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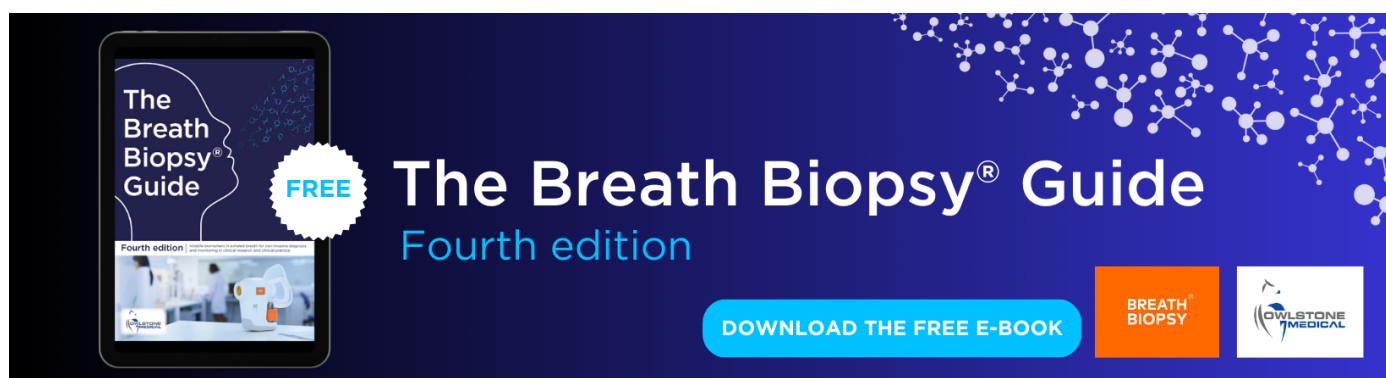
# Potential nitrogen mobilisation from the Yedoma permafrost domain

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# ENVIRONMENTAL RESEARCH
## LETTERS

**TOPICAL REVIEW**

# Potential nitrogen mobilisation from the Yedoma permafrost domain

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## Abstract

Permafrost regions, characterised by extensive belowground excess ice, are highly vulnerable to rapid thaw, particularly in areas such as the Yedoma domain. This region is known to freeze-lock a globally significant stock of soil nitrogen (N). However, the fate of this N upon permafrost thaw remains largely unknown. In this study, we assess the impact of climate warming on the size and dynamics of the soil N pool in (sub-)Arctic ecosystems, drawing upon recently published data and literature. Our findings suggest that climate warming and increased thaw depths will result in an expansion of the reactive soil N pool due to the larger volume of (seasonally) thawed soil. Dissolved organic N emerges as the predominant N form for rapid cycling within (sub-)Arctic ecosystems. The fate of newly thawed N from permafrost is primarily influenced by plant uptake, microbial immobilisation, changes in decomposition rates due to improved N availability, as well as lateral flow. The Yedoma domain contains substantial N pools, and the partial but increasing thaw of this previously frozen N has the potential to amplify climate feedbacks through additional nitrous oxide ($N_2O$) emissions. Our ballpark estimate indicates that the Yedoma domain may contribute approximately 6% of the global annual rate of $N_2O$ emissions from soils under natural vegetation. However, the released soil N could also mitigate climate feedbacks by promoting enhanced vegetation carbon uptake. The likelihood and rate of $N_2O$ production are highest in permafrost thaw sites with intermediate moisture content and disturbed vegetation, but accurately predicting future landscape and hydrology changes in the Yedoma domain remains challenging. Nevertheless, it is evident that the permafrost-climate feedback will be significantly influenced by the quantity and mobilisation state of this unconsidered N pool.

## 1. Introduction

Regions with a high amount of belowground excess ice are especially prone to rapid thaw and associated deep mobilisation of sedimentary organic matter (OM). A prime candidate for rapid and deep thaw processes is the focus region of this study: the Yedoma permafrost domain in Siberia and North America. This permafrost region, covering 2587 000 km² (Strauss *et al* 2021) consist of tens of metres of ice-rich silty soil intersected by ice wedges that developed in tundra-steppe environments of the late Pleistocene (as seen from the cliff shown in figures 1 and 2). Other deposits, such as thermokarst lake and drained lake sediments or Holocene cover layers started developing due to permafrost degradation and aggradation during the Late Glacial and the Holocene warm periods (Schirrmeister *et al* 2020). Because of the

region's relatively high OM content and substantial sedimentary volume, the Yedoma domain contains 327–466 Gt organic carbon (OC) and 37–45 Gt total nitrogen (N) (Strauss *et al* 2017, 2022), which amounts for 26% and 42% of the C and N stocks located in permafrost worldwide, respectively. The thawing of the Yedoma domain can mobilise the carbon reservoirs and release significant amounts of the greenhouse gases carbon dioxide ($CO_2$) and methane ($CH_4$) (Jongejans *et al* 2021, Schuur *et al* 2022). It can also enhance nutrient mobilisation, including a primary nutrient N. This is important, since despite the high abundance of N in soil OM, its availability in reactive forms is limited by low temperatures and slow mineralization rate in Arctic soils (Nadelhoffer *et al* 1991). The increased mobilisation of N due to thawing can promote primary productivity in both terrestrial and aquatic ecosystems (Sanders *et al* 2022). On the other hand, it can enhance soil decomposition processes, potentially counteracting the benefits of photosynthetic C-uptake by enhanced vegetation growth (Mack *et al* 2004). Consequently, alterations in N availability can influence the OC balance in the Yedoma domain through these feedback mechanisms, although the overall impact is uncertain.

In this study, motivated by the discovery of a significant N stock in the Yedoma domain (Strauss *et al* 2022), we discuss three main questions related to the fate of soil N, increasingly liberated from the frozen ground in the thawing Yedoma domain: (1) how does the thawed N become accessible for plants and microbes? (2) What are the most likely N-loss pathways through which the liberated N becomes inaccessible to these organisms?, and (3) which are the potential climate feedback loops associated with these different pathways of N uptake and release?

To address these questions we also develop a concept of N-mobilisation, where we include thaw, physical erosion processes, leaching and microbial transformations.

## 2. N quantity and quality: soil N forms in permafrost and N bioavailability

The ecosystem N cycle consists of multiple microbial and plant-related processes, which are responsible for transformations between numerous solid, soluble and gaseous forms of N (figure 1). The reactive N forms available for biological organisms include mineral N in the form of ammonium ($NH_4^+$), nitrite ($NO_2^-$) and nitrate ($NO_3^-$), as well as dissolved organic N (DON). From these reactive N forms, DON was found to be the most important in high-latitude soils because of the low abundance of mineral N (figure 1) (Jones and Kielland 2002, Fiencke *et al* 2022). DON comprises approximately half of total dissolved N stocks in a boreal wetland (Kane *et al*
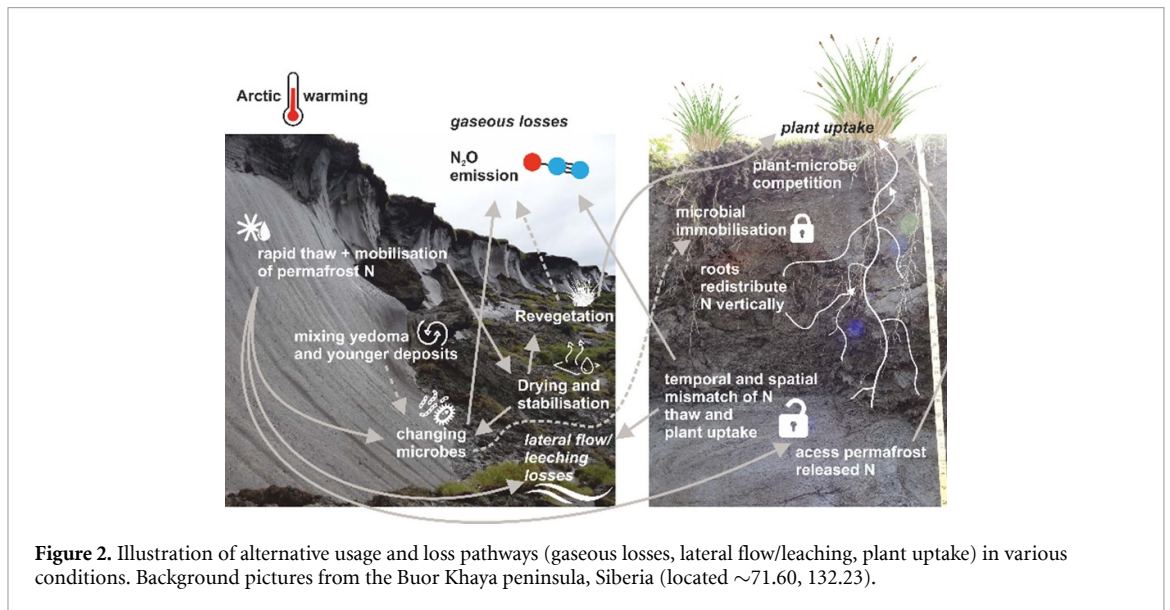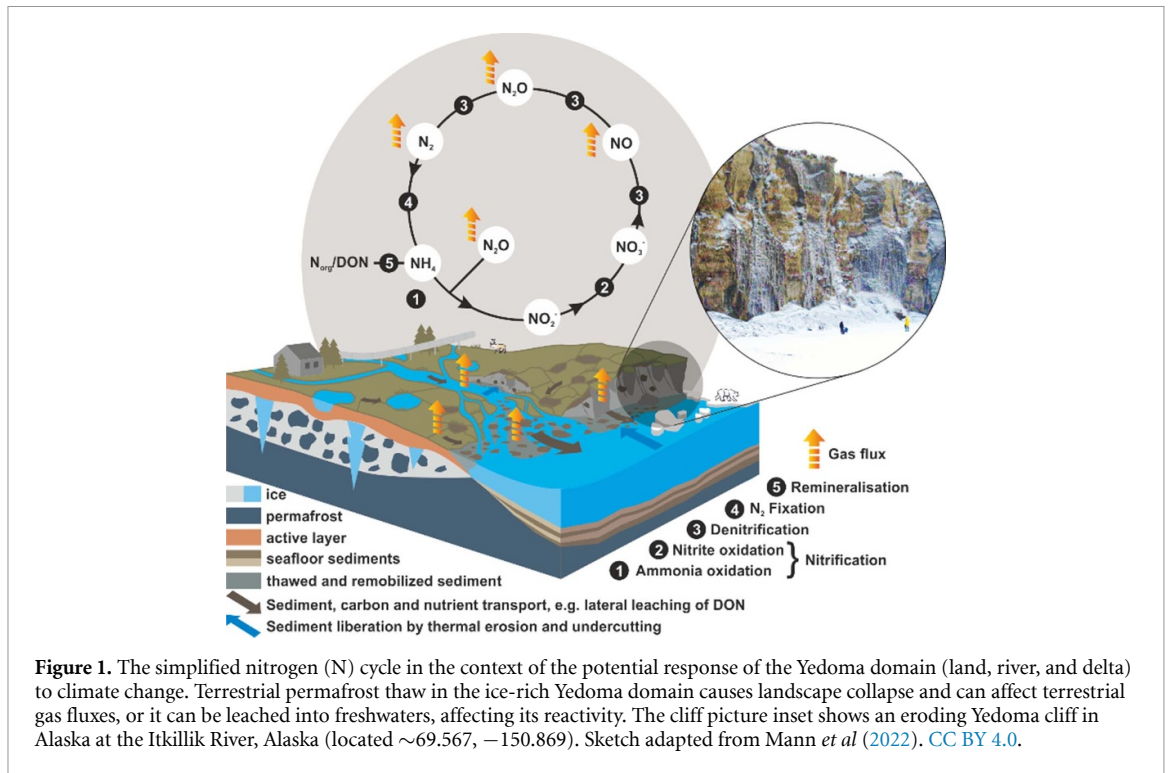
2010), which is a dominating ecotype of the Yedoma domain, especially in its southern parts.

In the ice-rich Yedoma domain, permafrost warming will increase the size of the active soil N pool due to an increase in seasonally thawed soil volume (figure 2) and more rapid N-cycling processes in warming soil (Schuur *et al* 2022). From a geomorphological perspective, the two processes determining the fate of N currently locked to permafrost are active layer deepening (gradual thaw), and rapid thaw processes, like thermokarst or thermo/thaw slump erosion (figure 3). This physical process of permafrost degradation is the first step of N-mobilisation through liberation from thawed soil, which needs to happen before any organisms can access the permafrost N. Although thermokarst and erosion caused by excess ice thawing are more prone to happen in ice-rich permafrost such as the Yedoma domain, gradual thaw is happening across the entire permafrost region, encompassing millions of square kilometres beyond the Yedoma domain, where active layers are deepening. This makes N liberation via gradual thaw a phenomenon spanning the circum-Arctic region

Studies on lability of N compounds in Yedoma deposits are sparse, but one of these rare studies, conducted in Siberian Yedoma deposits (Mack *et al* 2010), found a liberation of $250 \pm 107 \, \mu\text{g N g}^{-1}$ soil yr$^{-1}$ in a laboratory incubation experiment. Based on these N release rates, they assumed that thaw and decomposition of a 1 cm deep layer of frozen Yedoma deposits alone, if exposed to unfrozen, oxygenated conditions, could supply 3 g N m$^{-2}$ (Mack *et al* 2010) to microbial growth and metabolism as well as to vegetation growth. This amount is comparable to plant N uptake rates of 0.2–8.3 g N m$^{-2}$ yr$^{-1}$ reported for shrubby grass, tussock moss and forest tundra vegetation, summarised by Wild *et al* (2018), clearly demonstrating the importance of this added N liberated from permafrost. Additionally, significantly higher rates of net N mineralisation and nitrification were found in thawed Yedoma as compared to Holocene cover deposits (Marushchak *et al* 2021).

Differences in N density between the Yedoma domain's active layer (1.6 kg N m$^{-3}$) and the Yedoma domain's permafrost soils (0.9–2.2 kg N m$^{-3}$) were found to be small (Strauss *et al* 2022). While Arctic soils contain significant N stocks in soil OM, typically little of this N is biologically available (Shaver *et al* 1992, Buckeridge *et al* 2010, Beermann *et al* 2017). The fraction of readily biologically available dissolved N in Arctic ecosystems ranges from 0.01% to 3% of total soil N stocks (Shaver *et al* 1992, Buckeridge *et al* 2010).

A simple, first order proxy for the bioavailability of N following thaw is the C:N ratio. Compared to Pleistocene (Yedoma) and early Holocene permafrost deposits (Taberites), the active layer soils of the

**Figure 1.** The simplified nitrogen (N) cycle in the context of the potential response of the Yedoma domain (land, river, and delta) to climate change. Terrestrial permafrost thaw in the ice-rich Yedoma domain causes landscape collapse and can affect terrestrial gas fluxes, or it can be leached into freshwaters, affecting its reactivity. The cliff picture inset shows an eroding Yedoma cliff in Alaska at the Itkillik River, Alaska (located ∼69.567, −150.869). Sketch adapted from Mann *et al* (2022). CC BY 4.0.



**Figure 2.** Illustration of alternative usage and loss pathways (gaseous losses, lateral flow/leaching, plant uptake) in various conditions. Background pictures from the Buor Khaya peninsula, Siberia (located ∼71.60, 132.23).

Yedoma domain were found to have higher C:N ratios (Strauss *et al* 2022), implying a lower rate of N mineralisation there (Booth *et al* 2005, Liu *et al* 2017). Significantly higher rates of net N mineralisation and nitrification were found in thawed Yedoma as compared to Holocene cover deposits (Marushchak *et al* 2021). An accumulation of $NH_4^+$ was observed within Yedoma permafrost as compared to the active layer (Strauss *et al* 2022), likely due to mineralisation of OM with lower C:N ratios and delayed or lacking plant uptake (Uhlířová *et al* 2007). This elevated supply of $NH_4^+$ could also fuel the nitrification rates. Recently, Hansen and Elberling (2023) confirmed this

by stating that permafrost soils across the Northern Hemisphere contain larger concentrations of biologically available inorganic N (mainly as $NH_4^+$) than the active layer. Also in sub-Arctic peatlands, available N in near surface permafrost were seven times higher than in active layer permafrost; and higher rates of net N mineralisation and plant N uptake were also observed (Keuper *et al* 2012). For permafrost from the Tibetan Plateau, the opposite case was found, having more N in the active layer than in the permafrost below (Mao *et al* 2020).

The vegetation type dominating during the time Yedoma deposits accumulated can partly explain the

high lability of N compounds in Yedoma permafrost. Most of the Yedoma domain includes thick permafrost deposits that accumulated in the late Pleistocene, when grassland ecotype was dominating there (Zimov *et al* 2012). In their synthesis study on gross N mineralisation rates, Booth *et al* (2005) found that OM from grasslands appears to have lower C:N ratios and is inherently more productive for $NH_4^+$ than OM from forested or woody sites with higher C:N ratios. The mobilisation of the deeper still perennially frozen N rich Yedoma OM during permafrost thaw likely represents an important source of additional bioavailable N to the terrestrial as well as adjacent aquatic ecosystems.

## 3. Fate of N from thawed permafrost

### 3.1. Plant N uptake

Since plant growth in high-latitude ecosystems is usually N limited (Beermann *et al* 2015, 2017), N release from thawing permafrost deposits may boost plant productivity and thus $CO_2$ fixation from the atmosphere through photosynthesis. However, the strength of this feedback is strongly affected by how well the liberated nutrients including N will be accessible for plants (Pedersen *et al* 2020) or microbes (Baker *et al* 2023). The accessibility of nutrients is influenced by the spatial and temporal patterns of N release and transport, the presence or absence of plants, plant, species composition, plant rooting depth as well as soil characteristics. Seasonal variability plays an important role here: Plants and microbes are able to immobilise available N (figure 2) before photosynthetic activity sets in during the winter/spring transition (Edwards and Jefferies 2010). However, seasonal declines in microbial biomass may result in another pulse of available N (Bardgett *et al* 2007). Active layer deepening, apart from exposing more OM to microbial decomposition, leads to a longer thawing period, thereby prolonging the period with biologically available soil N.

Active layer deepening likely also results in direct N inputs to the ecosystem N cycle from newly thawed permafrost to the bottom of the active layer, as well as longer soil N availability, especially in the first years after thaw (Salmon *et al* 2016, 2018).

It has been shown, however, that due to a temporal mismatch between peak vegetation growth (mid-summer) and maximum thawing depth (late summer/autumn), there is incomplete utilisation of nutrients by plants near the permafrost table (Lacroix *et al* 2022). Also, plants will not necessarily be able to access the N released from permafrost, if they are located deeper down than their rooting zone (Keuper *et al* 2017). Incomplete plant N use can cause a nutrient oversupply near the permafrost table, which may lead to freely available N for microbial cycling processes such as nitrification and denitrification. This,

in turn, could lead to emissions of $N_2O$, a strong greenhouse gas and stratospheric ozone-depleting substance (figure 2 and Lacroix *et al* (2022)), or increased losses of N via downward vertical leaching and lateral flow (figure 2, chapter 3.2). This may be the case with gradual active layer deepening, while abrupt thaw exposes the newly thawed material to the surface, making it readily available for newly established vegetation on retrogressive thaw slumps (Marushchak *et al* 2021) or in thermokarst lakes (Walter Anthony *et al* 2014).

In retrogressive thaw slumps and other disturbed sites, however, development of full vegetation cover takes several years, and easily exceeds the capacity of plants to take up N during early stages of succession the mineral N supply (Marushchak *et al* 2021). This successional mismatch is probably also true for the process of surface water generation resulting from the melting of ground ice and subsequent subsidence, although there is limited literature on this topic. Thermokarst lake and gully formation leads to distinct vegetation dynamics, influencing the utilisation of newly available N by plants. The development of aquatic landscape features, such as small pools and troughs, requires colonisation by aquatic vegetation (primarily consisting of mosses and sedges) before they can effectively utilise the accessible N for carbon sequestration. Nevertheless, once the full vegetation cover is established on these disturbance sites, they exhibit the potential for considerable productivity.

Thus, increased N availability by permafrost thaw in soils could enhance net primary productivity and increase OC stocks in plant biomass, but this might not always be the case. Some experimental evidence confirms that plant growth increases with newly thawed deep N sources, while other studies show that effects on OC acquisition might be limited since only few deep-rooting plant species will be able to exploit the newly thawed N (Keuper *et al* 2017). Considering that a large part of the Yedoma domain lies within the continuous permafrost zone (with a shallow active layer depth of <1 m), it is likely that N in the soil layers exposed by active layer deepening may become accessible to deep rooting plants (see the gradual thaw pathway in figure 3), if there is no temporal mismatch.

Recently, a study of vegetation types in retrogressive thaw slumps (Buckeridge *et al* 2023) revealed that shrubs are the best candidate for plant N uptake as they have a deep vertical rooting potential (figure 2) and can reach the deep N stocks, as also found by Hewitt *et al* (2019). This is in line with the shrubification which has been observed in Arctic tundra due to recent warming (Frost *et al* 2013). Whether increased vegetation stocks may offset soil OC losses is therefore still uncertain (McGuire *et al* 2018, Mauritz *et al* 2021, Schuur *et al* 2021, 2022).

### 3.2. Lateral and vertical flow

In the Yedoma domain (and other ice-wedge-bearing permafrost), the thawing of ground ice frequently results in elevated surface water levels. This phenomenon becomes apparent through the degradation of ice-wedge polygonal landscapes, resulting in the formation of polygonal pools and ice wedge troughs, and sometimes leading to interconnected hydrological pathways (Liljedahl *et al* 2016). Importantly, this process is likely to serve as an increasingly significant source of nutrients (Vonk *et al* 2015). For instance, Koch *et al* (2018) observed a rapid decline in ammonium ($NH_4^+$) levels within deep trough ponds, attributable to biogeochemical cycling.

Runoff from Holocene cover on top of Yedoma uplands and some refrozen thermokarst basins sediments of the Yedoma domain can transport nutrients like $NO_3^-$ and $NH_4^+$ to aquatic systems. This runoff/lateral flow is limited in deeper strata, especially in Taberites beneath thermokarst lakes, as they are (at least partially) (re-)frozen. Vertical flow could occur as well if a groundwater connection is present, or through transport within plant roots in a throughgoing talik. Particulate N and DON originating from runoff could be deposited on floodplains, in river deltas, or in the nearshore sediments of the Arctic shelf seas (Ramage *et al* 2018, Marzadri *et al* 2021). If leached and transported to the aquatic systems, the fate of N strongly depends on the form and quality of N, as well as other stream network characteristics such as redox potential, oxygen status, availability of other nutrients, pH, temperature and microbial and plant community composition. Additionally, water transparency and sediment content are controlling the availability of light and thus nutrient uptake and primary productivity.

Nutrient losses through lateral flow and vertical leaching are potentially a major factor in overall tundra nutrient budgets (Mack *et al* 2004, Schaeffer *et al* 2013). Given the observed increases in tundra stream $NO_3^-$ export from 1978 to 2006 (McClelland *et al* 2007, Townsend-Small *et al* 2011), understanding mechanisms for N availability and losses in tundra soils is important. However, estimates of nutrient leaching losses from tundra soils remain limited (Harms and Jones Jr 2012, Treat *et al* 2016). Rates of N mineralisation, N assimilation and immobilisation vary seasonally due to interactions with plant biomass and microbes (Schmidt *et al* 2002, Sorensen *et al* 2008, Baker *et al* 2023) and further complicate estimates of N leaching losses. For example, soil N losses increased significantly during the late growing season at a high-Arctic tundra site as plants senesced (Schaeffer *et al* 2013).

Losses of DON account for the majority of soil N leaching to streams from pristine ecosystems (Hedin *et al* 1995, Perakis and Hedin 2007) like Arctic ecosystems (Lafrenière and Lamoureux 2008, McNamara

*et al* 2008). The export of dissolved OM, and therefore DON, is related to dissolved OM concentrations within the soils, dissolved OM retention within the soil, and hydrologic flux from the soil.

The export of dissolved OM is also controlled by the amount of runoff. Olefeldt and Roulet (2012) found substantially lower dissolved OM fluxes from a permafrost peatland than from other peatlands and concluded this was the result of less runoff due to presence of impermeable permafrost. Changes in the flow path of water due to permafrost thaw will alter dissolved OM and N inputs to aquatic ecosystems, resulting in predictions of increasing DON fluxes in Siberian watersheds (Frey *et al* 2007).

In streams, nutrient export is highly variable over time and space. The majority of nutrient export in Arctic rivers occurs during spring freshet (Holmes *et al* 2012, Juhls *et al* 2020). Holmes *et al* (2012) estimated dissolved N loading to be 1.26 Tg per year; roughly two-thirds (0.85 Tg) was organic N over the inorganic remainder ($NO_3^-$ and $NH_4^+$). Additionally, there is seasonal variability in the quantity of the dominant N form released in the Yedoma domain. As was found by Sanders *et al* (2022), who studied the Yedoma domain, DON is predominantly transported to the ocean in summer, while the concentrations of exported DON and $NO_3^-$ are similar during periods with ice cover.

Besides quantity, the quality of dissolved OM is also temporally variable. OM quality differs during the spring freshet from the growing season; 20%–46% of dissolved OM lost during spring freshet is degraded relatively rapidly (Michaelson *et al* 1998, Holmes *et al* 2008), while dissolved OM exported to the Arctic ocean during the summer is slow to degrade (Holmes *et al* 2008). N released by dissolved and particular OM mineralisation may result in increased stream productivity or N retention (Peterson *et al* 2001), denitrification (Peterson *et al* 2001), or export to the Arctic Ocean (Frey *et al* 2007, Mann *et al* 2022, Sanders *et al* 2022, Ogneva *et al* 2023). The net effect on climate, considering direct and indirect greenhouse gas emissions from both OC and N cycles is presently difficult to estimate from lakes and rivers in the Yedoma domain, and a solid estimation for $N_2O$ emissions from Arctic rivers is lacking until now.

### 3.3. Microbial immobilisation and changes in decomposition because of improved N availability

Excess N liberated during thaw will be partly immobilised by being incorporated into the microbial biomass following thaw, but with continued supply of N, the likelihood of excess N availability increases. This excess N is, depending on the micro-conditions, simultaneously available for various microbial transformation processes including $N_2O$ and molecular N ($N_2$) production as long as growth of vascular

plants remains hampered (Palmer *et al* 2012, Palmer and Horn 2012, Hetz and Horn 2021, Horn and Hetz 2021).

The effect of excess N is a subject of discussion, giving rise to two distinct phenomena: the concept known as the 'N mining theory' (Lovett *et al* 2018) and the 'N priming effect' (Mack *et al* 2004). The N mining theory suggests an increase in decomposition due to N limitation, where microbes are forced to mine for additional N-substrates from OM. The theory suggests that when N is limited, N-acquiring microbes can use OC as an energy source, thereby enhancing OM decomposition and increasing respiratory $CO_2$ losses to acquire the needed N (Chen *et al* 2014, Lovett *et al* 2018). The N priming effect, on the other hand, can be positive or negative, entailing a boost or a decrease in overall OM decomposition through enhanced N availability.

Notably, the N-priming effect not only enhances the decomposition of OM and stimulates further N-release, but also leads to higher N availability and enhanced decomposition of OM increase OC release (Mack *et al* 2004, Lavoie *et al* 2011). For example, Mack *et al* (2004) showed that aboveground OC storage increased following N-addition, but was offset by increased OC decomposition—and thus soil OC losses—belowground. Similarly, Zhang *et al* (2023) found that a warming-induced, enhanced soil N supply stimulated soil microbial activity and amplified soil OC losses from permafrost soils in the Tibetan Plateau. These findings support the 'stoichiometric decomposition theory', which suggests that N addition is beneficial for OM decomposition.

In contrast to these findings, Berg and Matzner (1997) and Riggs *et al* (2015) showed that increased N availability could lead to decreased OM decomposition and thus negative priming. Riggs and Hobbie (2016) hypothesised that negative priming can be caused by three mechanisms. First, increased N availability can improve OC use efficiency leading to OC use for microbial growth rather than respiration (Weintraub and Schimel 2003, Manzoni *et al* 2012, Chen *et al* 2018). Second, N addition might lead to decreased activity of oxidative enzymes, thereby limiting decomposition of complex OC molecules such as lignin (Eisenlord *et al* 2013). Third, soil acidification following N addition might lead to decreased microbial biomass and hence to decreased OM decomposition rates (Mueller *et al* 2012).

For Alaskan Arctic and boreal soils, Lavoie *et al* (2011) found that N addition could have a positive as well as a negative effect on OM decomposition. They showed that a positive effect was mainly observed for organic soils, whereas negative effects were mainly found for mineral soils, from which they concluded that the direction of priming in decomposition is highly dependent on the soils' labile OM fraction. Likewise, Wologo *et al* (2021) found that

addition of N (in the form of $NH_4^+$ and $NO_3^-$) and acetate, compounds abundant in permafrost including Yedoma (Mann *et al* 2022), triggered the breakdown of some dissolved OM compounds, but resulted in a net decrease in overall decomposition rate. Thus, depending on the OM degradability and the microbial composition, the N stock in the Yedoma domain might pose either a positive or a negative climate feedback upon thaw.

## 4. Newly thawed permafrost N: a positive or negative climate feedback?
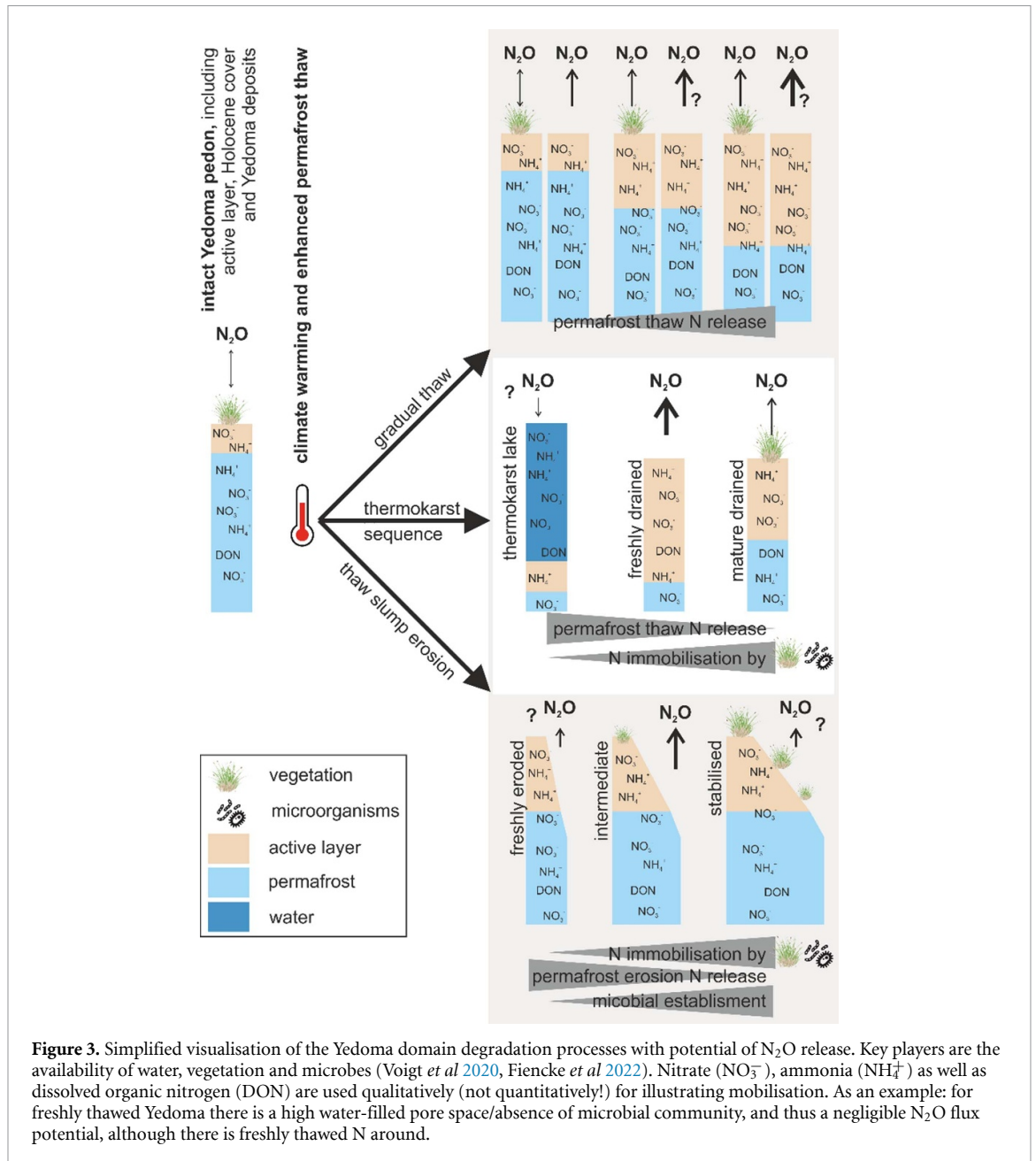
### 4.1. Likelihood for a negative feedback
Permafrost thaw will increase the amount of bioavailable N in an N-limited environment, which could therefore boost ecosystem productivity resulting in a negative climate feedback. Walter Anthony *et al* (2014) suggest that N and other nutrients such as P released from thawing Yedoma deposits have supported high lacustrine primary production and OC accumulation in thermokarst lake sediments during the Late Glacial to Holocene warming. In addition, in re-vegetated (stabilised) thermokarst basins, plants will be able to access former deep Yedoma N (see figure 3).

On the one hand, as mentioned before, abrupt thaw could increase OC sequestration, while gradual thaw poses the potential for incomplete nutrient use by plants (due to temporal and spatial mismatch). On the other hand, rapid thaw processes disturb or destroy the plant cover and thereby hinder the possibility of plants to catch the initial thaw liberates nutrient pulse. Therefore, it is possible that a considerable amount of N is not used to promote OC sequestration in the short-term. As a result, the possibility to create a negative feedback to climate via enhanced plant growth is limited in these regions with on-going thermokarst activity.

### 4.2. Likelihood for a positive climate feedback by gaseous losses
While part of the excess N liberated from thawing permafrost in the Yedoma domain will be used for plant growth and transformed into microbial biomass with continued N supply as described above (figure 2), part of it may become available for microbial transformation processes such as nitrification and denitrification (Horn and Hetz 2021, Ramm *et al* 2022). These microbial N transformation processes may cause gaseous N losses in the form of $N_2O$ as well as $N_2$. $N_2O$ is produced mainly by denitrification but also as a side product during the first step of nitrification, the ammonia oxidation. Further, nitrification has a crucial role for denitrification via $NO_3^-$ supply to serve as the electron acceptor in denitrification. Recently published data on high $N_2O$ emissions and potential $N_2$ losses from retrogressive thaw-slumps

**Figure 3.** Simplified visualisation of the Yedoma domain degradation processes with potential of $N_2O$ release. Key players are the availability of water, vegetation and microbes (Voigt *et al* 2020, Fiencke *et al* 2022). Nitrate ($NO_3^-$), ammonia ($NH_4^+$) as well as dissolved organic nitrogen (DON) are used qualitatively (not quantitatively!) for illustrating mobilisation. As an example: for freshly thawed Yedoma there is a high water-filled pore space/absence of microbial community, and thus a negligible $N_2O$ flux potential, although there is freshly thawed N around.

within Yedoma deposits demonstrate that this is a likely scenario for such permafrost thaw features in the Yedoma domain (Marushchak *et al* 2021).

There is increasing evidence from soils across the permafrost region that, despite their general N limitation due to slow N mineralisation in cold and often humid conditions, permafrost-affected soils can be substantial sources of $N_2O$ when three conditions are met (Repo *et al* 2009, Voigt *et al* 2017b, 2020, Marushchak *et al* 2021). First, a sufficient mineral N supply is a key factor controlling $N_2O$ emissions from soils (Parton *et al* 1996). In this context, the C:N ratio has been linked to $N_2O$ emissions from soils with highest emissions occurring at low to intermediate range C:N ratios, which support N mineralisation (Klemedtsson *et al* 2005, Liimatainen *et al*

2018). In the Yedoma domain, the C:N ratios ranged between 9–19 (medians of the different compartments in Strauss *et al* (2022), which is low enough to support $N_2O$ emissions as shown in Marushchak *et al* (2021).

Second, a lack of vegetation growth increases the mineral N availability for microbes and is thus favourable for $N_2O$ emissions. Previous studies reported high $N_2O$ emissions in locations where vascular plants are absent or N uptake by vegetation is otherwise disturbed, e.g. by thermokarst processes (Marushchak *et al* 2011, Gil *et al* 2017, Voigt *et al* 2017a). This is frequently the case in the Yedoma domain with its high abundance of eroded surfaces, disrupted plant growth, and disturbed site conditions due to abrupt thaw processes.

Third, an intermediate moisture content has been shown to promote $N_2O$ emissions from permafrost-affected soils (Voigt *et al* 2020). On the one hand, water-saturated conditions hinder N mineralisation and nitrification, which are aerobic processes, thereby limiting provision of mineral N species used for $N_2O$ production. At the same time, a high water content promotes denitrification as this is an anaerobic process. If denitrification is complete under water-saturated conditions, $N_2O$ is reduced to the inert $N_2$ gas, and complete denitrification may also lead to atmospheric $N_2O$ uptake (Butterbach-Bahl *et al* 2013, Voigt *et al* 2017b, 2020). On the other hand, an intermediate moisture range allows both $NO_3^-$ and $N_2O$ production via aerobic nitrification as well as $N_2O$ production via anaerobic denitrification to co-occur (Butterbach-Bahl *et al* 2013, Abbott and Jones 2015, Fiencke *et al* 2022). Thus, the magnitude of $N_2O$ emissions following permafrost thaw will largely depend on hydrology.

Limitations in microbially available OM together with accumulation of $NO_3^-$ associated with high nitrification rates might further enhance $N_2O$ production during denitrification (Hetz and Horn 2021). In favourable, intermediate soil moisture conditions, a microbial community capable of intensive mineral N cycling (by nitrification and denitrification) and substantial $N_2O$ production can be established in these mineral N rich sediments (Marushchak *et al* 2021). While for freshly thawed, wet Yedoma sediments, low $N_2O$ emissions were found due to low abundance of key functional groups, particularly nitrifiers, whereas high $N_2O$ emissions occurred after a few years of stabilisation, drying, partial re-vegetation and changes in microbial community (Marushchak *et al* 2021).

Based on these initial findings, we thus expect that the following areas are prime candidates for substantial $N_2O$ release (figure 3): thaw slumps, freshly drained lake basins, and thermo-erosional valleys. If thermokarst lakes drain, unfrozen sub-lake taliks can turn into zones of intermediate soil moisture levels. Nitze *et al* (2020) observed widespread lake drainage in the Yedoma domain over the past decades and predicted a similar trend of more lake drainage events in the future, especially for southern margins of continuous permafrost. With improved drainage, the OM in lake sediments is exposed to enhanced mineralisation, which will boost mineral N production and the microbial N transformation processes releasing $N_2O$.

## 5. Estimating the future net climate feedback from newly thawed N

The net effect on the climate of newly thawed N from permafrost degradation in the Yedoma domain strongly depends on local conditions (e.g. prevailing wetness, vegetation, microbes). These conditions will determine whether N in thawing permafrost is taken up by vegetation or microbes or if it will be subjected to vertical leaching or to microbial transformation processes, such as denitrification, leading to N losses in the gaseous form. In the short term, the gradual deepening of the active layer will affect only a small portion of the currently frozen N pool in the Yedoma domain. Most of this newly thawed N of the newly thawed active layer will be at depths interacting with plants, thus with a potential for enhancing the carbon sink capacity of these regions and limiting losses though lateral runoff and gaseous, vertical losses such as $N_2O$ emission. Speculative, but possibly further long-term climate warming beyond the 21st century will lead to an increasingly thawed N pool at depths that are below the root reach of plants. Even at present, a temporal mismatch of N supply and demand can leave part of the mobilised N inaccessible for plants. Furthermore, thermokarst lake initiation, coastal and riverbank erosion as well as erosion on thermokarst basins will continue to thaw deep Yedoma deposits, thereby mobilising substantial amounts of deep N below 3 m. The N at these soil depths could become available for microbes participating in N cycling under intermediate soil moisture levels, which might lead to $N_2O$ production.

Another difficulty for estimating $N_2O$ production based on environmental conditions is related to the process of stabilisation of rapid thaw (for example in thaw slumps and cliff erosion), which seems to be decoupled from hydrology parameters driving the $N_2O$ production elsewhere. Freshly thawed Yedoma from a permafrost exposure in Siberia was found to be inert for $N_2O$ production right after thaw with gradual but significant increase in $N_2O$ emissions within the first few years after thaw (Marushchak *et al* 2021). This temporal dimension of the already highly spatially variable $N_2O$ production in the landscape further increases the uncertainty for the estimation of the future net climate feedback in upscaling attempts. Similarly, Chen *et al* (2018) found that at the early stage of permafrost collapse, microbial N limitation is cancelled out because of enhanced microbial N mineralisation. This results in a lower C:N ratio and high N availability, which might lead to higher metabolic efficiency, thereby decreasing $CO_2$ release. Later on, due to N leaching or consumption, N may become again limited and $CO_2$ release will likely increase. This illustrates that these processes probably happen on different time scales. Besides these temporal complexities, uncertain future shifts in soil moisture conditions can crucially alter $N_2O$ production rates.

To wrap up the future the Yedoma domain pathway: There will be substantial mobilisation of N by deep permafrost thaw. This, in addition to the N release by gradual deepening of the active layer could provide a substantial amount of additional N.

According to a simplistic back-on-the-envelope calculation approach by Ramm *et al* (2020), we can illustrate the significance of thaw enhanced N cycling and $N_2O$ release in the Yedoma domain. If 10% (following the projected 9.6% Yedoma carbon loss over the 50 incubation year period from Strauss *et al* (2017)) of the N stored in the Yedoma domain (4.1 Gt, Strauss *et al* (2022)) is released between the present day and the year 2100 (assumption based on Schuur *et al* (2022); Schuur *et al* (2015)), and 1% (IPCC's default $N_2O$ emission factor from mineral soils) is emitted as $N_2O$ (0.4 Tg $N_2O$-N yr$^{-1}$, 31 Tg $N_2O$-N until 2100), this would be equivalent to ∼6% of the global annual rate of $N_2O$ emissions from soils under natural vegetation (6.6 Tg $N_2O$-N yr$^{-1}$ (Ciais *et al* 2013) already. For the total permafrost N stock of 97 Gt (Harden *et al* 2012, Strauss *et al* 2022), this would amount to 1.0 Tg $N_2O$-N yr$^{-1}$, 76 Tg $N_2O$-N in total for the 76 years to 2100 and 15% of the global annual rate of $N_2O$ emissions from soils under natural vegetation, which have not yet been accounted for. The release of $N_2O$ resulting from thawing permafrost, particularly Yedoma, is an additional contribution to the current $N_2O$ emissions originating from permafrost soils which have been estimated to range between 0.14 and 1.27 Tg $N_2O$-N (Voigt *et al* 2020). Thus, the thawing Yedoma domain is likely a neglected $N_2O$ source. Our study shows potential pathways of N release when we further 'open' the Yedoma-domain-permafrost freezer by human-caused climate warming. Future research should prioritize studying N flow paths post-thaw of permafrost deposits, along with physico-chemical and microbial stabilization/mobilization of these nutrient reservoirs. Additionally, developing process-based models to simulate N and carbon dynamics can enhance predictions regarding permafrost-climate feedbacks in vulnerable ecosystems.

## 6. Conclusion

The increasing release of N from the recently found, until now largely freeze-locked soil N pools in the Yedoma domain could further accelerate climate feedbacks from permafrost thaw through additional $N_2O$ emissions, or it could reduce climate feedbacks through promoting enhanced vegetation C sequestration. While the latter largely depends on how well the spatial and temporal pattern of plant N uptake matches with those of N release, the Yedoma deposits are a prime candidate for $N_2O$ production if the conditions are right (i.e./e.g. medium water content, establishment of microbial community capable of active N cycling, partial vegetation cover). More precisely, stabilising permafrost thaw sites with intermediate soil moisture content and disturbed vegetation cover likely have the highest potential for $N_2O$ release. However, making reliable predictions of future landscape and hydrology changes in the Yedoma domain remains a major challenge due to lack of data. In all cases, there is strong evidence that the permafrost-climate feedback will be affected by the amount and state of mobilisation of this previously unquantified N pool. Future research should focus on quantifying N flow post-thaw in permafrost and developing process-based models to improve predictions on permafrost-climate feedbacks.

## Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

## Contributions

J S designed the study and generated the first draft further improved by M E M, L v D, T S, C B, C V, L L J, and C T. All authors contributed significantly by revising and reviewing the manuscript drafts.

## Ethics declarations

The authors declare no competing interests.

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