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Nitrogen supply and physical disturbance shapes Arctic stream nitrogen uptake through effects on metabolic activity

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Abstract

1. Climate change in the Arctic is altering the delivery of nutrients from terrestrial to aquatic ecosystems. The impact of these changes on downstream lakes and rivers is influenced by the capacity of small streams to retain such inputs. Given the potential for nutrient limitation in oligotrophic Arctic streams, biotic demand should be high, unless harsh environmental conditions maintain low biomass standing stocks that limit nutrient uptake capacity.
2. We assessed the drivers of nutrient uptake in two contrasting headwater environments in Arctic Sweden: one stream draining upland tundra and the other draining an alluvial valley with birch forest. At both sites, we measured nitrate (NO_3^-) uptake biweekly using short-term slug releases and estimated rates of gross primary production (GPP) and ecosystem respiration from continuous dissolved oxygen measurements.
3. Catchment characteristics were associated with distinct stream chemical and biological properties. For example, the tundra stream maintained relatively low NO_3^- concentrations (average: $46 \mu\text{g N/L}$) and rates of GPP ($0.2 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$). By comparison, the birch forest stream was more NO_3^- rich ($88 \mu\text{g N/L}$) and productive (GPP: $1.7 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$). These differences corresponded to greater areal NO_3^- uptake rate and increased NO_3^- use efficiency (as uptake velocity) in the birch forest stream (max $192 \mu\text{g N m}^{-2} \text{ min}^{-1}$ and 96 mm/hr) compared to its tundra counterpart (max $52 \mu\text{g N m}^{-2} \text{ min}^{-1}$ and 49 mm/hr) during 2017. Further, different sets of environmental drivers predicted temporal patterns of nutrient uptake at these sites: abiotic factors (e.g. NO_3^- concentration and discharge) were associated with changes in uptake in the tundra stream, while metabolic activity was more important in the birch forest stream.
4. Between sites, variation in uptake metrics suggests that the ability to retain pulses of nutrients is linked to nutrient supply regimes controlled at larger spatial and temporal scales and habitat properties that promote biomass accrual and thus biotic demand.

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5. Overall, constraints on biotic potential imposed by the habitat template determined the capacity of these high latitude streams to respond to future changes in nutrient inputs arising from climate warming or human land use.

KEYWORDS

Arctic, catchment, metabolism, nutrient uptake, tundra

1 | INTRODUCTION

Climate change at high latitudes is currently altering key stream and river functions that regulate the transport and fate of nutrients exported from soils to freshwaters and oceans (Demars et al., 2016; Song et al., 2018). Terrestrial greening, earlier and stronger spring floods, and permafrost melting all affect the magnitude and timing of soil nutrient input to streams and rivers (Frey et al., 2007; Kendrick et al., 2018). Changes in these inputs to streams may directly influence nutrient retention by altering uptake kinetics (Mulholland et al., 2008; Ward et al., 2018), but also indirectly through effects of resource supply on metabolic rates (Hall et al., 2009). The relative influence of these drivers on nutrient uptake are poorly understood, especially in Arctic systems, where algal and microbial production is often nutrient limited and thus potentially sensitive to changes in terrestrial nutrient supply (Myrstener et al., 2018). However, Arctic streams may also be exposed to extreme physical conditions that constrain microbial biomass accrual and thus uptake (Huryn et al., 2005; Pastor et al., 2019). Identifying the biotic and abiotic factors that regulate nutrient uptake and understanding how they are organised across high latitude landscapes is crucial for predicting how climate-induced changes in a catchment propagate through aquatic networks and impact downstream ecosystems.

Hydrological, morphological, and biogeochemical processes interact to either promote or limit the biological uptake and retention of nutrients in stream ecosystems and, ultimately, their transport downstream. Thus, nutrient uptake metrics (areal uptake rate [U], uptake velocity [V_f], and uptake length [Sw]; see Table S1) are often sensitive to physical properties of streams that control biological access to dissolved resources. These factors include water residence time (Drummond et al., 2016; Zarnetske et al., 2012), the size of transient storage zones and the extent of hyporheic exchange (Gücker & Boëchat, 2004; Thomas et al., 2003), and the structure of turbulence in the water column (Grant et al., 2018, 2020). However, patterns of uptake in streams are also sensitive to variance in the strength of biological demand and therefore can be altered by the stoichiometric balance of nutrient supply (Cross et al., 2005; Schade et al., 2011; Tromboni et al., 2018) and by the overall rates of metabolic activity, including gross primary production (GPP) and ecosystem respiration (ER) (Fellows et al., 2006; Hoellein et al., 2007; Tank et al., 2018). Finally, fluctuations in discharge alter all of the physical and biological factors described above and regulate the overall nutrient supply and longitudinal flux at catchment scales (Wollheim et al., 2018).

At regional scales, variance in uptake parameters appear largely explained by specific discharge, nutrient concentrations, and metabolic processes (Hall et al., 2009) but the relative importance of specific drivers may vary at small spatial and temporal scales (Day & Hall, 2017).

Streams draining Arctic and sub-Arctic regions may vary considerably in nutrient availability and the physical drivers that influence nutrient uptake (Shogren et al., 2019). Arctic waters are generally oligotrophic, leading to widespread nutrient limitation (Myrstener et al., 2018), and stream metabolic rates that tend to fall at the lower end of global averages (Myrstener et al., 2021; Rocher-Ros et al., 2020). Further, potentially extreme physical conditions of streams at high latitudes, including strong hydrologic variability, low temperatures, and loading of glacial sediments may constrain nutrient uptake rates by simultaneously depressing biotic activity and the contact time between solutes and the biological communities associated with stream sediments (Blaen et al., 2014; Docherty et al., 2018). However, depending on the regional and/or local geomorphic setting, high latitude streams can also be physically stable and nutrient rich, supporting relatively high rates of metabolic activity and nutrient uptake (Huryn et al., 2014; Schade et al., 2016). These distinct end-members underscore the importance of the *physical habitat template* (Southwood, 1977) across high-latitude landscapes (e.g. Huryn et al., 2005), which may regulate the relationship between stream nutrient supply and demand (Covino et al., 2018) by limiting how biological communities develop.

The physical habitat template of Arctic streams encapsulates hydrologic, chemical, and morphologic catchment characteristics that produce distinct disturbance and nutrient regimes (Huryn et al., 2005). In general, high latitude streams supported by surface water run-off from precipitation or glacial meltwater are characterised by strong physical disturbance, low channel stability, low temperatures, and a high likelihood of bottom freezing in winter (Parker & Huryn, 2013; Pastor et al., 2019). Combined with low nutrient concentrations, these conditions suppress autotrophic productivity and consumer biomass (Huryn et al., 2005). Such conditions are typical for upland tundra streams, which lie near the nutrient-poor and low-productivity end of the habitat gradient in Arctic landscapes. By comparison, streams with strong groundwater connections or in close proximity to solifluction tend to be nutrient enriched and more hydrologically stable, and typically support higher rates of metabolism and biomass accrual (Huryn et al., 2005; Myrstener et al., 2021; Pastor et al., 2020). At the extreme end of this habitat gradient are

spring-fed streams, which sustain flow throughout the year, are comparatively rich in nutrients, and are home to notably productive biological communities (Huryn et al., 2014). Parker and Huryn (2013) used this variation in the habitat template to explain and organise spatial variability in community composition and food web properties across Arctic streams. Here, we explore whether these same features underpin patterns of stream nutrient uptake in high latitude landscapes.

We assess the relative importance of hydrological, geomorphological, and ecological properties as drivers of nutrient uptake in streams of the Fennoscandian Arctic. To explore these controls, we conducted nitrate (NO_3^-) releases throughout the spring, summer, and autumn in two geomorphically distinct streams within the same catchment in the Fennoscandian Arctic. Nitrate was chosen for uptake measurements based on previous observations of nitrogen (N) limitation for streams in the same area (Myrstener et al., 2018) and the general dominance of NO_3^- over ammonium (NH_4^+) in these systems (Myrstener et al., 2021). We compared uptake between an upland tundra stream that experiences relatively high physical stress and low N concentrations and an alluvial valley bottom stream draining birch forest that is more physically stable and has comparatively high N concentrations. Combined, these represent end members along a gradient of morphological and biogeochemical properties observed for headwaters in this region. We hypothesised that these different hydrogeomorphic settings would support distinct rates and patterns of nutrient uptake owing to differences in rates of metabolic activity. Specifically, we predicted that the physically harsh tundra stream would have low rates of areal uptake (i.e. U) and

nutrient use efficiency (i.e. V_f) because flow disturbance and low nutrient supply limit biological standing stocks and associated demand for nutrients. In contrast, we expected the more benign and nutrient rich stream to accrue greater benthic biomass, sustain higher metabolic activity, have high areal uptake rates, and use available nutrients more efficiently through the growing season.

2 | METHODS

2.1 | Site description

The studied streams are part of Miellajokka catchment situated 200 km north of the Arctic Circle close to Abisko Scientific Station, northern Sweden (Figure 1). While various terms are applied to this region (e.g. arctic, sub-arctic, oroarctic; see Virtanen et al., 2016), it lies within the Arctic boundaries defined by the Arctic Monitoring and Assessment Programme on the basis of latitude, elevation, vegetation, and occurrence of permafrost (AMAP, 1998). Temperature measured at the Abisko Scientific Research Station averages -1°C over the last climatic period (1960–1990), but is now above 0°C , and annual precipitation is around 350 mm/yea, of which 60% falls outside the summer months (Kohler et al., 2006). Discontinuous permafrost exists at elevations above 800 m in this region (Gisnås et al., 2017). We worked in two sub-catchments of the Miellajokka, one just above tree line at 750 m above sea level (hereafter: tundra stream, M6) and one in the birch forest (hereafter: birch forest stream, M18) at 400 m above sea level to represent common yet

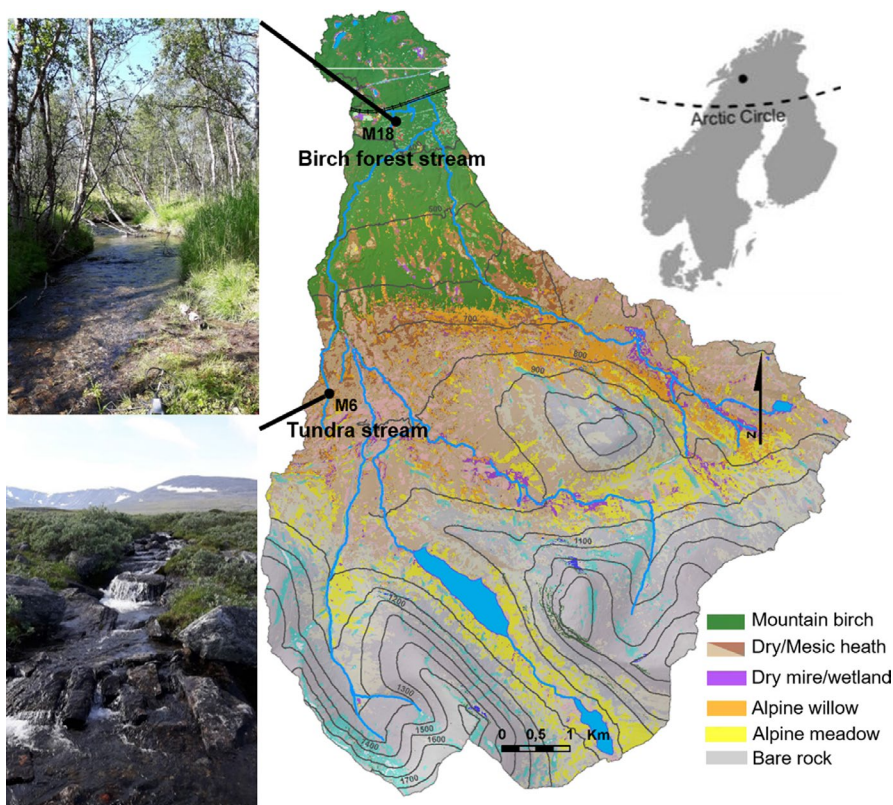


FIGURE 1 Location of the studied catchment in Sweden, and tundra (M6) and birch forest stream (M18) within the catchment. The green area shows mountain birch forest cover and roughly corresponds to the tree line [Colour figure can be viewed at wileyonlinelibrary.com]

distinct stream types in this regional landscape (Table 1). Overall, the tundra stream represents a comparatively low nutrient, high disturbance environment while the birch forest stream is less physically stressful and more enriched with nitrogen and phosphorus (P, see below).

Differences in important habitat features between these two streams reflect their distinct catchment settings (Table 1). The catchment of the tundra stream is dominated by cryoturbated soils and supports Fennoscandian highland tundra vegetation, which is

TABLE 1 Physical and chemical characteristics of the streams. Median substrate size (d50) is determined from measurements of 300 particles. Discharge and temperature show the full range during the open water season. Flood response represents the percent increase in discharge during a flood event as compared to the previous 7 days. For detailed methods see Myrstener et al. (2021). Biomass accrual represents average growth rate over 5 weeks on tiles during 2017–2018

Variable	Unit	Stream	
		Tundra stream (M6)	Birch forest stream (M18)
Slope	m/m	0.04	0.02
Vegetation		Tundra	Birch forest
Substrate (D50)	cm	11	3
Discharge total range	L/s	9–178	19–158
Discharge during slugs	L/s	9–111	31–93
Flood response	%	80–320	25–70
Temperature	°C	0–12	2–9
Snow cover	months	6	2
Winter conditions		Dry/frozen	Partially flowing
Biomass accrual	$\mu\text{g Chl-}a/\text{cm}^2$	0.3	0.7
Gross primary productivity	$\text{g O}_2 \text{ m}^{-2} \text{ year}^{-1}$	47	222

floristically similar to tundra ecosystems in other parts of the Arctic (Virtanen et al., 2016), and includes dwarf shrubs such as *Empetrum hermaphroditum* and *Betula nana*. By contrast, the catchment of the birch forest stream is located in the valley bottom of this landscape and is underlain by glaciofluvial sediments that support productive mountain birch forest (*Betula pubescens* spp. *Czerepanovii*) and herbaceous understory. Compared to the birch forest stream, the channel of the tundra stream is steeper (slope 0.04 vs. 0.02 m/m) and has larger bottom substrates (e.g. median/90th percentile in substrate size: 11/53 vs. 3/7 cm). Average summer water temperature from 2015 to 2018 was similar between the two streams (6 ± 2 vs. $7 \pm 1^\circ\text{C}$) but the temporal variability and range in temperature was greater in the tundra stream (0–12 vs. 2–9°C; Figure 2). Similarly, mean discharge from 2015 to 2018 was 44 vs. 59 L/s in the tundra and birch forest stream respectively; yet the hydrographs are notably different (Figure 2). For example, tundra stream experienced five floods with an 80%–300% increase in discharge compared to the previous 6 days during 2016, while discharge in the birch forest stream never increased by more than 60%. In addition to a distinct flow regime, the tundra stream has as much as three times longer duration of ice cover than the birch forest stream (6 vs. 2 months), probably due to different water sources and the decrease in temperature with increasing elevation (c. 0.5°C per 100 m Sundqvist et al., 2011). Finally, field observations suggest that the tundra stream can freeze completely and cease flowing during winter (Myrstener et al., 2021; Rocher-Ros et al., 2020), whereas the perennial flow in the birch forest stream is supported by continuous groundwater influx and less soil freezing (R. Giesler, personal communication).

In addition to differences in physical properties, the tundra and birch forest stream also have distinct nutrient, light, and metabolic regimes. Overall, nutrient concentrations in the tundra stream tend to be low: soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN, $\text{NO}_3^- + \text{NH}_4^+$) averaged $0.7 \mu\text{g P/L}$ and $36 \mu\text{g N/L}$, respectively, during open water seasons of 2017 and 2018. Concentrations in the birch forest stream are low to moderate; SRP and DIN averaged $1 \mu\text{g P/L}$ and $84 \mu\text{g N/L}$, respectively, during open water seasons of 2017 and 2018. These differences are also reflected in the terrestrial surroundings, where tundra catchment is

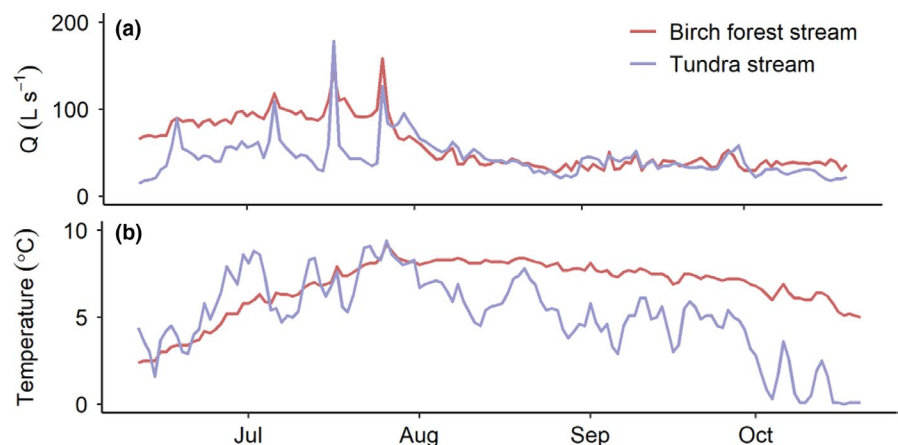


FIGURE 2 Daily discharge (Q, panel a) and temperature (panel b) in the birch forest stream (red) and the tundra stream (blue) during the open water season of 2016 [Colour figure can be viewed at wileyonlinelibrary.com]

dominated by heath vegetation poor in N (Björk et al., 2007) while the valley bottom stream drains a highly productive birch forest catchment, with an understory of herbaceous plant and more available soil N (Weih, 1998). There is also a strong seasonal pattern in DIN in both streams with high winter (up to 200 $\mu\text{g N/L}$) and low summer concentrations of 11 versus 36 $\mu\text{g N/L}$ in the tundra and birch forest stream, respectively. Light availability is lower in the birch forest stream compared to the tundra (average 10 vs. 40 $\text{mol m}^{-2} \text{day}^{-1}$) from June to September and it is possible that the birch forest stream experiences slightly limiting conditions for parts of the season, but is usually well above saturation (c. 7 $\text{mol m}^{-2} \text{day}^{-1}$, Hill et al., 1995). At annual time scales, the birch forest stream has higher average daily GPP ($1.2 \pm 0.5 \text{ SD}$ vs. $0.3 \pm 0.2 \text{ SD}$ $\text{g O}_2 \text{ m}^{-2} \text{day}^{-1}$) as well as annual GPP (222 vs. 47 $\text{g O}_2 \text{ m}^{-2} \text{year}^{-1}$) compared to the tundra stream (Myrstener et al., 2021). Consistent with this, estimates of biomass accrual on tiles during this project period (summer 2016) show nearly 3-fold greater rates of net growth in the birch compared to tundra stream in early summer (Lindberg, 2016).

2.2 | Metabolism estimates

To evaluate the influence of metabolic rates on N uptake, we estimated GPP and ER at both sites from June to October 2016 and additionally from April to October 2018 in the birch forest stream. We selected reaches that did not gain or lose more than 5% water over a 500-m stretch to minimise hydrologic inputs from groundwater and tributaries because uncertainty in lateral inflow can bias estimates of ER and GPP (Hall & Tank, 2005). Ultimately, all nutrient releases were performed well within the footprint of the oxygen sensors and associated metabolic estimates (e.g. 66% footprint: 500–1,000 m, see Demars et al., 2020). At five locations within each stream reach, we recorded light every hour using HOBO pendant loggers (Onset Computer Corporation) and converted lux to an estimate of photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) using a conversion factor of 0.0185 (Thimijan & Heins, 1983).

We recorded dissolved oxygen (DO) and water temperature continuously at 10-min intervals with miniDOT oxygen loggers (Precision Measurement Engineering Inc.). Each oxygen sensor was inter-calibrated three times: before, during, and after deployment with DO saturated water (100% DO after air bubbling) and DO depleted water (0% DO using dry yeast) and there was no drift above instrumental accuracy ($\pm 5\%$). We estimated GPP and ER from one station, open water metabolism using Bayesian inverse modelling (Hall & Hotchkiss, 2017) based on the time series of O_2 , water temperature and light (from Abisko Scientific Research station), and daily estimates of gas exchange rate coefficient (K) and stream depth (z). The main equation we used was:

$$\frac{d\text{O}_2}{dt} = \frac{\text{GPP} + \text{ER}}{z} + K(\text{O}_{2\text{sat}} - \text{O}_2)$$

where the change in oxygen over time ($\text{g O}_2/\text{m}^3$) equals all oxygen produced by photosynthesis (GPP, $\text{g O}_2 \text{ m}^{-2} \text{day}^{-1}$) minus all oxygen

consumed by respiration of both autotrophs and heterotrophs (ER, $\text{g O}_2 \text{ m}^{-2} \text{day}^{-1}$) and the rate of gas exchange between the water and air (K, day^{-1}). We modelled three parameters (GPP, ER, and K) but with tight priors set on K to reduce the problem of equifinality (Appling et al., 2018), i.e. where the same O_2 curve can be modelled with different combinations of the three parameters. To do so, we based priors for daily K estimates on propane releases and nighttime regression analysis (following Rocher-Ros et al., 2020). We selected days when the night-time regression produced K values with an $r > 0.6$, and then constructed linear models between K and discharge, to obtain daily estimates of K . Note that for both sites, propane releases following Wallin et al. (2011) generated estimates of K that agreed well with the night-time regression-based K . Finally, we filtered data for erroneous model days by using the mean average error between the observed and the modelled O_2 concentrations. All days with a mean average error larger than 0.2 were removed (Lupon et al., 2019). When GPP is very low, a poor model fit can still produce a small error; thus, we also visually inspected all remaining days to exclude clearly erroneous estimates. Finally, we averaged GPP and ER for 5–10 days around each nutrient release, depending on the number of available model days, to use for all statistical analyses.

2.3 | Nitrogen uptake measurements

In each stream, along the same reach where O_2 was measured, we conducted short-term nutrient additions (i.e. slugs) to estimate in-stream uptake of NO_3^- , where uptake represents the downstream loss of a nutrient compared to a conservative tracer (chloride, Cl^-). We conducted nine releases in each stream between the first week of June and last week of October 2016 and an additional six releases in the birch forest stream during 2018 to capture the full open water season in spring. Each release involved a short-term NO_3^- addition, with a 15–25 min travel time, and a target enrichment of 500 $\mu\text{g N/L}$. We based the reach lengths on travel time and discharge so that reach lengths averaged 250 m (± 100 m).

We used sodium chloride (NaCl) as the conservative tracer to assess hydrological parameters and made initial discharge estimates using the salt slug method following Moore (2005). All releases were performed between 10:00 and 15:00 in the day. We sampled water for background NO_3^- and Cl^- concentrations at the bottom of the reach before each release. In the first few releases, we also analysed water samples from the top of the reach and found no significant decreases in NO_3^- concentration between top and bottom stations. During each release, we manually recorded conductivity with a YSI Pro30 conductivity meter (Yellow Springs, OH, USA) and took water samples for NO_3^- and Cl^- on average every other minute with 30-s intervals at the peak of the breakthrough curve. We ran all NO_3^- samples from 2016 on an automated flow injection analyser (FIA star 5000, FOSS Analytical) and all samples from 2018 on a QuAAtro39 (Seal analytical). Chloride samples were run by Dionex DX-300, equipped with an AS14 column using electrical suppression (Dionex Corp.).

We used One-Dimensional Transport with Inflow and Storage (OTIS) to model hydrologic parameters based on Cl^- and NO_3^- removal in the main channel and storage zone area (Runkel, 2000). OTIS models the solute concentration through the downstream breakthrough curve by optimising parameter estimates and minimising the differences between modelled and observed concentrations (Figure S1). In the OTIS model for hydrological parameterisation of dispersion, main channel area (A), storage zone area (A_s), and exchange rate between main channel and storage zone (alpha, α), we used Cl^- calculated from electrical conductivity (EC). We based the EC to Cl^- correction on lab calibrations with the EC instrument as well as Cl^- concentration measured from the water samples during the releases, which both generated a conversion factor of 0.31. When modelling N uptake in OTIS, the hydrological parameters for dispersion, area, A_s and α can be used to estimate uptake in both the main channel (λ_1) and storage zone (λ_2 , Runkel, 1998). Here, the storage zone is defined by areas of slow flowing water and regions within the streambed infiltrated by stream water (i.e. hyporheic zones). We performed two sets of modelling exercises for NO_3^- uptake in OTIS. First, we estimated both λ_1 and λ_2 to compare main channel and storage zone uptake. Following this exercise, we modelled main channel uptake alone, in this case forcing all uptake, including that in the storage zone into the main channel uptake term to enable estimates of uptake metrics (S_w , V_f and U) based on the removal of NO_3^- in the entire ecosystem.

We followed conventions established by Webster and Valett (2006) when referring to and calculating nutrient uptake metrics, including: uptake length (i.e. the average length a solute travels before being removed from the water column; S_w , m); areal uptake rate (the flux of nitrogen to the stream bed; U , $\mu\text{g m}^{-2} \text{min}^{-1}$); and uptake velocity (a metric of nutrient use efficiency; V_f , mm/hr). Of these, V_f standardises uptake for changes in flow ($V_f = \text{discharge}/S_w \times \text{width}$) but also reflects the efficiency with which nutrients are used by the biological community (e.g. $V_f = U/\text{nutrient concentration}$), facilitating cross-system comparison. Finally, we estimated two additional metrics, which help describe the effect of the storage zone on nutrient uptake: the proportional size of the storage zone area compared to the main channel (A_s/A) and the average time a particle spends in the storage zone (t_{stor}), based on the storage zone exchange rate (α):

$$t_{\text{stor}} = \frac{1}{\alpha} \times \frac{A_s}{A}$$

2.4 | Nitrogen demand

We estimated the overall metabolic N demand for the purpose of having an integrated assessment of uptake by stream GPP and ER. We interpret these estimates in a relative sense as the absolute values are highly variable depending on chosen respiratory quotient, C:N molar ratios, growth efficiencies, and assumptions regarding autotrophic respiration. Units for N demand were expressed as $\mu\text{g N m}^{-2} \text{min}^{-1}$ so that they are directly comparable to

estimates of areal uptake (U). We based estimates of biological N demand on daily rates of GPP and ER with a respiratory quotient of one (1 mol $\text{O}_2 = 1$ mol C). For autotrophic demand we used a C:N molar ratio of 20 based on stream epilithon and filamentous algae (see Hall & Tank, 2003) and assumed net autotrophic production to be between 60% and 80% of total GPP, with the other 20%–40% being autotrophic respiration (Hall & Beaulieu, 2013; Thomas et al., 2005). This results in the following equation using moles of N:

$$\text{Autotrophic N demand} = \text{GPP} - (\text{GPP} \times \text{autotrophic respiration}).$$

In the same way, heterotrophic C assimilation is represented as heterotrophic production (HP) minus heterotrophic respiration (HR), where HR equals ER minus autotrophic respiration. For heterotrophic demand we assume C:N molar ratio of 5 for benthic, freshwater bacteria and fungi (Cross et al., 2005) but acknowledge that this ratio is highly variable. Heterotrophic production was based on a range of heterotrophic growth efficiencies (HGE) from 5% to 20% (Del Giorgio et al., 1997) and the equation:

$$\text{HP} = (-\text{HR} \times \text{HGE}) / (1 - \text{HGE})$$

In the end, the effect of varying the estimate of autotrophic respiration (40%–20%) on total N demand was <2%, so heterotrophic N demand was based on the assumption of 40% autotrophic respiration.

2.5 | Statistical analyses

We assessed the drivers of uptake velocity (V_f) during the full experimental period in each stream and in both streams together using partial least square regressions (PLSR) using the R package *pls* and leave-one-out cross-validation. PLSR identifies linear, multivariate correlations between predictor and response variables and produces latent variables to maximise the explained variability in Y and reduce the original multidimensionality, similar to a principal component analysis (Carrascal et al., 2009). PLSR is particularly strong in our situation with a sparse modeling problem here there are more covariates (X-variables) than estimates of V_f (Y-variable). We identified the most important predictors based on variables important in projection (VIP) scores above 0.9 (Mehmood et al., 2012). We included light (PAR), temperature, discharge, NO_3^- concentration, proportional storage zone area (A_s/A), the average time a particle spends in storage zone (t_{stor}), GPP and ER in the model. We further used linear regressions to test for relationships between GPP, ER, and independent variables such as NO_3^- , light, temperature, and Q. All results are presented ± 1 SD. All regression models were initially checked for possible serial autocorrelation in the residuals using the Durbin-Watson test in R (package *lmtest*) and no significant autocorrelations were found.

3 | RESULTS

3.1 | Stream templates (chemical, hydrological, physical, and morphological properties)

Considering both sites, stream habitat conditions during nutrient releases spanned broad gradients in discharge (9–111 L/s), temperature (0–12°C), estimated instantaneous light (15–600 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and background concentrations of NO_3^- (11–213 $\mu\text{g N/L}$). Note that two releases were performed during ice formation or under ice and snow cover with extremely low discharge: these included the last release in the tundra stream (in October) and the first release in 2018 in the birch forest stream (April); otherwise, all releases reflect *open water* conditions. Overall, and as expected, physical and chemical properties at these two sites were distinct throughout this study period (Figure 1; Table 1; Table S2). In addition to these differences, the proportional storage zone area (A_s/A) was on average 0.08 (± 0.01) in the tundra stream and twice that in the birch forest stream (0.2 ± 0.03); however, the average time a particle spent in storage zones (t_{stor}) was similar; 176 ± 86 versus 157 ± 61 s in the tundra and birch forest stream, respectively.

3.2 | Metabolic rates

Daily GPP differed 10-fold between the two streams and over the whole experimental period, averaging $0.1 \pm 0.07 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the tundra stream, $1.0 \pm 0.5 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the birch forest stream during 2016, and $1.4 \pm 0.5 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the birch forest stream during 2018 (Table S2). Daily GPP on the days of the releases captured the seasonal range in GPP well and was 0.01–0.2 $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the tundra stream and 0.04–1.7 $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the birch forest stream. Average gas transfer velocity (k_{600}) in the birch forest site was 16.4 day^{-1} in 2018 and 17 day^{-1} in 2016 while average k_{600} in the tundra stream was 21.3 day^{-1} . Differences in GPP bracketing nutrient release days were linearly related to variation in background NO_3^- concentration during summer and early autumn in the tundra stream ($r^2 = 0.88$, $n = 7$, slope = 0.003, intercept = 0.03, $p = 0.002$), but not when accounting for the full season that included the first and last releases close to ice off and under ice ($r^2 < 0.01$, $n = 9$, $p = 0.9$). GPP during releases in the birch forest stream on the other hand was unrelated to all measured environmental variables (N, light, temperature and Q, $r^2 < 0.1$, $p > 0.05$). ER rates were orders of magnitude higher than GPP in both streams and averaged $3.4 \pm 1.4 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the tundra, $8.6 \pm 3.3 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the birch forest stream during 2016, and $12.4 \pm 3.1 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ in the birch forest stream during 2018. ER in the tundra stream was not significantly related to any of the environmental variables, including GPP (or NO_3^- , temperature or light), except for a weak positive, linear relationship with Q ($r^2 = 0.33$, $n = 9$). In the birch forest stream on the other hand, ER was closely related to GPP ($r^2 = 0.63$, $n = 15$) when including both years, but was not linearly related to any other environmental variables, including Q.

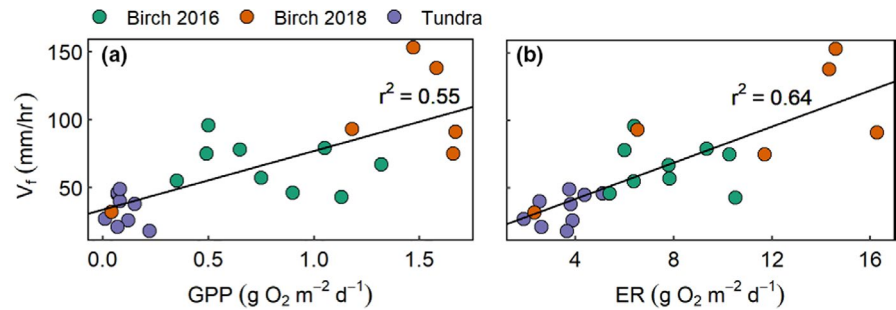
3.3 | Nitrogen uptake parameters from OTIS

The main channel NO_3^- removal rate (λ_1), as estimated from OTIS, was 0.20–0.32 hr^{-1} in the tundra stream and 0.11–0.8 hr^{-1} in the birch forest stream (Table S1). Storage zone NO_3^- removal rates (λ_2) were similar between the streams and occasionally higher than in the main channel, ranging from 0.04 to 1.61 hr^{-1} in the tundra stream and 0.01 to 1.73 hr^{-1} in the birch forest stream. The highest storage zone removal rates were observed during releases under ice or close to ice-on periods for both the tundra and birch forest stream, and the overall percentage of V_f attributed to uptake in transient storage zones was higher in the birch forest stream compared to in the tundra. The tundra stream also experienced elevated storage zone removal rates on a few occasions during the open water season; however, the contribution to V_f (i.e. total uptake) was always lower than in the birch forest stream.

3.4 | Uptake length, areal uptake, and uptake velocity

Uptake length (S_w), areal uptake (U), and uptake velocity (V_f) was calculated based on OTIS modelling accounting for uptake in both the storage zone and the main channel. Here, NO_3^- uptake was consistently lower in the tundra stream compared to the birch forest stream, considering all three uptake metrics (Table S3), and uptake in 2018 was considerably higher compared to 2016. Average uptake length (S_w) was 2,324 m in the tundra stream but was only 1,552 m in the birch forest stream during 2016. During the open water season (excluding under ice releases), U averaged $17 \pm 7 \mu\text{g N m}^{-2} \text{ min}^{-1}$ in the tundra stream, $77 \pm 49 \mu\text{g N m}^{-2} \text{ min}^{-1}$ in the birch forest stream in 2016, and $172 \pm 85 \mu\text{g N m}^{-2} \text{ min}^{-1}$ in the birch forest stream 2018. Similarly, V_f averaged $36 \pm 11 \text{ mm/hr}$ during the open water season in the tundra stream, $66 \pm 18 \text{ mm/hr}$ in the birch forest stream during 2016, and $110 \pm 39 \text{ mm/hr}$ in the birch forest stream during 2018. There was a seasonal trend in U in both streams with highest uptake in spring and autumn and lowest uptake in summer, which as driven by the positive, linear relationships between U and NO_3^- concentration ($r^2 = 0.78$ and 0.92 in the birch forest and tundra stream respectively, Figure S3). Uptake velocity (V_f), which reflects the efficiency with which nutrients are used, was best explained by ER, GPP and the relative size of the storage zone (A_s/A) when analysing both streams together (PLSR, correlation scores ≥ 0.8 , VIP score > 1.3 , Figure S4). Individually, GPP and ER explained 50%–60% of the variability in V_f across both sites (linear regression, $r^2 = 0.55$ and 0.64 respectively, $p < 0.001$, Figure 3). When the streams were separated, regressions between V_f and GPP and ER were only significant in the birch forest stream ($r^2 = 0.31$ and 0.64, $p = 0.03$ and $p = 0.007$ for GPP and ER respectively), and not the tundra stream (negative slope, $r^2 = 0.13$, $p = 0.3$ and $r^2 = 0.24$, $p = 0.18$ for GPP and ER, respectively). Areal uptake (U) was not related to GPP or ER in any of the streams ($p = 0.16$ –0.6).

FIGURE 3 Uptake velocity (V_f) against gross primary productivity (GPP, panel a) and ecosystem respiration (ER, panel b) during the open water season. Regression lines include all data and are significant at $p < 0.001$ (GPP) and $p < 0.001$ (ER). The slope of the regression line is 43 for GPP and 7 for ER [Colour figure can be viewed at wileyonlinelibrary.com]



When analysing the streams separately, V_f in the tundra stream was instead best explained by Q , temperature, and PAR (VIP score = 1.4 to 1.0, correlation score = 0.90) and NO_3^- (VIP score = 1.2, correlation score = -0.9) with a seasonal pattern of highest V_f during summer (PLSR, 76% of variance explained by first component, Figure 4). There was no clear seasonal trend in the birch forest stream, where V_f was best explained by ER (VIP score = 1.9, correlation score = 0.9), GPP (VIP score = 1.6, correlation score = 0.9) and t_{stor} (VIP score = 1.1, correlation score = -0.7, Figure 4). The birch forest stream was more efficient at removing NO_3^- from transport compared to the tundra stream when they had similar background concentrations of NO_3^- : at 60–70 $\mu\text{g N/L}$, the tundra stream had an areal uptake rate of 19–31 $\mu\text{g N m}^{-2} \text{min}^{-1}$, while the birch forest stream removed 50–150 $\mu\text{g N m}^{-2} \text{min}^{-1}$ (Figure S3).

3.5 | N demand

Autotrophic demand as calculated based on GPP and ER was 0–7 $\mu\text{g N m}^{-2} \text{min}^{-1}$ in the tundra stream and 1–54 $\mu\text{g N m}^{-2} \text{min}^{-1}$ in the birch forest stream. Average autotrophic N demand in the tundra and birch forest stream together ranged from 16 to 23 $\mu\text{g N m}^{-2} \text{min}^{-1}$ using 40% and 20% autotrophic respiration, respectively. Heterotrophic N demand was 5–52 $\mu\text{g N m}^{-2} \text{min}^{-1}$ in the tundra and 6–161 $\mu\text{g N m}^{-2} \text{min}^{-1}$ in the birch forest stream. Average

heterotrophic N demand in the tundra and birch forest stream together ranged from 17–68 $\mu\text{g N m}^{-2} \text{min}^{-1}$ using 5 and 20% bacterial growth efficiency, respectively. Combined, autotrophic and heterotrophic demand matched areal uptake rates (U) well during summer when using the higher heterotrophic growth efficiency of 0.2 ($r^2 = 0.51$, $p = 0.001$, Figure S5) but in early spring and late autumn in the birch forest stream, N demand based on GPP and ER were lower than measured areal uptake rates. Note that the background concentrations of DIN are higher during early spring and late autumn, which increases areal uptake rates. Demand correlated more strongly with uptake velocity ($r^2 = 0.64$, $p < 0.001$, Figure S6) across the full season, including all releases, compared to areal uptake rates.

4 | DISCUSSION

Nutrient uptake in streams and rivers can alter the timing and magnitude of nutrient fluxes from soils to downstream ecosystems (Bernhardt et al., 2005; Bernal et al., 2019). Identifying the factors that regulate the capacity for nutrient uptake in high-latitude streams is thus important for understanding how climate-driven changes in soil nutrient cycling and export (e.g. Kendrick et al., 2018; Salmon et al., 2016) may be propagated downstream in these landscapes. Here, we show how differences in catchment setting can lead to distinct patterns of nitrate uptake in two high

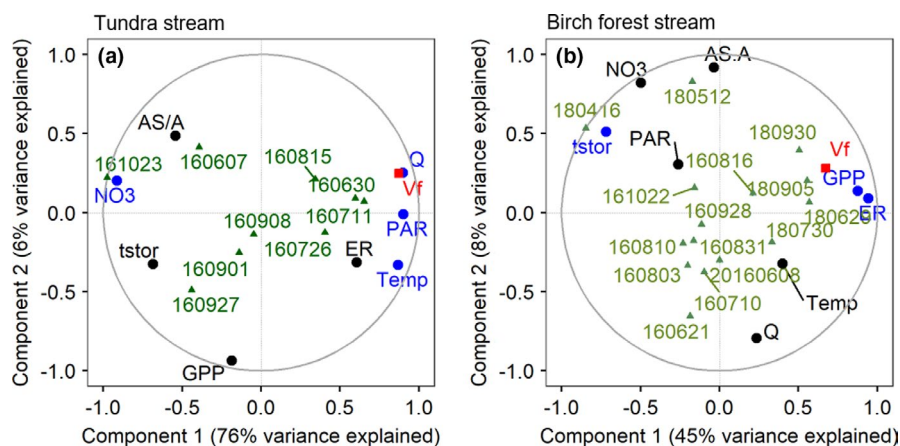


FIGURE 4 Results from a partial least square regression (PLSR) using uptake velocity (V_f) as the response variable in the tundra stream (a) and birch forest stream (b). Plotted are correlations between predictors (blue being most important in projection and black non-important) and the response variable (N uptake, red) against the model scores of each NO_3^- release (presented as dates in year-month-day, green). Each stream model score on the two components is normalised to fit the -1 to 1 axes [Colour figure can be viewed at wileyonlinelibrary.com]

latitude streams through the effects of geomorphology, stream nutrient concentrations, and metabolic activity. Specifically, instantaneous uptake, both in terms of efficiency and total removal, was greatest in the birch forest stream, which had higher background NO_3^- concentration and greater metabolic rates compared to the tundra counterpart. Although our spatial scope of inference is limited, these results suggest that Arctic and sub-Arctic streams have the potential to take up nutrients at rates comparable to streams in other biomes, but their potential is highly sensitive to local habitat features that constrain biomass accumulation and biotic demand.

4.1 | Drivers of nitrate uptake

Our observations support the hypothesis that trends in uptake for the tundra stream were shaped by physical drivers and NO_3^- concentration rather than by variation in metabolic demand. Overall, both metabolic rates, areal NO_3^- uptake (U) and uptake velocity (V_f) at this site were low compared to global rates (Hall et al., 2009; Rocher-Ros et al., 2020), and with little variation throughout the study period, even though habitat factors such as discharge and nutrient concentration varied and co-varied considerably. These conditions make interpreting the relationship between individual drivers and specific uptake metrics a challenge. However, low GPP and biomass standing stocks in this tundra stream have been attributed to low stream nutrient concentrations, long ice cover duration, and regular flooding (Myrstener et al., 2018). Such low biotic potential and variable NO_3^- concentrations resulted in a negative relationship between uptake velocity (V_f) and NO_3^- concentration (Figure 4; Figure S2), presumably because metabolic rates fail to keep pace with relatively large and/or rapid changes in N supply in spring and autumn. Furthermore, even though there was a strong linear relationship between NO_3^- and GPP during the open-water season, ER did not follow this pattern, and thus the total N demand was poorly associated with stream NO_3^- concentrations. Although speculative, the relationship between measured uptake and estimated demand suggests that the tundra stream approached N saturation in spring and autumn, when NO_3^- concentrations were slightly higher, and other factors probably limit biomass accrual and demand at that time (Hoellein et al., 2007). Altogether, our results suggest that metabolic activity, and thus demand for N, were relatively low in this tundra stream and that physical and chemical properties best predicted rates of nutrient uptake. Given that this stream is representative of a large fraction of the drainage network in this region (Myrstener et al., 2021), we suspect these physico-chemical forces probably act as important drivers of nutrient cycling across this broader landscape. Confirmation of these results in other Arctic regions will be important to understanding how these streams will respond to future climate conditions.

At the other end of the our habitat template, the small birch forest stream, with *spring-like* characteristics, and relatively low chemical and physical variability, represents a less common habitat type

in the Fennoscandian Arctic landscape (Myrstener et al., 2021; Weih, 1998). At this site, our observations support the hypothesis that metabolic demand can control variation in uptake metrics, ostensibly because habitat conditions were more suitable for benthic biomass accrual and associated biological activity. Indeed, rates of ER and GPP were significantly higher in the birch forest stream compared to the tundra counterpart, and were similar to rates in other biomes (Hoellein et al., 2013). These differences in metabolic rate are also mirrored by patterns of chlorophyll-*a* accumulation and standing stocks throughout the year (Table 1; Myrstener et al., 2021). At this site, metabolic rates were positively correlated with uptake velocity (V_f ; Figure 3), as observed in other nutrient poor streams (Hall & Tank, 2003), but were not significantly related to areal uptake rate (U). This counterintuitive result may simply be an artifact of the different times scales associated with our measurements of metabolism (a multi-day average) versus nutrient uptake (an hour during midday) and the noise that this can create. Areal uptake rates did increase with estimated metabolic demand across sites, particularly during the open water season, but this relationship was weak when considering all observations (Figure S5). The relationship between metabolic rates and the efficiency with which nutrients were used was considerably stronger (as reflected by V_f ; Figure S6). Understanding exactly why this discrepancy arises is beyond our scope of inference but may relate to complexities associated with nutrient co-limitation. Recent work suggests that metabolic rates at this site are more strongly correlated with the availability P than N (Myrstener et al., 2021). In fact, both the tundra and birch forest stream are likely to reside close to N and P co-limitation (Myrstener et al., 2021). While we are not able to directly assess this here, others have shown how N and P supply interact to shape patterns of uptake and how limitation by one nutrient impacts the nutrient use efficiency of a non-limiting nutrient (Piper et al., 2017; Schade et al., 2011; Tromboni et al., 2018). Regardless, biotic potential is large enough in the birch forest stream that biological activity, rather than NO_3^- supply, appears to control the efficiency of NO_3^- use. Such patterns illustrate how longer-term nutrient supply regimes, which promote the accrual and activity of benthic biomass, can regulate how high latitude streams respond to short-term changes in nutrient supply, whether those occur naturally or through fertilisation (e.g. Slavik et al., 2004).

4.2 | Among site drivers of nitrate uptake

Uptake rates in Miellajokka were comparable to streams with similar metabolic rates and background N concentrations (e.g. Fellows et al., 2006; Hall & Tank, 2003; Hall et al., 2009). This finding suggests that the capacity to remove N in these streams did not differ drastically when compared to streams in other biomes. However, when exploring differences between our two streams, we find that, contrary to the commonly observed negative relationship between uptake velocity and N concentration (Hall et al., 2009; Mulholland

et al., 2008), uptake velocity was instead higher in the higher N, birch forest stream. We suggest that this deviation from the expected relationship reflects the greater biomass standing stock and metabolic activity achieved in the birch forest stream, which arise from increased nutrient supply and greater hydrological and thermal stability. In addition to these biological factors, our results also suggest that distinct geomorphic features between the upland tundra and valley bottom stream contributed to the observed differences in uptake capacity. For example, transient storage zones accounted for a larger fraction the V_f in the birch compared to the tundra stream. These differences exist despite similar hydrologic residence times in the transient storage zones of each stream, suggesting that associated biota in the birch stream were particularly efficient in retaining NO_3^- . The greater contribution of the transient storage zone to V_f in the birch stream may be driven by substrate properties that facilitate vertical exchange, but also by the relatively stable thermal and hydrological conditions that characterise this site. Combined, these features lead to higher areal uptake rates and uptake velocities in the birch stream compared to the tundra counterpart, even during periods of similar ambient N concentration. These observations suggest that in-stream NO_3^- concentration can be a poor predictor of nutrient uptake efficiency, as recently observed in Greenlandic streams, where other factors also appear to limit biomass accrual and activity (Skovsholt et al., 2020).

While based on just two sites, the higher V_f in the stream with greater NO_3^- concentrations illustrates how differences in biotic potential, as reflected in biomass standing stocks and metabolic rates, can shape spatial variation in nutrient removal efficiency. The commonly reported reduction in V_f with increasing nutrient concentrations occurs because nutrient supply often outpaces the ability of the biotic community to upregulate removal from the water column. Thus, for situations where biomass and metabolic activity are weakly linked to nutrient supply and/or limited by some other factor (e.g. a different element, light, and/or temperature), uptake velocity will decline as nutrient availability increases (Hall et al., 2009), which is what we observed over time in the tundra stream during open water conditions. However, variation in V_f can also be driven by changes in uptake (U), and thus increase with rates of metabolic activity (e.g. O'Brien et al., 2007; Plont et al., 2020), as we observe across our streams. Importantly, for catchments like the Miellajokka, where among-site variation in biotic activity is driven in part by the availability of limiting nutrients (Myrstener et al., 2021), the emergent variation in biological demand can overwhelm patterns of uptake efficiency, leading to positive relationships between V_f and nutrient concentrations across sites. Given that differential nutrient supply has been identified as a driver of biomass accrual across Arctic streams elsewhere (Huryn et al., 2005), this positive relationship between V_f and background nutrients may be common for this biome. While this idea requires additional study, our results support the premise that metabolically derived estimates of nutrient demand (e.g. Webster et al., 2003) help explain variance in the relationships between uptake efficiency and concentration across streams and better inform our

understanding of how nutrient supply and demand are related in stream ecosystems (Covino et al., 2018).

4.3 | Applying the Arctic habitat template to biogeochemistry

We broadly aimed to incorporate ideas from the habitat template approach, which has proven useful for understanding variance in Arctic stream food webs (Huryn et al., 2005), into a framework for understanding nutrient uptake. Although we only did this at two streams, we show that the stable, more nutrient rich stream (birch forest stream), supports relatively high periphytic biomass, rates of GPP, rates of nutrient use (as areal N uptake) and the efficiency of nutrient use (as V_f) compared to the more physically dynamic stream with lower ambient nutrient concentrations (tundra stream). Support for this framework can also be found in the uptake patterns reported for other Arctic streams that display distinct habitat properties. For example, the high physical stability and elevated nutrient side of this template includes Arctic springs (Huryn et al., 2014) as well as small Yedoma and floodplain streams in Siberia (Schade et al., 2016), which all support relatively high nutrient uptake rates. By comparison, studies from Arctic streams with intermediate levels of stress have shown low but measurable N uptake, potentially supported by higher bed stability that promotes some autotrophic or heterotrophic biomass (Blaen et al., 2014) and/or elevated rates of sediment respiration (Docherty et al., 2018). Finally, at the other end of this habitat template, many streams in eastern Greenland and Svalbard have no measurable nutrient uptake using enrichment approaches due low biomass, high physical stress, and/or limiting levels of other (non-target) nutrients (Blaen et al., 2014; Docherty et al., 2018). Combined, these studies highlight how differences in the habitat template and geomorphic setting shape Arctic streams in ways that influence when and where biotic versus abiotic drivers govern nutrient uptake.

Variation in the Arctic habitat template has predictable implications for how streams function and how this may change under future climate conditions. For example, we hypothesise that in streams where biomass and nutrient use is limited by stressful physical or chemical conditions, areal nutrient uptake rates will be largely insensitive to short-term changes in environmental drivers (e.g. isolated increases in temperature) because benthic standing stocks are too small to produce strong responses. Similarly, to the extent that biotic processes during the open water season are constrained by physical drivers in the winter and spring (e.g. freezing, ice cover), streams may have limited capacity to respond efficiently to summertime nutrient increases (e.g. via permafrost thaw). By comparison, streams with more benign habitat templates hold the potential to increase nutrient uptake in response to higher temperatures and/or increases in nutrient supply from warming upland soils. Under stable habitat conditions, our findings suggest that the efficiency of nutrient removal can increase

with nutrient supply if biomass accrual and activity equals or exceeds changes in nutrient availability. We argue that this relationship is driven by differences in the physico-chemical template of these streams and its influence on how biomass accrual and activity change with nutrient supply. Further work is necessary to evaluate the generality of these findings but we posit that the habitat template framework may prove to be a powerful tool for predicting the biogeochemical impacts of multiple environmental changes expected under climate change in high latitude landscapes.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from Zenodo at <https://zenodo.org/record/4604633#YE8-DWhKpY>, reference number <https://doi.org/10.5281/zenodo.4604633>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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