among denitrification, DNRA, anammox, and abiotic reduction. Each pathway channels nitrite toward distinct outcomes, from nitrogen retention to irreversible gaseous loss (Zumft, 1997; Lam & Kuypers, 2011). Abiotic reactions extend this network: reduction of nitrite by ferrous iron generates NO and $N_2O$ independently of enzymatic control, competing with biological pathways (Jones et al., 2015; Grabb et al., 2017; Robinson et al., 2021).

The defining characteristic of this configuration is redistribution, not accumulation. Nitrite operates as a flux junction: its concentration reflects the balance between upstream formation and downstream consumption, while its turnover rate determines the direction and magnitude of nitrogen transfer. In spatially heterogeneous environments, nitrite produced in one microdomain may be consumed in an adjacent zone within short diffusion distances (Firestone & Davidson, 1989). Accumulation arises primarily when this coupling is disrupted by kinetic limitation, redox fluctuation, or imbalance in electron donor and acceptor supply. The fate of reactive nitrogen is determined at the stage where nitrite flux is partitioned among competing biological and abiotic transformations.

## Kinetic control of nitrite turnover and gaseous nitrogen speciation

The direction and magnitude of nitrogen redistribution at the nitrite node depend on the kinetic balance between gross production and gross consumption. When these proceed at comparable rates, net concentration change approaches zero while flux through the intermediate remains substantial; pool size therefore provides limited information about pathway activity (Margalef-Marti et al., 2026).

Residence time at the nitrite stage is determined by the degree of kinetic coupling between sequential reactions. Tight coupling in oxic systems constrains accumulation and shortens residence time; disruption by fluctuating oxygen supply, transport limitation, or electron donor imbalance prolongs residence time and increases the probability of accumulation. Shifts in environmental conditions reorganize flux distribution at the nitrite node even when nitrate or ammonium pools exhibit minimal change.

Gaseous nitrogen production represents the most consequential downstream outcome of nitrite turnover. In biological denitrification, the relative gross rates of successive reductions — from nitrite to NO, $N_2O$, and ultimately $N_2$ — determine the $N_2O$:$N_2$ ratio. Sustained electron supply and active nitrous oxide reductase favour completion of the sequence and $N_2$ dominance; partial decoupling enhances expression of intermediate products, particularly $N_2O$ (Firestone & Davidson, 1989; Zumft, 1997; Lewicka-Szczebak et al., 2020). During oxygen-limited nitrification, nitrite generated from ammonium oxidation may be partially reduced within ammonia oxidizers, producing $N_2O$ under fluctuating oxygen conditions (Wrage et al., 2001).

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Abiotic reduction of nitrite by ferrous iron and reduced mineral phases generates NO and $N_2O$ independently of enzymatic control (Jones et al., 2015; Grabb et al., 2017). Although $N_2O$ is not a primary product of canonical anammox metabolism — hydrazine oxidation yields $N_2$ directly — anammox activity modifies the nitrite pool available to co-occurring denitrifiers and nitrifier-denitrifiers, indirectly shaping $N_2O$ production in mixed-metabolism environments (Kartal et al., 2011). Therefore, the $N_2O$:$N_2$ ratio, and the speciation of nitrogen loss more broadly, is controlled by turnover intensity and kinetic coupling at the nitrite stage rather than by pool size.

**Isotopic constraints on gross nitrite turnover**

Stable isotope measurements provide direct constraints on nitrogen transformations at the stage where flux redistribution occurs: the nitrite node. Isotopic composition responds to gross production and gross consumption rather than to net pool change alone. Constant concentration does not imply constant $\delta^{15}N$: progressive isotopic shifts may occur under steady-state pool conditions, revealing turnover intensity undetectable in concentration data (Fig. 2).

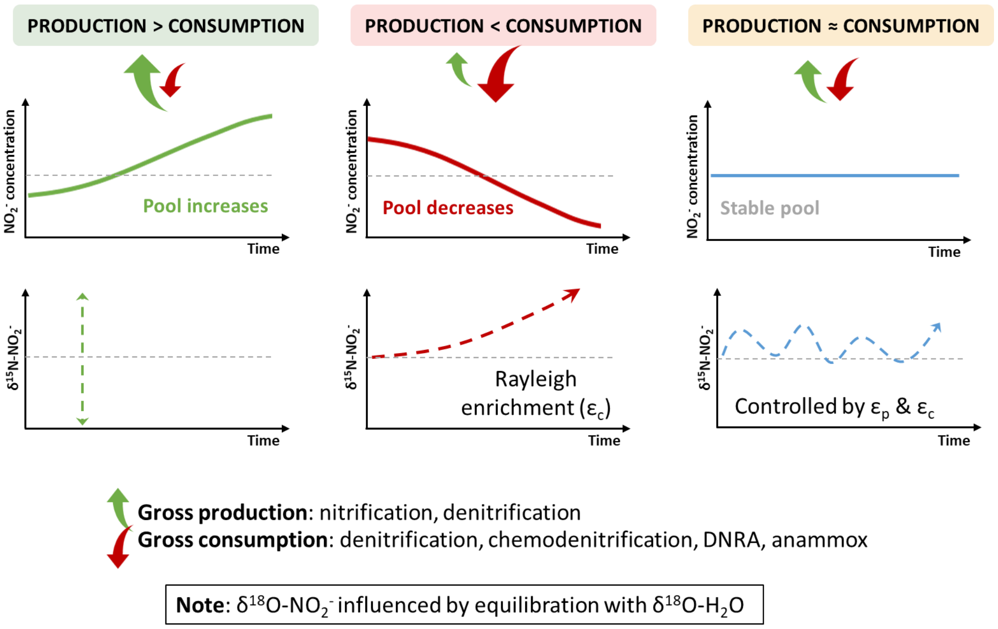

**Figure 2. Isotopic expression of gross nitrite turnover under contrasting production–consumption regimes.** Top panels show nitrite concentration ($[NO_2^-]$) as a function of time, reflecting the net balance between gross production (P) and gross consumption (C): accumulation when P > C, depletion when P < C, and quasi-steady state when P ≈ C despite high internal fluxes. Bottom panels illustrate conceptual trajectories of $\delta^{15}N(NO_2^-)$. In contrast to concentration, isotopic composition responds to gross turnover rather than net change. $\delta^{15}N(NO_2^-)$ evolves according to the isotopic signatures of contributing sources and the combined effects of isotope fractionation during production

(εP) and consumption (εC). The direction of isotopic change is therefore process-dependent and not universal (e.g. inverse isotope effects during nitrite production by nitrification).
When consumption dominates, residual nitrite may become $^{15}$N-enriched if fractionation is expressed, whereas under conditions of balanced production and consumption ($P \approx C$), $\delta^{15}N(NO_2^-)$ may drift despite constant concentration, reflecting ongoing gross turnover. Oxygen isotope signals ($\delta^{18}O$) may be partially overprinted by exchange with water, increasing the diagnostic primacy of $\delta^{15}N$.

Each pathway imposes a characteristic kinetic isotope fractionation. During ammonia oxidation, inverse nitrogen isotope effects may enrich newly formed nitrite relative to its ammonium source (Casciotti et al., 2003; Santoro & Casciotti, 2011). During nitrite oxidation to nitrate, preferential removal of lighter isotopes enriches the residual pool in both $^{15}$N and $^{18}$O (Casciotti, 2009; Buchwald et al., 2012). Reductive pathways generate distinct fractionation patterns associated with nitrite reductase activity (Brunner & Bernasconi, 2005; Casciotti et al., 2010). Abiotic reduction by ferrous iron produces additional nitrogen isotope effects governed by surface-mediated electron transfer (Jones et al., 2015; Grabb et al., 2017). Overlapping fractionation factors across biological and abiotic pathways preclude simple end-member mixing and require integration with environmental and redox context. The direction of $\delta^{15}N\text{-}NO_2^-$ evolution is not universal and depends on the relative contributions of concurrent production and consumption pathways, their associated isotope effects (εP, εC), and the isotopic composition of the source substrate.
Oxygen isotopes introduce an additional dimension. Exchange between nitrite oxygen atoms and ambient water may proceed on timescales comparable to biological turnover (Buchwald & Casciotti, 2010; Casciotti et al., 2010; Granger & Wankel, 2016), attenuating the independence of $\delta^{18}O$ as a pathway tracer. Nitrogen isotopes do not undergo analogous exchange, preserving sensitivity to pathway-specific fractionation. Under conditions of significant oxygen isotope exchange, $\delta^{15}N$ provides the more robust constraint on gross turnover.
Isotopic signatures propagate to gaseous products. The bulk $\delta^{15}N$ of $N_2O$ reflects fractionation associated with nitrite reductases and kinetic coupling among successive reduction steps. Intramolecular $^{15}$N site preference (SP) provides additional mechanistic resolution: because SP is largely independent of the isotopic composition of precursor nitrite, it records enzyme-specific reaction pathways involved in $N_2O$ formation (Brunner & Bernasconi, 2005; Toyoda et al., 2017). Variations in SP discriminate among nitrifier-denitrification, canonical denitrification, and partial reduction sequences downstream of nitrite. Isotopomer signatures must account for subsequent $N_2O$ reduction and mixing, which may overprint primary fractionation signals. Direct determination of natural-abundance $\delta^{15}N$ and $\delta^{18}O$ in nitrite is achievable using azide-based conversion methods which reduce it to $N_2O$ (McIlvin & Altabet,

2005; Sebilo et al., 2019), whereas analytical approaches optimized for nitrate do not independently preserve nitrite information without prior chemical conversion.

### Sensitivity across environmental gradients

Environmental systems differ not in whether nitrite turnover operates, but in how sensitively flux redistribution at the nitrite node responds to perturbation. Sensitivity is highest where oxidative and reductive metabolisms overlap at redox transition zones, and attenuates where reaction coupling is constrained to a single redox regime. Small shifts in oxygen supply, electron donor availability, or hydrological residence time can reorganize pathway partitioning at the nitrite node without producing detectable changes in bulk nitrogen pools. The nitrogen cycle is therefore most vulnerable to mechanistic misinterpretation precisely where nitrite turnover is most intense.

In fully oxic environments, nitrite is produced during ammonia oxidation and rapidly oxidized to nitrate, reflecting tight coupling between nitrification steps (Casciotti, 2016). Redox transition zones — oxic–anoxic interfaces in soils, sediments, riparian zones and stratified water columns — represent the most dynamic settings (Burgin et al., 2011). Simultaneous production from ammonia oxidation and nitrate reduction, combined with kinetically constrained consumption, promotes nitrite accumulation and amplifies sensitivity to environmental change (Buchwald & Casciotti, 2010; Bristow et al., 2016). These zones are recognized as hotspots of $N_2O$ production, consistent with the central role of nitrite in regulating the $N_2O:N_2$ ratio (Butterbach-Bahl et al., 2013; Babbin et al., 2020). In persistently anoxic environments — deep sediments, saturated soils and oxygen minimum zones — nitrite is predominantly generated via nitrate reduction and consumed through denitrification, DNRA or anammox (Zumft, 1997; Lam & Kuypers, 2011; Ward et al., 2009; Dalsgaard et al., 2012; Kalvelage et al., 2013). Hydrological and transport processes further modulate this coupling across all settings: long residence times favor complete turnover, whereas rapid transport can decouple production from consumption, allowing accumulation or downstream export (Sebilo et al., 2006).

### Nitrite as the control point of nitrogen fate

Nitrogen cycling is commonly interpreted through the distribution of dominant inorganic pools. This perspective captures accumulation and export; it does not identify where transformation trajectories are decided. The reaction network places that decision at the stage of nitrite turnover. Environmental conditions regulate this distribution by modulating the rates of nitrite production and consumption.

This reframing resolves several persistent ambiguities. Similar nitrate or ammonium concentrations can arise from fundamentally different internal configurations of production and consumption. $N_2O$ emissions cannot be predicted from pool size alone because their magnitude depends on the completeness of reduction downstream of nitrite. Redox transition zones emerge as hotspots not because they contain larger pools, but because they intensify flux redistribution at this intermediate. A nitrite-centred framework shifts emphasis from storage to flux (Fig. 3), from accumulation to coupling, and from static pools to dynamic turnover, linking microbial metabolism, abiotic reactivity, redox heterogeneity, and atmospheric exchange within a single mechanistic perspective. Because both production and reduction of $N_2O$ depend on nitrite availability and turnover, resolving dynamics at this node provides a direct mechanistic link between microbial processes and climate-relevant gas fluxes.

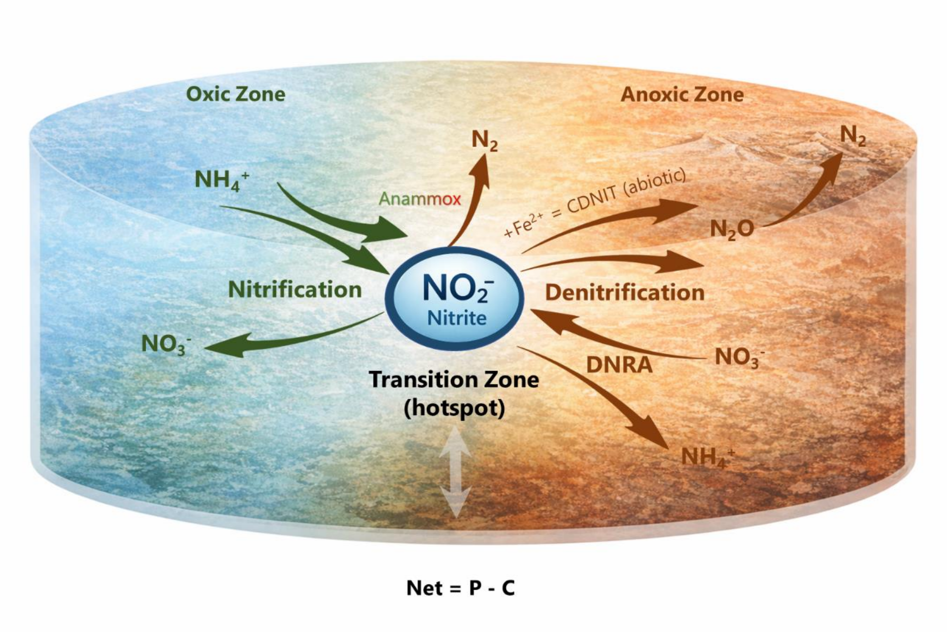

**Figure 3. Conceptual synthesis positioning nitrite turnover as the control point linking redox gradients, gross flux redistribution, isotopic expression, and nitrogen fate.** Nitrite integrates oxidative and reductive processes across environmental gradients. Gross production and gross consumption determine residence time and flux partitioning among retention, recycling, and gaseous loss. The $\delta^{15}N$ of $NO_2^-$ records turnover intensity, whereas the $\delta^{18}O$ may be modified by exchange with water. Isotopic signals propagate to $N_2O$ and inform pathway attribution. Nitrogen fate is therefore governed at the nitrite stage rather than by the size of accumulated nitrate or ammonium pools.

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Concentration reflects net balance between production and consumption. $\delta^{15}N$ records the imprint of concurrent production and consumption even when pool size remains constant. Oxygen isotope exchange constrains interpretation but reinforces the diagnostic primacy of nitrogen isotopes. Incorporating nitrite isotopes converts an otherwise unobservable internal turnover into a measurable quantity.

Translating this framework into practice requires prioritising direct nitrite isotope measurements alongside conventional concentration measurements, particularly in redox-dynamic systems where net fluxes are most ambiguous. Dual $\delta^{15}N$–$\delta^{18}O$ approaches, combined with isotopomer analysis of $N_2O$, offer the most diagnostic power. At the modelling scale, representing nitrite explicitly as a state variable, rather than collapsing nitrification and denitrification into net transformations, would improve mechanistic fidelity in biogeochemical models applied to nitrogen budgets and greenhouse gas inventories. The measurement and modelling strategies that follow from this reorientation are those organised around the node where nitrogen fate is actually decided.

As environmental systems experience increasing redox variability under climate change and land-use intensification, sensitivity at the nitrite stage is likely to amplify. Understanding nitrogen cycling at Earth-system scale requires resolving where and how nitrite flux is redistributed. Without explicit consideration of turnover at this branching node, interpretations of nitrogen budgets, greenhouse gas emissions, and isotopic signals remain incomplete.

## Author contribution

MS and RM jointly conceived the perspective and wrote the manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

## Data and code availability

No new data or code were generated for this study. The perspective is based exclusively on bibliographic sources, all of which are cited in the reference list.

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