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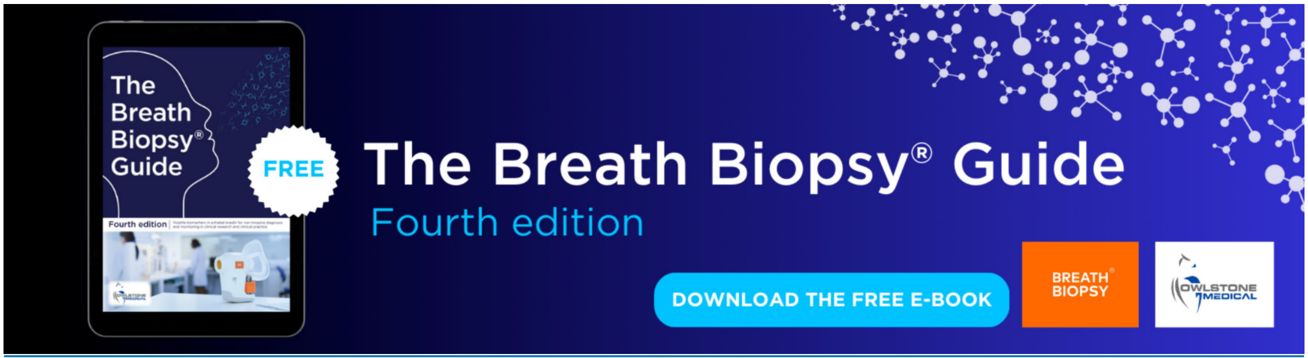

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Missing nitrogen source during ecosystem succession within retrogressive thaw slumps in Alaska

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Abstract

Retrogressive thaw slumps (RTS)—thermal erosion of soil and vegetation after ground ice thaw—are increasing. Recovery of plant biomass after RTS is important for maintaining Arctic carbon (C) stocks and is regulated by nutrient availability for new plant growth. Many RTS are characterized by verdant shrub growth mid-succession, atypical of the surrounding nutrient-limited tundra. Here, we investigated the potential for internal and external sources of nitrogen (N) and phosphorus (P) to support mid-successional shrub growth at three Alaskan RTS chronosequences. We assessed patterns of soil and microbial CNP, soil NP cycling rates and stocks, N inputs via biological N_2-fixation, and thaw leachate over time after disturbance. We found a clear transfer of P stocks from mineral to organic soils with increasing site age, yet insufficient N from any one source to support observed shrub growth. Instead, multiple mechanisms may have contributed to mid-successional shrub growth, including sustained N-cycling with reduced plant biomass, N leaching from undisturbed tundra, uninvestigated sources of N_2-fixation, and most promising given the large resource, deep mineral soil N stocks. These potential mechanisms of N supply are critical for the regulation of the Arctic C cycle in response to an increasingly common climate-driven disturbance.

1. Introduction

Disturbances in Arctic systems undermine the stability of a pool of permanently frozen soil (permafrost) carbon (C) that is large (∼1000 Pg C in top 0–3 m (Tarnocai *et al* 2009, Schuur *et al* 2022)), and vulnerable to climate change (Ping *et al* 2015, Schuur *et al* 2015). This is particularly the case with thermokarst disturbance, the incidence of which is increasing with a warming climate (Osterkamp 2005, Lantz and Kokelj 2008, Belshe *et al* 2013, Segal *et al* 2016, Kokelj *et al* 2017, Ward Jones *et al* 2019). Thermokarst occurs when permafrost abruptly thaws and subside. On river and lake slopes, thermal erosion by water, combined with sustained air temperatures, thaws soil ice wedges and can result in various types of thermokarst features, including retrogressive thaw slumps (RTS; (Schuur *et al* 2008, Abbott and Jones 2015)). In a RTS, the active layer soil and vegetation slides off the underlying ice leaving the disturbed slope devoid of soil organic matter, or it retains 'rafts' of tundra organic matter that float on the now-melted mineral slurry (Lantuit and Pollard 2008, Pizano *et al* 2014). The spatial cover and persistence of these rafts is not consistent across the Arctic and will vary with slope and ground-ice patterns. These slope disturbances vary in size from small local slump scars (∼1–5 m) to very large scars (∼ha) and are evident on the landscape for 100+ years after the initial disturbance (Lantuit *et al* 2012, Segal *et al* 2016). The process of landscape recovery is slow and the few studies that have investigated scars of different age to understand landscape recovery processes indicate shifts in vegetation succession that are different than those normally found in undisturbed Arctic vegetation (Burn and Friele 1989, Lantuit *et al* 2012, Pizano *et al* 2014, Cray and Pollard 2015).

Nitrogen (N) and phosphorus (P) limit primary productivity in most terrestrial ecosystems and their availability determines the pattern of ecosystem recovery after disturbance (Vitousek *et al* 1993, Chapin *et al* 1994, Van Cleve *et al* 1996, Rastetter *et al* 2020). The mechanisms that control N and P availability during recovery vary with the initial extent of the disturbance (Vitousek *et al* 1989). Primary succession, which begins with complete removal of soil organic matter (i.e. recovery after glacial retreat or volcanic activity), is strongly dependent on external N inputs (i.e. N fixation and deposition) for initial ecosystem development. Secondary succession, in which soil organic matter remains, typically has a large stock of N remaining in the organic or mineral soil (Yanai *et al* 2013) (i.e. clear cut logging), and initially loses nutrients but recovers rapidly; the most limiting nutrients are retained while non-limiting nutrients continue to be lost during ecosystem recovery (Rastetter *et al* 2020). Both types of ecosystem development are also dependent on ecosystem state factors, vegetation feedbacks (i.e. facilitation) and possibly, allochthonous inputs (Jenny 1941, Chapin *et al* 1994, Van Cleve *et al* 1996, Vitousek *et al* 2010). Recovery from many ecosystem disturbances including RTS, however, do not fall easily into either of these end-point categories of succession type, but rather fall somewhere between primary and secondary succession, with varying amounts of soil organic matter retention (Walker *et al* 1996, 2009, Schuur and Mack 2018). This makes it more difficult to predict the mechanisms controlling N and P cycling and availability in a recovering ecosystem. Understanding these mechanisms within the framework of a rapidly-changing Arctic is important because climate feedbacks, including thermokarst, are just as important as primary climate drivers for controlling the vast Arctic C store (Schuur and Abbott 2011, Schuur *et al* 2015).

Arctic ecosystems are renowned for their strong nutrient limitation for plant growth and microbial activity (Shaver and Chapin 1980, McLaren and Buckeridge 2019). In these strongly nutrient-limited ecosystems, the sources of N and P for ecosystem recovery after thermokarst are unclear, particularly when most of the organic matter is lost during the initial slump disturbance. Further, given the hypothesized limited nutrient availability, it is particularly startling that the typical trajectory in this region of vegetation succession 15–50 years after thermokarst is characterized by large and abundant shrub growth (especially *Salix glauca*, but also *Salix pulchra and Betula nana*), with aboveground biomass production far exceeding that of the surrounding tundra (Pizano *et al* 2014, Huebner and Bret-Harte 2019). In northern Canada, this shrub-stage of succession can persist for close to a century (Lantz *et al* 2009). Therefore, we have an overarching research question: where do the nutrients come from to support this verdant shrub growth relatively soon after extensive ecosystem disturbance?

We propose that the nutrients required for this shrub growth are supplied both internally, such that nutrients are elevated in the organic and mineral soils within the RTS through various mechanisms, and externally, in which nutrients enter the RTS from outside the RTS spatial boundaries (figure 1). We also propose that the importance of internal vs externally sourced inputs increases through successional time. In earlier stages of succession, drained, thawed, and warmed rafts of organic matter remain dotted across exposed mineral soil after slumping. The warmer temperatures and aerated soil on these rafts of organic soil may support enhanced microbial activity and vegetation feedbacks, as compared to the surrounding mineral soil, seeding future plant growth (figure 1, H1). In latter stages of succession this internal cycling may increase as early successional plants produce litter and contribute nutrients to SOM and the pool of organic matter increases in the soil over time (figure 1, H1alt). Internal N and P resources also include extant and newly available NP-stocks from thawed permafrost, which may transfer from below to above ground over successional time (enhanced initially by increases in thaw depth, (Salmon *et al* 2016)) (figure 1 H2). Externally, biological N fixers, which provide an important allochthonous source of N in early primary succession landscapes (Chapin *et al* 1994, Rastetter *et al* 2001, Vitousek *et al* 2002), should decrease across succession as they become out-competed by shrubs and sedges (figure 1 H3). Finally, the importance of external (allochthonous) inputs will decrease across the slump recovery area over time as increased organic matter and vegetation cover will result in higher top-slope interception of leachate inputs in late succession as nutrient cycles becomes progressively less open (Rastetter *et al* 2020) (figure 1 H4). Resolving the mechanisms in these RTS across time clarifies the drivers of post-thaw ecosystem recovery in Alaskan permafrost ecosystems.

To examine the importance of these hypothesized internal and external processes on ecosystem succession, we examined how N and P cycling, stocks and inputs changed across RTS recovery chronosequences in Alaskan arctic tundra. In three nearby RTS chronosequences with different underlying geology but

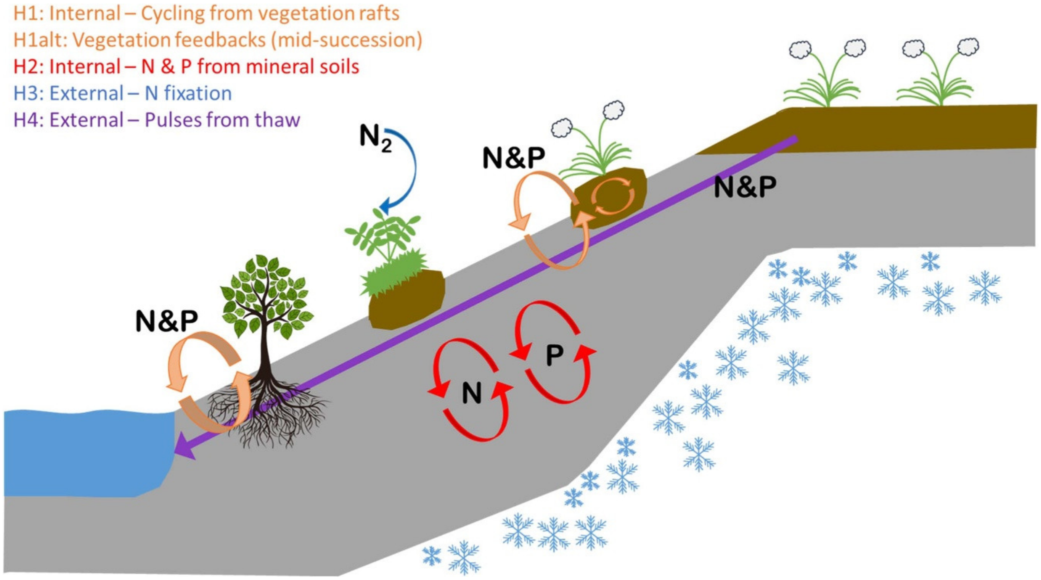

Figure 1. Hypothesized internal and external processes that may supply nutrients to ecosystem succession. Internally resourced nutrients include (H1) microbial and vegetation feedbacks (orange arrows) from vegetation rafts in early stages of succession, or from (H1alt) shrub communities in mid-succession and (H2) nitrogen and phosphorus in the mineral soil stocks, including possible newly released soil from thawing permafrost (red arrows). Externally acquired nutrients include (H3) biological N_2-fixation (blue arrows) from mosses and legumes which may be higher in abundance in earlier stages of succession, and (H4) leachate from non-disturbed organic soils at the top of the thaw slump (purple arrows) which flows down the slope.

similar climate, vegetation, and slope aspect, we investigated the above four mechanistic hypotheses of nutrient sources required to fuel shrub growth. We test H1 by measuring gross ammonium mineralization and net N and P mineralization rates, as well as microbial biomass C, N and P stocks, with the prediction that rates will be higher in the early-chronosequence organic soils (the organic rafts, H1) or mid-succession (H1alt); H2 using data on C, N and P-stocks in organic and mineral soil, with the prediction that soil N and P should increase in the organic soil and decline in the mineral soil with time since disturbance; H3 using data on legume and moss cover and nodule abundance, with the prediction that both will be higher in early succession; and H4 using ion-exchange resin bags deployed beneath the snowpack (subnivean), over the course of snowmelt, with the prediction that N inputs and outputs will be higher in early succession, but with net higher inputs.

2. Methods and materials

Methods and materials are explained in more detail in supplemental material (Buckeridge 2023). Briefly, we investigated patterns of ecosystem succession at three upland RTS chronosequences near Toolik Lake, Alaska. Each chronosequence (table 1) contained 2–4 scars of varying age since disturbance (age determined as in (Pizano *et al* 2014)).

Young scars (‘Recent’) were dominated by exposed mineral soil formed from the permafrost slurry after thawing, dotted by rafts (~0.2 m^2) or stripes of tundra vegetation (‘Recent organic’) with exposed mineral soil (‘Recent mineral’) between them. Mineral soil was either bare, or covered in biocrusts, thin moss, *S. glauca* seedlings or, in the spring, mats of *Equisetum* and varied in pH, bulk density and total C and N (table 1). Mid-succession scars (‘Shrub’) had a thin layer of organic soil (‘Shrub organic’) above mineral soil (‘Shrub mineral’) and were dominated by shrubs (*B. nana, S. glauca* and *S. pulchra*) denser and taller (up to 2 m) than those on the undisturbed tundra. The vegetation and topography of very old scars (~150 years; ‘Old’) were almost indistinguishable from the surrounding tundra and were detected only through remote sensing (Google Earth images) by the headwall shadow and scar edges. Transects were established in the central, stable part of the slump or the undisturbed tundra above with five plots along transects.

For H1, we collected two adjacent organic and mineral cores in June for determining net N and P mineralization rates and microbial biomass C (MBC), N (MBN) and P (MBP) stocks. The second (‘final’) core was immediately re-deployed into the original hole in a polypropylene tube with an ion exchange resin bags above and two below the soil (DeMarco *et al* 2011) and then collected in September (71–76 d incubation). After

Table 1. Properties of the retrogressive thaw slumps (RTS).

					Organic soils			Mineral soils				
RTS	Age category	Age (y)[a]	Vegetation cover (%)[a]	Organic horizon depth (cm)	pH	Bulk density (g cm^{-3})	Gravimetric soil water content (kg m^{-2})	pH	Bulk density (g cm^{-3})	Gravimetric soil water content (kg m^{-2})	Max. organic soil temp. (°C)[b]	Min. organic soil temp. (°C)[b]
NE-14 (68.68 N, 149.62 W)	Recent	5	43	9.3	6.8	0.25	7.1	8.4	1.15	15.8	15.0	−5.5
	Shrub	44	100	5.2	7.6	0.14	9.9	8.2	1.28	24.7		
	Shrub	50	100	7.3	7.1	0.09	13.5	7.4	1.07	29.2		
	Old	~150	100	8.3	6.7	0.19	42.6	7.4	1.06	29.7		
	Undisturbed	>1000	100	6.0	6.6	0.15	27.4	6.6	0.91	49.5	13.5	−15.5
Iminus-1 (68.55 N, 149.58 W)	Recent	8	17	8.6	5.2	0.25	7.5	6.5	0.93	23.8	13.5	−7.0
	Shrub	16	17	8.0	5.9	0.20	3.8	7.3	1.00	26.4		
	Shrub	25	33	8.3	5.6	0.26	9.5	6.4	0.77	30.7		
	Old	~150	100	7.5	6.4	0.10	17.2	6.8	0.93	43.5		
	Undisturbed	>1000	100	9.1	5.0	0.18	37.8	4.6	0.59	52.5	12.5	−18.0
Itkillik 2 (68.67 N, 149.82 W)	Recent	8	67	9.7	7.3	0.19	29.8	7.8	1.30	21.3	15.0	−12.0
	Undisturbed	>1000	100	8.5	7.4	0.17	35.6	7.1	0.70	51.6	13.5	
Itkillik 3 (68.67 N, 149.84 W)	Shrub	54	100	7.4	7.8	0.13	15.9	8.2	1.28	32.1	12.0	−5.5
	Undisturbed	>1000	100	6.1	6.5	0.18	28.5	7.1	0.99	26.6	14.5	−8.5

[a] for details: Pizano *et al* (2014), ages estimated by oldest shrub growth ring count.

[b] i-Buttons taped to cores at 5 cm depth.

collection, soil subsamples from 'initial' and 'final' cores were extracted with 0.5 M K_2SO_4, 0.5 M K_2SO_4 + 0.5 ml of $CHCl_3$, 0.5 M $NaHCO_3$ or 0.5 M $NaHCO_3$ + 0.5 ml $CHCl_3$ and resins extracted with 2 M KCl. Extractable NH_4^+-N, NO_3^-N were determined from K_2SO_4 extracts ('non-fumigated') and KCl extracts using automated flow analysis (Lachat). Extractable organic C (EOC) and total N (ETN) contents in the K_2SO_4-$CHCl_3$ ('fumigated') and K_2SO_4 ('non-fumigated') extracts were determined using a TOC-TN autoanalyzer (Shimadzu, Kyoto, Japan) and extractable PO_4^{3-}-P from $NaHCO_3$ extracts (fumigated and non-fumigated) using the malachite green method (D'Angelo *et al* 2001). Net rates of N and P mineralization were estimated by calculating final core nutrients plus core leachate (middle resin bag) and subtracting initial core nutrients, divided by incubation time. MBC, MBN and MBP were calculated as the difference between EOC, ETN or PO_4-P in fumigated and non-fumigated extracts (Fierer and Schimel 2002).

To measure gross ammonium mineralization, we collected two additional adjacent organic and mineral cores and injected them with a 0.1 (organic) or 0.4 (mineral) mM solution of 99% $^{15}NH_4Cl$. Initial cores were extracted in 0.5 M K_2SO_4 as above. Final cores were incubated at 10 °C for 6 h (organic soils) or 24 h (mineral soils), then processed as initial cores. ^{15}N content of the gross mineralization extracts was analyzed at the Stable Isotope Facility, University of California, Davis. Gross rates were estimated via the dilution of the initial core $^{15}NH_4{}^+$-N pool by the final core $^{14}NH_4{}^+$-N in the extracts.

For H2 we used data on C, N (Carla Erba CN analyzer) and P-content (ICP-AES, UC Davis Analytical Lab) in organic and mineral soil. CNP stocks were calculated using bulk density multiplied by depth, using average horizon depth per transect for the organic and 10 cm depth for the mineral horizon. Actual mineral stocks are much higher but cannot be extrapolated without deeper sampling. In contrast, the 'recent organic' stocks were not corrected for the incomplete spatial cover of organic soil on the mineral slurry (e.g. raft density) and thus actual stocks are much lower than presented.

For H3 we used data on legume and moss cover and legume nodule abundance to estimate biological N_2 fixation. For H4 we used winter thaw N overland flow input versus output balance (NE-14 and I-minus only). Resin bags were placed on the tundra surface at the base of the snowpack in March on the control and upper, mid and lower slopes of the RTS and then collected after snow and soil surface thaw. Overland flow was characterized based on differences in extractable total N recovery at each slope position. Resin N retention was upscaled from resin area (18 cm^2) to N per m^2.

We used the 'lm' function in R (R version 4.2.1) to fit linear models to all variables across the four categorical levels of RTS age separately for organic and mineral soils. Non-normally distributed data were log-transformed before model fitting. If the log transformation was insufficient, we replaced the linear model with a non-parametric Kruskal–Wallis rank sum test (function 'kruskal.test'). For significant ($P < 0.05$) linear models, post-hoc comparisons between levels (least squares means) were tested with function 'emmeans' in the package 'emmeans'. Variance in resin data between age categories was assessed with the function 'leveneTest' in package 'car'.

3. Results

3.1. Hypothesis 1: NP cycling rates and microbial biomass CNP

We found no difference in gross and net rates of N and net rates of P cycling, between age categories (figure 2). Microbial biomass C, N and P (MBC, MBN, MBP; figures 3(a)–(c)) in the organic horizon increased with age (C: $P = 0.004$, N: $P < 0.0001$, P: $P = 0.004$). The MBC:N ratio did not change with time in the organic or mineral soils. Mineral soil microbial biomass was less responsive and only MBP ($P = 0.04$) increased with time. Although the smaller biomass logically results in higher biomass-specific activity rates early in succession (not shown), there was no significant specific NP rate differences across succession.

3.2. Hypothesis 2: NP stocks

C and N stocks followed similar patterns of accumulation with time (figure 4). C accumulated in the organic ($P < 0.0001$) and mineral ($P < 0.0001$) soil. In the organic soil, C did not differ between recent and shrub age categories, but both were lower than old and undisturbed soil C and old soil C was less than undisturbed soil C (all $P < 0.05$; figure 4(a) left panel). In the mineral soil, recent soil C was less than the undisturbed soil C ($P < 0.0001$), and shrub soil C was less than undisturbed soil C ($P < 0.0001$; figure 4(a) right panel).

N accumulated in the organic ($P < 0.0001$) and mineral ($P < 0.0001$) soil with time. In the organic soil, N did not differ between recent and shrub age categories, but both were lower than old and undisturbed soil N and old soil N was less than undisturbed soil N (all $P < 0.05$; figure 4(b) left panel). In the mineral soil, recent soil N was less than the undisturbed soil N ($P < 0.0001$), and shrub soil N was less than undisturbed soil N ($P < 0.0001$; figure 4(b) right panel).

Total P increased in organic soils with time ($P < 0.0001$; figure 4(c) left panel) and declined in mineral soils with time ($P = 0.0001$; figure 4(c)

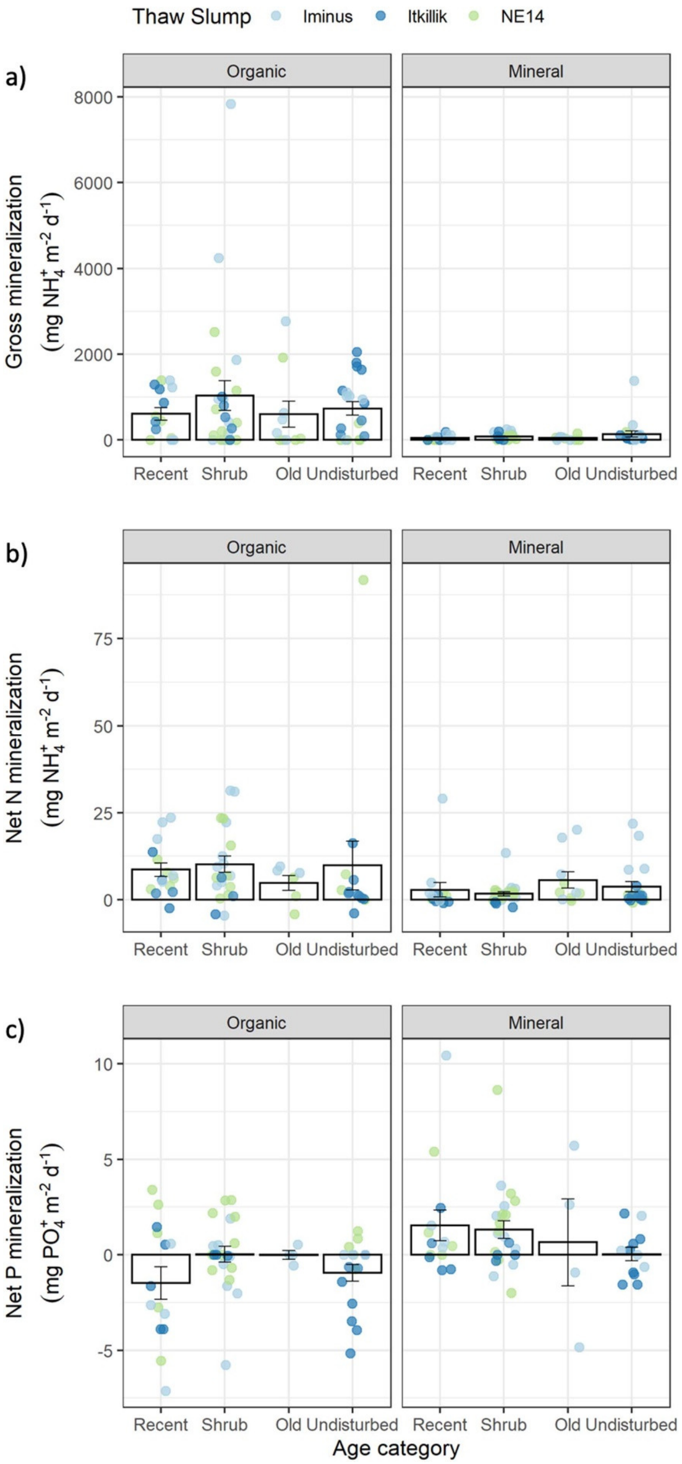

Figure 2. Gross (a) and net (b) soil nitrogen cycling rates (mg NH_4^+-N m^{-2} d^{-1}), and net soil phosphorus cycling rates (c) (mg PO_4-P m^{-2} d^{-1}), in recent (5–8 y since RTS), shrub (16–54 y since RTS), old (∼150 y since RTS) and undisturbed (>1000 y since RTS) transects at I-minus, Itkillik and NE-14 RTS.

right panel). The organic horizon soil P did not differ between the recent and shrub age categories or between the shrub and the old age categories, but recent soil P was less than old and undisturbed soil P, and shrub and old soil P were less than undisturbed soil P (all $P < 0.05$). In the mineral soil, recent ($P = 0.0001$) and shrub ($P = 0.02$) soil had higher P than the undisturbed soil.

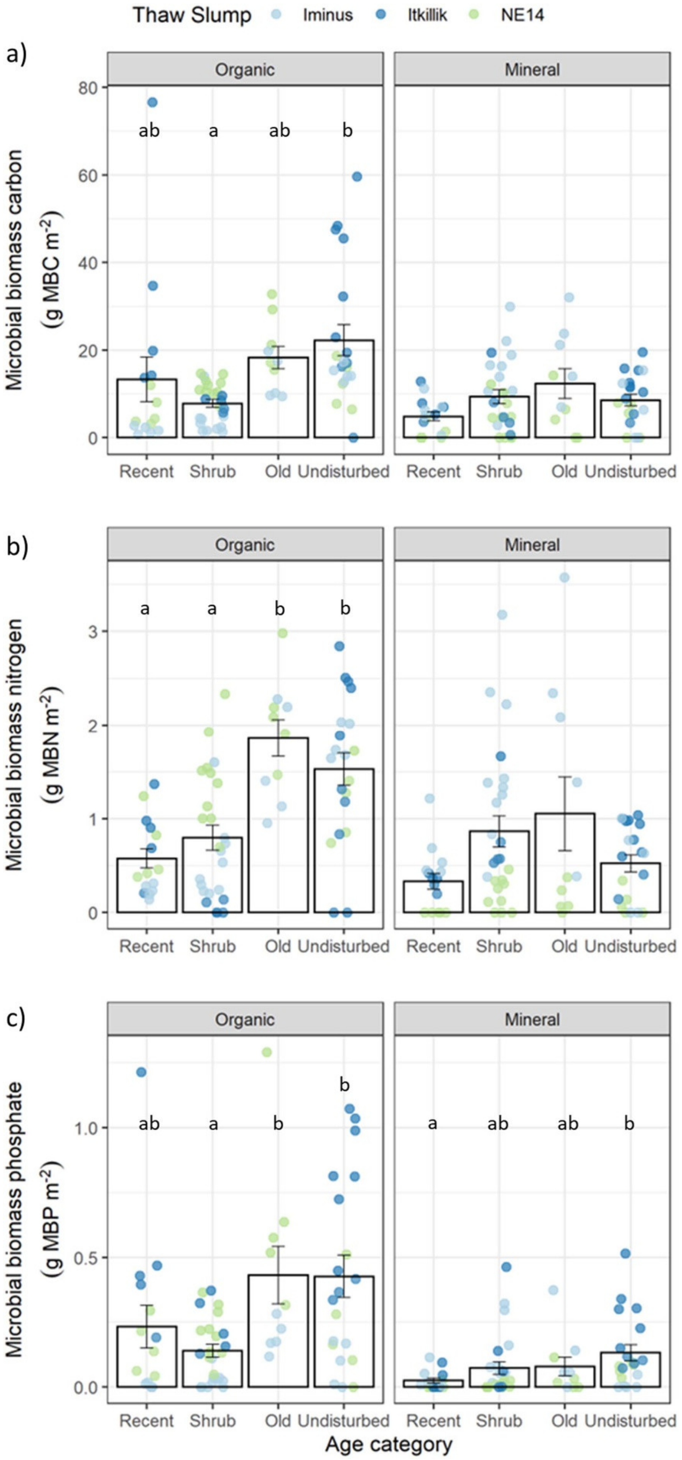

Figure 3. Microbial biomass flush carbon (a), nitrogen (b) and phosphate (c) (g m^{-2}) in recent (5–8 y since RTS), shrub (16–54 y since RTS), old (∼150 y since RTS) and undisturbed (>1000 y since RTS) transects at I-minus, Itkillik and NE-14 RTS.

3.3. Hypothesis 3: moss cover and legume nodule mass

Moss cover increased with age ($P < 0.0001$), because the recent age category had less moss cover than all other categories (all, $P < 0.05$), and the other categories did not differ from each other (figure 5(a)). Legume nodule mass increased with age ($P < 0.007$), as the recent ($P = 0.02$) and shrub ($P = 0.01$) age category nodule mass was less than the undisturbed soil nodule mass (figure 5(b)).

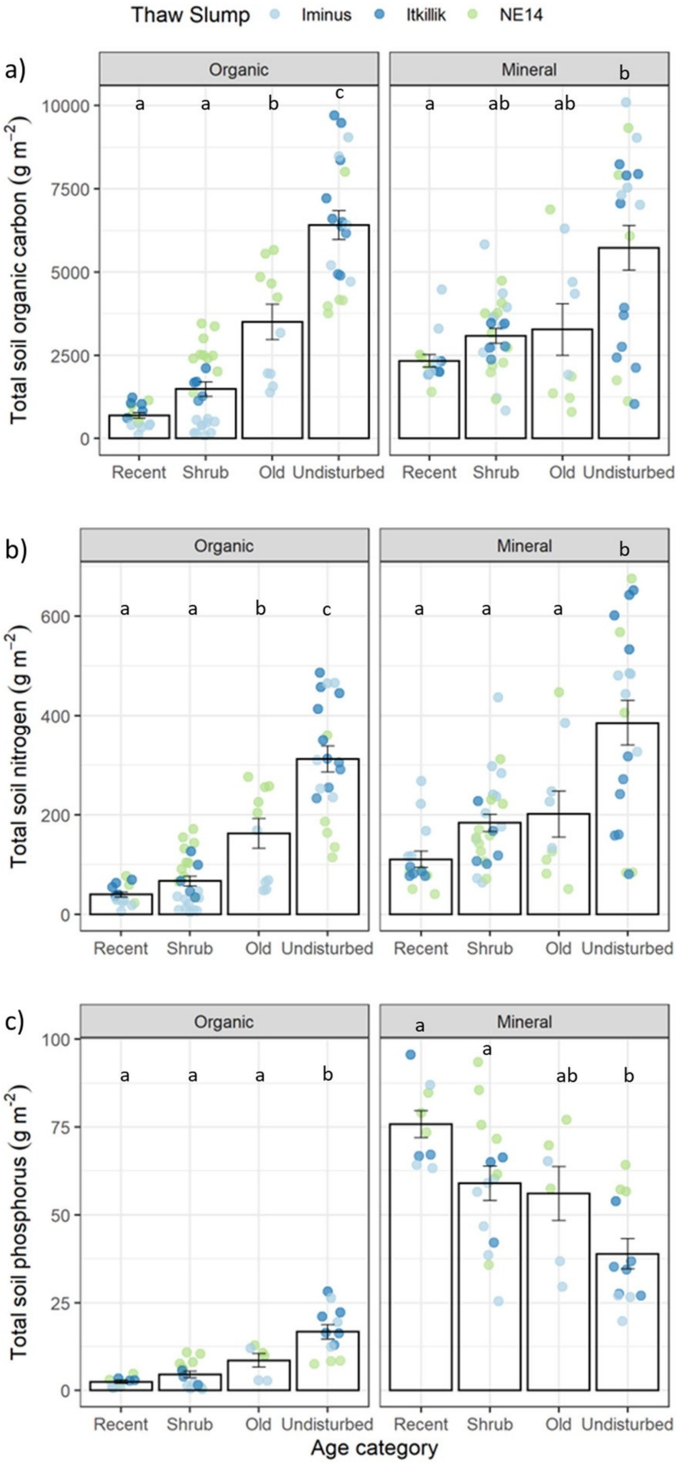

Figure 4. Stocks of total soil carbon (a), nitrogen (b), and phosphorus (c) (g m^{-2}) in recent (5–8 y since RTS), shrub (16–54 y since RTS), old (∼150 y since RTS) and undisturbed (>1000 y since RTS) transects at I-minus, Itkillik and NE-14 RTS. Recent organic soils have not been reduced to represent incomplete coverage of the RTS (table 1), and mineral stocks represent only the top 10 cm of mineral soil.

3.4. Hypothesis 4: winter resins

Inputs of N captured on resins (top of slope) did not differ from outputs (bottom of slope) and did not differ by age category (figure 6). There was a trend for variance to differ across age categories ($P = 0.09$), with more variance in the recently slumped transect.

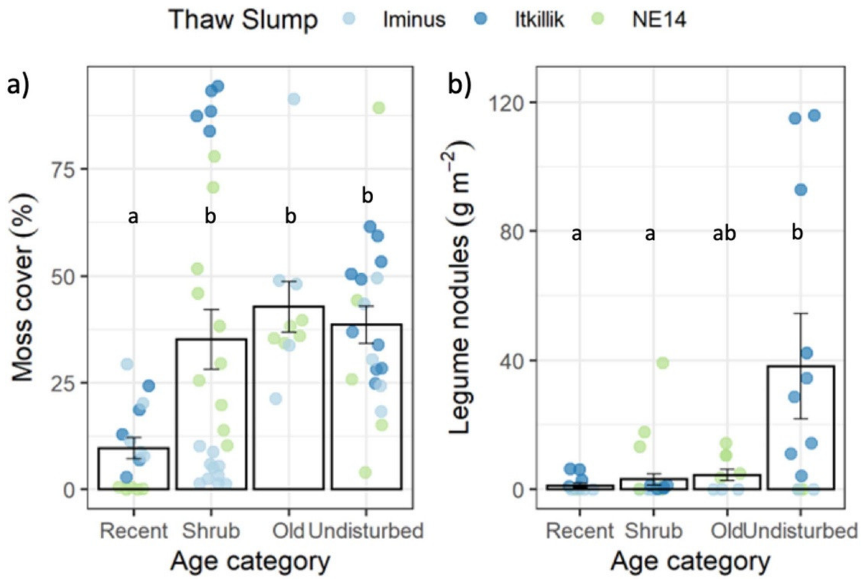

Figure 5. Moss cover (%) (a) and legume nodule mass (g m^{-2}) (b) in recent (5–8 y since RTS), shrub (16–54 y since RTS), old (∼150 y since RTS) and undisturbed (>1000 y since RTS) transects at I-minus, Itkillik and NE-14 RTS. No legumes were observed at I-minus RTS. One high value is not shown for legume nodule mass (beyond *y*-axis limits, 310 g m^{-2}).

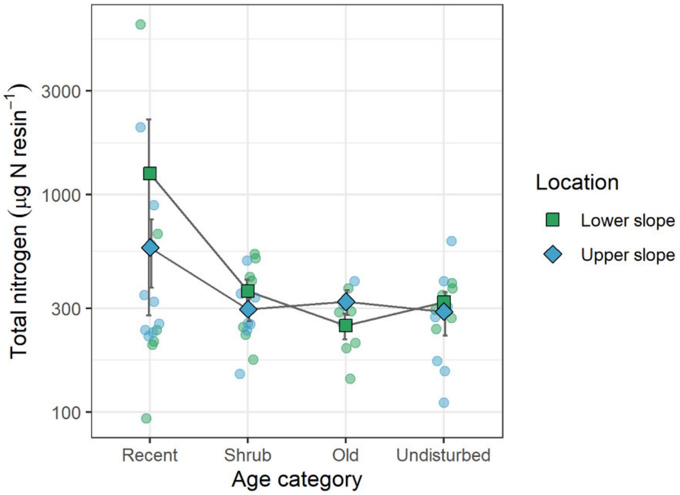

Figure 6. Total N (NH_4^+-N, NO_3^-N, DON) accumulation on resins planted at the bottom of the snowpack over thaw (60 d), in Iminus and NE-14 at the upper (input) and lower (output) slope. Log scale on *y*-axis. Itkillik was not (logistically) accessible during snow thaw.

4. Discussion

4.1. Internal nutrient supply hypotheses

Our first hypothesis, that the source of N and P for shrub growth after thermokarst was sourced by early successional nutrient cycling rates (figure 1(a), orange arrows), was not supported (figure 2). Our expectation for higher N availability early in succession was built from the idea that a system is 'leakier' in N-cycling when recently disturbed (i.e. leakier, because cycling is faster or sporadic, such that transfer between microbial and plant pools is inefficient and more nutrients may be lost from the system as leachate or gaseous emissions (Rastetter *et al* 2020)). This leakiness is driven by either elevated or continuous microbial activity with no vegetation to take up the N. This concept is largely driven by secondary succession studies (Davidson *et al* 2007, Bowden *et al* 2008, Lafrenière *et al* 2017), and is less pervasive in primary succession sites (de Vries *et al* 2021) or in disturbed sites with mixing of organic and mineral soils (Harms *et al* 2014). In primary succession studies, internal soil NP cycling typically increases with succession, with vegetation feedbacks (Tateno and Hirose 1987, Crews *et al* 1995). Although our sites had low total C and N and high P in the recently disturbed mineral soil (figures 4(a) and (b)), like a primary succession landscape, the rafts of organic matter left on top of the mineral soil slurry post-RTS ('recent organic') acted as a secondary succession remnant. This hypothesis could be described as partially supported because although we saw no changes in NP cycling rates with successional time, the low vegetation biomass during the early successional stage with continuous microbial N cycling rates means that there was potentially excess N available for the shrub growth that followed in the next successional stage.

Positive vegetation feedbacks are common in nutrient-constrained systems, promoting increased NP availability and cycling rates (Buckeridge *et al* 2010, McLaren and Turkington 2010, Demarco *et al* 2014). Therefore, we proposed an alternative hypothesis to early succession enhanced NP cycling rates, in which nutrient cycling and microbial biomass increased mid-succession fueled by vegetation feedbacks (figure 1(b), orange arrows under shrubs). However, this hypothesis was not supported, and we found no shrub-stage increase in gross N cycling and net NP mineralization rates (figure 2). Instead, we found a lower organic soil MBCNP in the shrub stage (16–55 years post-RTS), relative to the undisturbed tundra. Tall shrub systems have previously been recorded to have lower MBC than low shrub systems, associated with a higher MBC:N ratio and high fungal dominance (Chu and Grogan 2010), although we did not find differences in microbial C:N across these RTS chronosequences.

The large stock of N in the mineral soil is a potential source for plant growth (Yanai *et al* 2013), if shrub roots and their mycorrhizal symbionts can access deeper soil. Shrub and sedge roots primarily acquire their nutrients in surface soils (Yang *et al* 2021). However, rooting can be quite deep and is constrained ultimately by the active layer depth (Iversen *et al* 2015). In this study, the amount of N in just the surface mineral soil of the recent slumps (110 g N m^{-2}) was adequate to support shrub growth, estimated to require ~2.3 g N m^{-2} y^{-1}, multiplied by ~50 years (Shaver and Chapin 1991). However, if upper mineral soils were providing the full quota of N required, there would be a noticeable depletion the mineral soil N stocks from the recent to the shrub stage of development, which did not occur at least in the top 10 cm (figure 4(b)). If shrub roots acquired nutrients from below the top 10 cm of mineral soil, then the N resources are more than adequate to support shrub growth. Furthermore, this opportunity is increased if thaw deepens under the RTS, allowing access to large new sources of mineral soil N (Salmon *et al* 2018). As we often observed deeper rooting shrubs, deep mineral soil N stocks require greater attention in future studies.

Soil total P appears to have been important for fueling shrub growth, as total P increased in organic soils and declined in mineral soils with time, implying a transfer from belowground to aboveground. This is consistent with a study in the Tibetan Plateau that found greater increases in plant P than N after thermokarst recovery (Yang *et al* 2021). Deep-rooting shrubs may be responsible for this transfer. Alternatively, the high *Equisetum* coverage in the recently slumped transects may be responsible, as *Equisetum* can operate as a P pump through its deep rooting, high P content, and rapid litter decomposition (Marsh *et al* 2000). Regardless of the mechanism, mineral soil P stocks in the recent slumps in this study (75.8 g P m^{-2}) and under shrubs (59.0 g P m^{-2}) were much larger than required for annual shrub growth, and shrub requirements (~0.2 g P m^{-2} y^{-1*} ~50 y) (Shaver and Chapin 1991) may be easily encompassed in the measurement error (~10 g P m^{-2}).

4.2. External nutrient supply hypotheses

Our third hypothesis suggested that the source of N supporting shrub growth could be from N_2-fixation. We hypothesized that legume abundance and moss cover would be high early in succession which would support theories (Rastetter *et al* 2001, Vitousek *et al* 2002) and evidence (Vitousek and Walker 1989, Blundon and Dale 1990, Chapin *et al* 1994, Kohls *et al* 2003) of high levels of N_2-fixation early in succession. However, here we found that legumes and mosses both had low cover early in succession and are therefore unlikely N sources for shrubs (figure 5(a)). Further, we found that there was an increase in legume (*Lupinus, Oxytropis, Astragalus* and *Hedysarum* spp.) cover and root nodulation in later successional stages (figure 5(b)), and nodulation is often correlated with N_2-fixation rates (Weisz *et al* 1985, Voisin *et al* 2003).

There are several other potential sources of N_2-fixation that we did not assess. We observed (but did not quantify) high abundance of *Equisetum* and biological soil crusts in the recently disturbed successional stage, and others have described *Equisetum* as being an important component of the vegetation community early in RTS succession (Burn and Friele 1989). Multiple species of *Equisetum* with a pan-arctic distribution have been found to fix N_2 (Fuji *et al* 1984). Further, biocrust N_2-fixation rates have been gathered from multiple types of arctic tundra, which although highly variable, are substantial enough to contribute to the N-needs of the plant community (Zielke *et al* 2002, Sorensen *et al* 2006, Stewart *et al* 2011). N_2-fixation in sites dominated by biocrusts can be on the same order of magnitude as those dominated by mosses with epiphytic cyanobacteria (Zielke *et al* 2002), and frost-heaved sorted circles dominated by lichen and *Equisetum* had N_2-fixation rates of ca. 1 g N m^{-2} per growing season (Sorensen *et al* 2006), almost half of the estimated shrub N budget (Shaver and Chapin 1991). Further investigations of Arctic diazotroph activity are encouraged.

Our fourth hypothesis tested whether nutrients to fuel shrub growth may be supplied from overland flow during thaw from the undisturbed tundra above the slump (figure 1, purple arrows). High nutrient export in the early stages of RTS recovery and in tundra during thaw is common (Buckeridge and Grogan 2010, Yano *et al* 2010, Harms and Ludwig 2016, Lafrenière *et al* 2017, McLaren *et al* 2017, Turner *et al* 2021). If we upscale from N collected on subnivian resins (N resin-1*resin m^{-2}), the N inputs at the top of the slump were in the range of 0.1–1.1 g N m^{-2} per spring thaw (recent: 0.7; shrub: 0.4 older disturbed: 0.3, and undisturbed tundra: 0.3 g N m^{-2}). The N collected on resins at the top of the slope (i.e. inputs) did not differ from the amount collected at the bottom (i.e. outputs), suggesting that the overland flow was not a significant net input of nutrients into the disturbed system. The difference between input and output also did not differ with time since thermokarst, however, the variance was higher in the most recently disturbed system (figure 6). This variance may be due to surface soil microbes interacting with overland flow of C and N, creating hotspots and hot moments of N mobilization and mineralization downslope (Kuzyakov and Blagodatskaya 2015). Our experimental design captured time-averaged responses at decadal (chronosequence C, N, and P stocks), seasonal (net mineralization cores and subnivean resins), and daily (gross N mineralization cores) rates, and was not set-up to accurately portray these hot moments in N cycling. Although there would not be enough nutrient inputs into the system through this overland flow mechanism alone to support plant growth, this variance may play a role in supporting early thermokarst succession shrub growth and deserves further investigation.

5. Conclusions: what is the nutrient source for mid-successional shrub growth?

We proposed a number of possible mechanisms to explain the source of N and P for verdant shrub growth in the mid-successional stage of ecosystem recovery after RTS. We found clear transfer of P from mineral to organic soils, possibly promoted by deep-rooting shrubs, or *Equisetum* at an early successional stage. We did not find a single N source, instead, indications of a collection of potential sources. These include possible *Equisetum* and biocrust N_2-fixation, downslope N inputs during thaw and sustained (although not higher) microbial activity in the early successional tundra remnants. We also propose that shrubs tapping into the existing deep mineral soil N—as with P—is the best candidate for future investigation, as this N stock is large, possibly more so with deeper thaw under the RTS. Across three RTS chronosequences with different soil types and underlying geologies, we provide vegetation and microbial mechanisms that explain the source of nutrients for ecosystem recovery after RTS. These mechanisms play a pivotal role in the slow accumulation of soil C after an increasingly common Arctic tundra climate disturbance.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://zenodo.org/record/7586804.

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