I appreciate the effort by the authors to reposition nitrite as a central node governing nitrogen fate across redox gradients. The conceptual framework is interesting and potentially valuable for linking microbial metabolism, isotope dynamics, and nitrogen loss pathways.

That said, I found some sections repetitive and occasionally overly abstract, which made the manuscript difficult to follow at times. Several lines and concepts would benefit from clearer wording and additional explanation, particularly for readers who may be less familiar with isotope systematics or nitrite turnover dynamics. The manuscript would also benefit from incorporating more concrete environmental examples to contextualize better and illustrate the conceptual arguments being made.

A major point that I think deserves stronger discussion is the practical limitation associated with natural-abundance nitrite isotope approaches. Although the manuscript advocates for shifting focus from accumulated pools to nitrite turnover and coupling, these approaches are inherently biased toward environments and transition zones where nitrite accumulates to detectable concentrations. In many natural systems, nitrite concentrations remain below detection despite active nitrogen cycling, owing to extremely rapid turnover and tight coupling between production and consumption processes. As a result, many oxic-anoxic transition zones are spatially narrow, transient, and analytically challenging to resolve. This limitation is important because it constrains where nitrite natural-abundance isotope techniques can realistically be applied. I therefore think the manuscript would benefit from a more explicit discussion of current analytical detection limits, the concentration ranges typically required for robust d15N and d18O measurements of nitrite, and future methodological developments aimed at improving sensitivity toward nanomolar-level nitrite detection and isotope analysis.

We thank Reviewer 2 for the careful and constructive reading of our manuscript. The reviewer raises one major point, the practical limitations of natural-abundance nitrite isotope approaches in environments where nitrite does not accumulate to analytically tractable concentrations, and a series of specific comments on clarity, terminology, and structure. We fully acknowledge the analytical limitation raised and have addressed it explicitly by adding a dedicated paragraph in the concluding section. We have also acted on the large majority of specific comments, reformulating several passages to improve clarity and reduce apparent repetition, adding brief environmental examples, and correcting terminological imprecisions. On one point, the description of nitrite as the "only" inorganic nitrogen species produced under both oxidative and reductive regimes, we maintain our position with a qualification: while nitric oxide (NO) participates in both regimes, it is extremely short-lived in aqueous solution and does not accumulate to measurable concentrations. Nitrite is therefore the only stable dissolved inorganic intermediate fulfilling this dual role, and we have revised the text to make this specificity explicit. Our responses to each comment are detailed below.

Specific comments:

Lines 24–26: “Nitrogen retention, recycling and atmospheric loss are resolved at the stage of nitrite turnover, where competing pathways partition fluxes under kinetic and environmental constraints.” Not sure what the authors are getting at here. The framing feels overly complicated.

We have reworded the sentence to “Nitrogen retention, recycling, and losses to the atmosphere are determined during nitrite turnover, where competing pathways partition fluxes according to kinetic and environmental constraints” to improve clarity (lines 26-27).

Lines 41–42: Another timely study to consider, as it discusses the impact of climate change on denitrification in an aquatic environment: https://doi.org/10.1038/s41564-026-02349-9

We thank the reviewer for drawing our attention to this study. We note that our initial manuscript was submitted on 15 April 2026, prior to the publication of Callbeck et al., on 22 May 2026, which explains its absence from the original version. We have nevertheless incorporated this reference in the revised manuscript (line 44) as it provides a timely illustration of climate-driven impacts on denitrification in aquatic systems.

Lines 55–62: “Nitrite is the only inorganic nitrogen species produced by both oxidative and reductive processes…” I agree that nitrite plays a central role in the nitrogen cycle, but I would suggest being a little cautious with the wording here. Nitric oxide (NO) also participates in both oxidative and reductive branches of the nitrogen cycling, and is an even more reactive and transient intermediate that is often difficult to measure. So while I agree with the overall point being made, describing nitrite as the “only” inorganic nitrogen species linking these processes may be somewhat overstated.

We thank the reviewer for this important observation. Nitric oxide (NO) does indeed participate in both oxidative and reductive branches of the nitrogen cycle. However, NO is extremely short-lived in aqueous solution, with a half-life of seconds in the presence of dissolved oxygen, and does not accumulate to measurable concentrations under environmental conditions. It therefore cannot function as a diagnosable intermediate for natural-abundance isotope approaches. We note that this issue was also raised by Reviewer 1. We have introduced the qualifiers "stable" and "dissolved" to make explicit that the uniqueness of nitrite resides in its being the only dissolved inorganic intermediate that is both stable enough to accumulate and produced under both oxidative and reductive regimes — a combination that NO does not fulfil.

The sentence (lines 57-62) is now “Nitrite is the central stable dissolved intermediate linking oxidative and reductive nitrogen transformations and the obligatory precursor to downstream nitrate, ammonium and gaseous nitrogen products (Burgin & Hamilton, 2007; Lam & Kuypers, 2011; Kraft et al., 2014).” We have also stated “Despite NO also participates in both oxidative and reductive branches of the nitrogen cycle it is extremely short-lived in aqueous solution and does not accumulate to measurable concentrations under environmental conditions.”

Lines 63–64: “Current diagnostics rely on concentration measurements of nitrate, ammonium and gaseous products.” A bit repetitive.

We agree that this sentence was partly redundant with the preceding argument. We have merged it with the following sentence and added a brief environmental example to ground the argument concretely, addressing both this comment and the reviewer's request for illustration at lines 67-71.

The new sentence is: “Concentration measurements of nitrate, ammonium and gaseous products integrate multiple processes, masking mechanistic controls on pathway partitioning: similar nitrate concentrations can arise from fundamentally different combinations of nitrification, denitrification and DNRA (e.g. in riparian zones where both processes operate simultaneously), leading to divergent outcomes in nitrogen retention and N_2O emissions.”

Line 64: “metrics” Did you mean nutrients? Not sure what is meant by metrics?

Lines 64–67: “These metrics integrate multiple processes, masking mechanistic controls on pathway partitioning…” The sentence is a bit vague. Could the authors provide more clarity by illustrating an environmental example?

We agree that "metrics" was ambiguous and that the sentence was partly redundant with the preceding argument. We have rewritten the paragraph, replacing "metrics" with an explicit reference to "concentration measurements", and have added a brief environmental example (riparian zones with simultaneous nitrification and denitrification) to illustrate how similar nitrate pool sizes can arise from fundamentally different internal process configurations, addressing both comments simultaneously (lines 67-71).

Lines 70–71: “its isotopic composition records concurrent production and consumption…” To provide a bit of pushback here, it is precisely because nitrite is simultaneously produced and consumed that analyzing nitrite using natural abundance isotopes becomes very complicated. This may be worth acknowledging in this passage.

The simultaneous occurrence of production and consumption does indeed complicate isotopic interpretation. This complexity is precisely what motivates the dual $\delta^{15}N$–$\delta^{18}O$

framework developed in the dedicated section. We have added a brief acknowledgement of this interpretative challenge at this location and directed the reader to the relevant section (line 76).

Lines 71–72: “Recent methodological advances…” Is it still appropriate to describe this as “recent” if the method was reported in 2005?

We agree that describing a 2005 method as "recent" is no longer appropriate. We have replaced "recent methodological advances" with "available methods", which better reflects the current state of the field while retaining the references to the original and most recent analytical developments (line 76).

Lines 73–74: “Oxygen isotopes are partially modified by exchange with water, increasing the diagnostic importance of d15N.” For the uninitiated reader, this likely requires further explanation.

We have expanded this sentence to briefly explain the mechanism of oxygen isotope exchange for readers less familiar with isotope systematics. The full treatment of this phenomenon is provided in the Isotopic constraints section.

The sentence is now: “Oxygen isotopes of nitrite are partially reset due to equilibrium with oxygen isotopes of ambient water, modifying the primary biological signal.” Lines 79-80.

Lines 78–79: “a basis accessible only when nitrite is treated as a control point rather than a transient residual.” Not sure what the authors mean by treating nitrite as a “control point.” This needs additional elaboration.

We have modified the sentence for clarification “This basis relies on considering nitrite as a central component of the nitrogen cycle rather than a transient residual.”. Lines 84-85.

Line 103: “outcomes” Perhaps “end points” would be clearer?

We agree that "outcomes" was insufficiently precise in this context. We have replaced it with "fates", which better reflects the biogeochemical framing of the manuscript. Line 111.

Line 107: “this configuration is redistribution, not accumulation.” This is a bit vague. Also, what exactly is meant by “this configuration”?

Line 108: “flux junction” This term could benefit from further clarification.

Lines 108–109: Nitrite operates as a flux junction: its concentration reflects the balance between upstream formation and downstream consumption. It's a bit repetitive.

We have clarified the antecedent of "this configuration" by replacing it with "this convergence–divergence architecture", referring explicitly to the dual role of nitrite described in the preceding paragraph. We have also expanded the definition of "flux junction" inline to make the term self-explanatory for readers less familiar with reaction network terminology. Lines 115-117.

Lines 109–115: A lot of this comes across as repetitive and reiterates the same concepts multiple times.

We have addressed the apparent repetition in two ways. First, we removed the closing sentence of the "Branching node" section ("The fate of reactive nitrogen is determined at the stage where nitrite flux is partitioned among competing biological and abiotic transformations"), which reiterated points already made. Second, we added a transitional sentence at the opening of the "Kinetic control" section to make explicit the logical progression from the structural argument (nitrite as the reaction network node) to the kinetic argument developed in this section (gross production and consumption rates as the determinants of flux direction and magnitude). The two sections address different levels of analysis — structural and kinetic — and we hope this transition now makes that distinction clear. Lines 123-128.

Lines 118–122: “The direction and magnitude of nitrogen redistribution…” Again, this feels like the same concept discussed above.

This comment is addressed by the transitional sentence added at the opening of the "Kinetic control" section in response to the preceding comment. The apparent repetition reflects the absence of an explicit link between the structural argument of the "Branching node" section and the kinetic argument developed here. We believe the added transition now clarifies that these two sections operate at different levels of analysis.

Lines 123–128: “Residence time at the nitrite stage…” Could the authors point to a concrete environmental example of this?

We have modified the sentence to “Accumulation and persistence along time of nitrite”, for clarification. We have also included “see Sensitivity across environmental gradients section”, because examples are provided there. Line 136.

Line 129: “Gaseous nitrogen production…” I would suggest explicitly stating the two gases being discussed upfront — i.e., dinitrogen (N2) and nitrous oxide (N2O).

We have explicitly stated the gases. Line 143.

Line 129: “the most” I do not fully understand why this is framed as “the most” important aspect of nitrite turnover. Perhaps the authors mean from a biogeochemical perspective. From an environmental perspective, nitrite oxidation to nitrate — thereby sustaining denitrification pathways — is also critically important. I would suggest dropping “the most.”

We agree that framing gaseous nitrogen production as "the most consequential" outcome is an overstatement — nitrite oxidation back to nitrate, which sustains nitrification and fuels further denitrification, is equally important from a biogeochemical standpoint. We have replaced "the most consequential" with "a relevant" to reflect this more balanced view. Line 143.

Line 130: “biological” I might refer to these processes as “microbial” rather than “biological.”

We have replaced "biological" with "microbial" as suggested. Line 144.

Line 132: “electron supply” Could you be a bit more specific?

We have specified "organic donor supply (such as organic matter)" in place of the more generic "electron supply" to improve precision, as organic carbon is the primary electron donor driving complete denitrification to N_2 in most environmental settings. Lines 145-146.

Line 132: “completion of the sequence and” Could be worded to favor complete nitrate reduction to N2.

We respectfully note that the current phrasing already conveys this meaning. "Completion of the sequence" refers explicitly to the stepwise reduction from nitrite through NO and N_2O to N_2, and "N_2 dominance" directly expresses the outcome the reviewer requests. We have retained this formulation as it captures both the mechanistic process (sequential reduction) and its biogeochemical outcome (N_2 as the dominant product) more precisely than a simpler reference to "complete nitrate reduction to N_2" would.

Lines 140–142: “indirectly shaping N2O production in mixed-metabolism environments…” Anammox also directly contributes to N2 production using nitrite, which would also fit into the importance of nitrite. The connection of anammox to nitrite and linking this to N2O is a bit of a stretch. Why not connect anammox to nitrogen loss via N2 production?

We thank the reviewer for this correction. We agree that the primary biogeochemical significance of anammox at the nitrite node is its competition with denitrifiers for nitrite, which directly governs the partitioning between N_2 and N_2O production. We have reformulated this sentence to place this competition at the center, while retaining the implication for N_2O in mixed-metabolism environments. Lines 155-158.

Line 142: “the speciation” Not sure I understand this, might need rewording

We have replaced "the speciation of nitrogen loss" with "the relative production of N_2 versus N_2O" for clarity. Line 158.

Line 147: “Stable isotope measurements…” Perhaps specify “stable isotope measurements of nitrite” for clarity.

We have added "of nitrite" to avoid any ambiguity about which isotope measurements are being referred to at the opening of this section. Line 163.

Lines 209-211: Might be worth specifically referring to the oxic-anoxic transition zones.

We have specified "oxic-anoxic transition zones" in place of the more generic "redox transition zones" as suggested. Line 233.

Lines 212-213: “In fully oxic environments, nitrite is produced during ammonia oxidation and rapidly oxidized to nitrate, reflecting tight coupling between nitrification steps (Casciotti, 2016).” I think an important practical limitation should be acknowledged here. In many fully oxic environments, nitrite turnover is so rapid that nitrite concentrations may remain below detection or at levels insufficient for natural-abundance isotope analyses. For example, in stratified water column systems, we often observe elevated nitrate concentrations alongside undetectable nitrite, despite clear evidence for active ammonium oxidation based on 15NH4+ tracer-rate experiments and metagenomic data. Thus, the absence of measurable nitrite does not imply the absence of nitrification activity. This highlights one of the major challenges of using natural-abundance nitrite isotopes to assess nitrogen cycling: the approach is only feasible when sufficient nitrite accumulates for analysis, which often restricts applications to narrow oxic–anoxic transition zones where nitrite transiently accumulates. It may therefore be helpful for the review to discuss the current analytical limits for natural-abundance nitrite isotope measurements. What nitrite concentrations are presently required for robust d15N and d18O analyses, and what represents the current cutting edge in analytical sensitivity? More broadly, it would be interesting to discuss whether the field is moving toward the ability to quantify nitrite isotopes at nanomolar concentrations, analogous to recent advances enabling oxygen measurements at picomolar levels. Without such advances, natural-abundance NO2- isotope approaches may remain restricted to relatively localized environments with

micromolar nitrite accumulation, which can be spatially and temporally very constrained.

Lines 218-220: “2016). These zones are recognized as hotspots of N2O production, consistent with the central role of nitrite in regulating the N2O:N2 ratio (Butterbach-Bahl et al., 2013; Babbin et al., 2020).” One challenge worth acknowledging here is that many environmental hotspots of N2O and N2 production occur under conditions where nitrite itself remains below detection. In such systems, strong nitrogen turnover may clearly be occurring, yet the direct application of natural-abundance nitrite isotope approaches becomes extremely difficult or even impossible. This limitation is fundamentally tied to analytical sensitivity at multiple stages: first, the chemical detection of nitrite itself; second, the efficiency and sensitivity of converting NO2- to an analyzable gas species (e.g., N2O or N2, depending on the analytical approach); and finally, the detection limits and precision of the isotope ratio mass spectrometer. As a result, although nitrite may mechanistically regulate these processes, the practical ability to use nitrite natural-abundance isotopes as a tracer is often restricted to environments where nitrite transiently accumulates to sufficiently high concentrations for robust analysis.

Line 241: “from accumulation to coupling…” As mentioned above, an important practical limitation is that natural-abundance nitrite isotope approaches are inherently biased toward environments and transition zones where nitrite accumulates to detectable concentrations. In many systems, these zones are spatially narrow, transient, or characterized by NO2- concentrations below analytical detection limits despite active nitrogen cycling. This analytical constraint may be worth acknowledging more explicitly when advocating for a shift from accumulation-based to coupling-based interpretations of nitrogen cycling.

We thank the reviewer for raising this important practical limitation, which is indeed central to an honest appraisal of the framework we advocate. We fully agree that natural-abundance nitrite isotope approaches are currently constrained to environments where nitrite accumulates to analytically tractable concentrations, and that many oxic-anoxic transition zones, precisely the settings where nitrite turnover is most intense, are spatially narrow, transient, and often characterized by nitrite concentrations below current detection limits. We have addressed this limitation explicitly by adding a dedicated paragraph in the Isotopes section (and briefly in the concluding section). We believe that acknowledging these constraints directly, rather than dispersing brief caveats across multiple sections, provides a more coherent and honest treatment of the gap between the conceptual framework and its current analytical reach.

The paragraph added in the Isotopes section (lines 214-227): “Despite their strong mechanistic potential, nitrite isotope measurements are only feasible when sufficient nitrite accumulates for analysis and remain analytically challenging. Nitrite is chemically unstable and may undergo rapid oxidation or reduction during sampling and storage, potentially altering its isotopic composition before analysis. Reliable

preservation therefore requires rapid processing and carefully controlled storage conditions, often under alkaline conditions that minimize transformation rates. In many terrestrial and aquatic systems, low nitrite concentrations restrict isotope analyses to zones where nitrite transiently accumulates. This emphasizes the need for continued development of high-sensitivity analytical approaches (Lewicka-Szczebak et al., 2021; Deb and Lewicka-Szczebak, 2025). For instance, a recent study developed a method for freshwater samples by coupling anion-exchange resin preconcentration with the azide reduction method for nitrite isotopic characterization at concentrations of 0.02 μmol L^{-1} or higher (Jiang et al., 2026). These analytical limitations likely contribute to the still limited application of nitrite isotope measurements in environmental studies despite their considerable interpretative potential."

The paragraph added in the concluding section (Lines 298-302): "Although nitrite isotope measurements offer strong mechanistic insight, their application is constrained by low concentrations and analytical challenges. Recent advances in high-sensitivity methods are expanding their feasibility in natural systems. Nonetheless, these limitations continue to restrict their widespread use in environmental studies".

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 losses to the atmosphere are determined during nitrite turnover, where competing pathways partition fluxes according to 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; Callbeck et al., 2026). 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 central stable dissolved intermediate linking oxidative and reductive nitrogen transformations and the obligatory precursor to downstream nitrate, ammonium and gaseous nitrogen products (Burgin & Hamilton, 2007; Lam & Kuypers, 2011; Kraft et al., 2014). Despite NO also participates in both oxidative and reductive branches of the nitrogen cycle it is extremely short-lived in aqueous solution and does not accumulate to measurable concentrations under environmental conditions. 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; Denk et al., 2017; Deb et al., 2024).

Concentration measurements of nitrate, ammonium and gaseous products integrate multiple processes, masking mechanistic controls on pathway partitioning: similar nitrate concentrations can arise from fundamentally different combinations of nitrification, denitrification and DNRA (e.g. in riparian zones where both processes operate simultaneously), leading to divergent outcomes in nitrogen retention and N_2O emissions.

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, though disentangling these overlapping signals requires the dual $\delta^{15}N$–$\delta^{18}O$ approach described in

detail in the Isotopic constraints section below. Available methods advances permit direct determination of natural-abundance $\delta^{15}N$ and $\delta^{18}O$ in nitrite (McIlvin & Altabet, 2005; Sebilo et al., 2019; Deb & Lewicka-Szczebak, 2025; Hu et al., 2026). Oxygen isotopes of nitrite are partially reset due to equilibrium with oxygen isotopes of ambient water, modifying the primary biological signal and thereby increasing the diagnostic importance of $\delta^{15}N$.

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. This basis relies on considering nitrite as a central component of the nitrogen cycle 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.

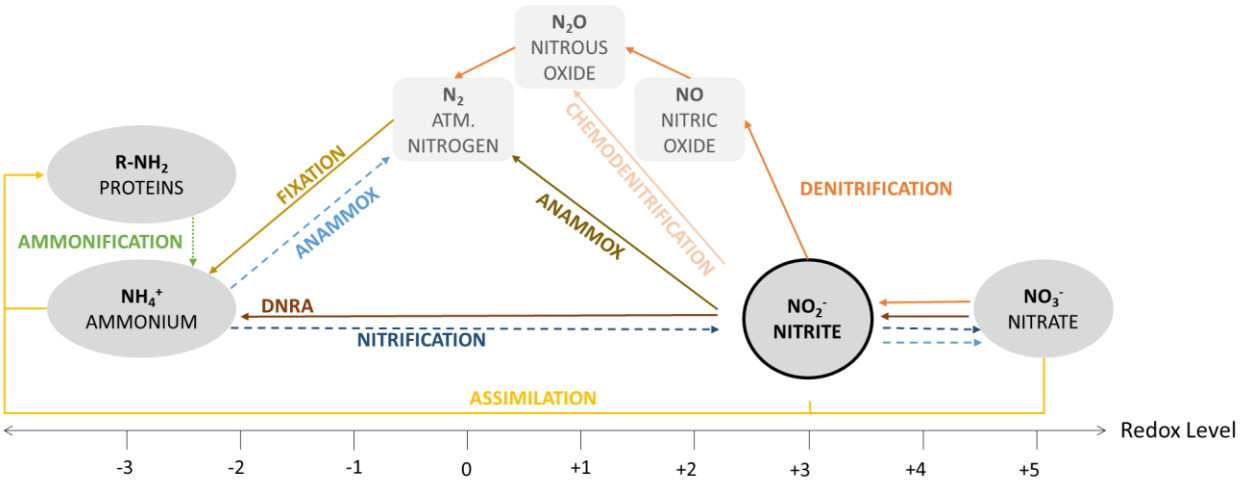

Figure 1. Nitrite-based nitrogen cycling reactions across redox gradients. Oxidative pathways are presented in blue arrows, reductive ones in orange/brown and those involving organic matter in yellow/green. To simplify the scheme, hydroxylamine has not been included in the figure. Hydroxylamine is also involved in oxidative and reductive pathways. It can be produced during ammonia oxidation and nitrite reduction. It is primarily oxidized by nitrifying microorganisms to nitrite, with minor

side production of nitric oxide and nitrous oxide, and it can be reduced to ammonium. However, it is highly reactive, it is usually rapidly oxidized before accumulating in the environment, limiting its influence at the ecosystem scale.

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 fates, 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 convergence-divergence architecture is redistribution, not accumulation. Nitrite operates as a flux junction, a node at which inputs from multiple upstream pathways are portioned among competing downstream transformations, so that 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.

Kinetic control of nitrite turnover and gaseous nitrogen speciation

If the structural position of nitrite determines where pathway divergence occurs, the kinetic balance between gross production and gross consumption determines how. 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). Such tightly coupled nitrite turnover has recently been observed in nitrate-rich groundwater systems using combined isotope and microbial approaches (Deb et al., 2025).

Accumulation and persistence along time of nitrite 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 (see Sensitivity across environmental gradients section). Shifts in

environmental conditions reorganize flux distribution at the nitrite node even when nitrate or ammonium pools exhibit minimal change.

Gaseous nitrogen (i.e., NO, N_2O and N_2) production represents a relevant downstream outcome of nitrite turnover. In microbial 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 donor supply (such as organic matter) 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). 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 competes with denitrifiers for the available nitrite pool, thereby influencing the partitioning of nitrite between N_2-producing and N_2O-producing pathways in mixed-metabolism environments (Kartal et al., 2011). Therefore, the N_2O:N_2 ratio, and the relative production of N_2 versus N_2O 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 of nitrite 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).

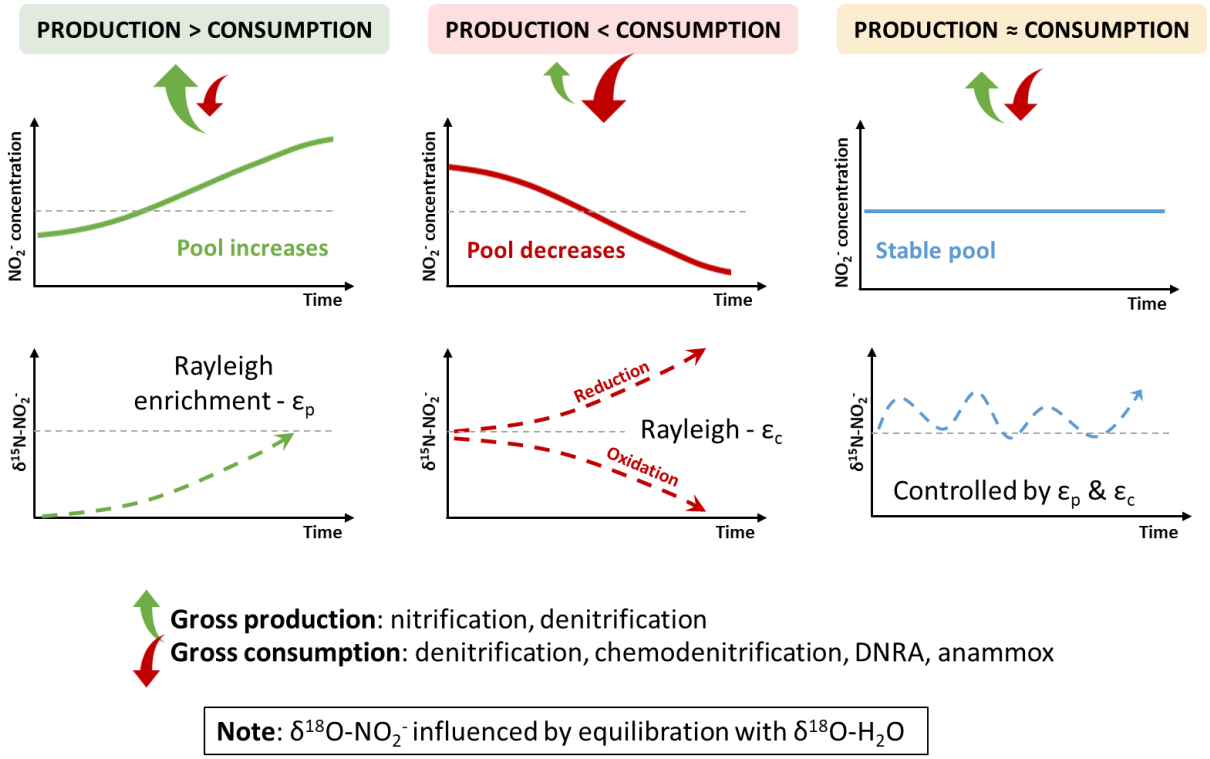

Figure 2. Isotopic expression of gross nitrite turnover under contrasting production–consumption regimes. Top panels show nitrite concentration ([NO_2^-]) as a function of time, reflecting the net balance between gross production (P) and gross consumption (C): accumulation when P > C, depletion when 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). Under conditions of balanced production and consumption (P ≈ 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.

Despite their strong mechanistic potential, nitrite isotope measurements are only feasible when sufficient nitrite accumulates for analysis and remain analytically challenging. Nitrite is chemically unstable and may undergo rapid oxidation or reduction during sampling and storage, potentially altering its isotopic composition before analysis. Reliable preservation therefore requires rapid processing and carefully controlled storage conditions, often under alkaline conditions that minimize transformation rates. In many terrestrial and aquatic systems, low nitrite concentrations restrict isotope analyses to zones where nitrite transiently accumulates. This emphasizes the need for continued development of high-sensitivity analytical approaches (Lewicka-Szczebak et al., 2021; Deb and Lewicka-Szczebak, 2025). For instance, a recent study developed a method for freshwater samples by coupling anion-exchange resin preconcentration with the azide reduction method for nitrite isotopic characterization at concentrations of 0.02 μmol L^{-1} or higher (Jiang et al., 2026). These analytical limitations likely contribute to the still limited application of nitrite isotope measurements in environmental studies despite their considerable interpretative potential.

Isotopic signatures of nitrite 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 (Toyoda et al., 2017; Lewicka-Szczebak et al., 2020).

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 oxic-anoxic 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; Denk et al., 2017; Deb et al., 2024). 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.

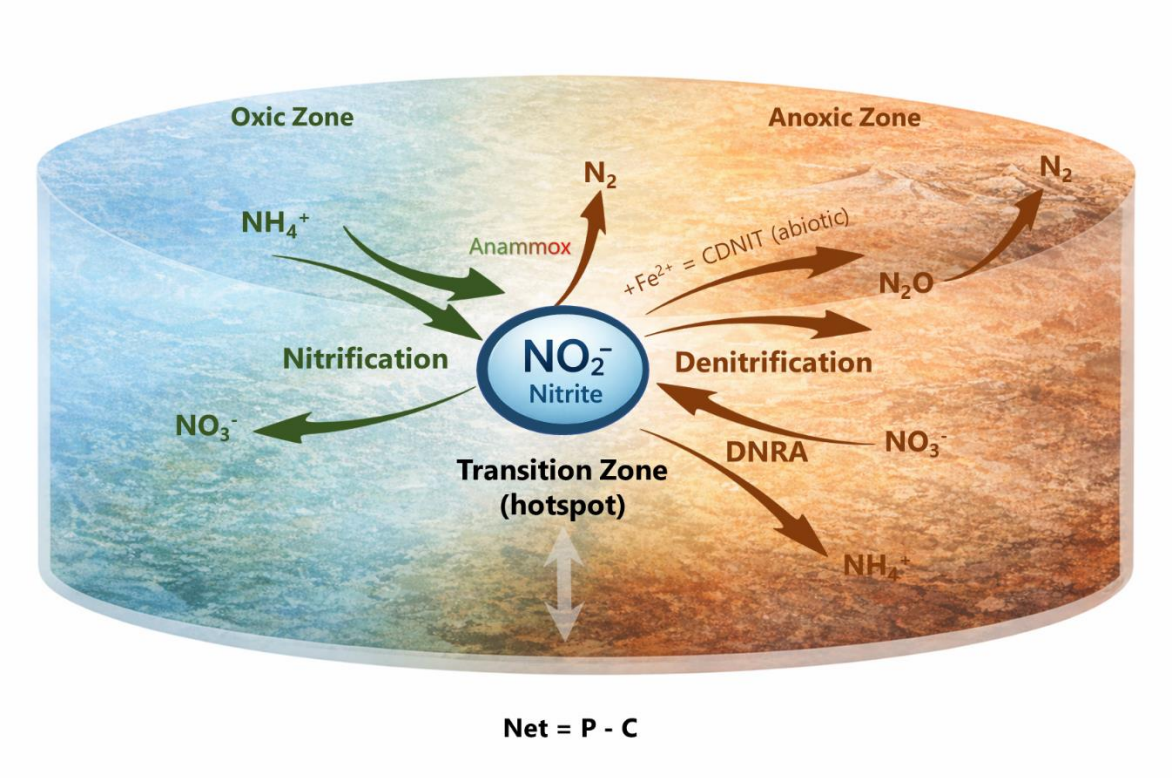

Figure 3. Conceptual synthesis positioning nitrite turnover as the control point linking redox gradients, gross flux redistribution, isotopic expression, and nitrogen fate. Nitrite integrates oxidative and reductive processes across environmental gradients. Gross production and gross consumption determine 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.

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. At the same time, the extent of oxygen exchange with water may provide information on nitrite residence times and the relative rates of biological turnover versus abiotic exchange (Buchwald and Casciotti, 2013; Lewicka-Szczebak et al., 2021). 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. Although nitrite isotope measurements offer strong mechanistic insight, their application is constrained by low concentrations and analytical challenges. Recent advances in high-sensitivity methods are expanding their feasibility in natural systems. Nonetheless, these limitations continue to restrict their widespread use in environmental studies.

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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