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Trees out-forage understorey shrubs for nitrogen patches in a subarctic mountain birch forest

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Nitrogen (N), acquired by roots and mycorrhizal fungi and supplied to plant foliage, is a growth-limiting nutrient at the subarctic treeline. Due to this limitation, interspecific competition and acquisition of N is an important control on plant community composition and distribution. The ability of trees and shrubs to access N shapes community dynamics at this ecotone undergoing species range shifts and changes in primary productivity driven by climate change. Using ^{15}N soil labelling we investigate the fate of soil inorganic N, and spatial distances over which trees and understorey shrubs access soil N, in a treeline forest. ^{15}N was injected into soil rooting zones in discrete 1 m^2 patches and foliar samples were collected from trees between 1 and 50 m away, and understorey shrubs between 0.5 and 11 m away from labelled soil. The ^{15}N label was found in mountain birch trees up to 5 m, and in understorey shrubs up to 2 m, away from labelled soil. We estimate that 1.27% of pulse-derived N was found in foliage of birch trees, compared to 1.16% in the understorey. However, mountain birch trees contributed only 31% of ecosystem leaf area index (LAI), thus there was a disproportionate allocation of added label to the birch canopy compared with its contribution to ecosystem LAI. The difference in root and mycorrhizal exploration distances and community N partitioning between mountain birch trees and understorey shrubs may confer competitive advantage to trees with respect to nitrogen and nutrient patches, which may alter plant community structures within these forests. This is particularly important considering predicted climate-driven tree and tall shrub expansion in subarctic regions, with likely consequences for ecosystem N and carbon (C) cycling, as well as for community composition and biodiversity.

Keywords: *Betula pubescens*, ^{15}N labelling, nitrogen partitioning, shrubs, treeline forest

Introduction

Nitrogen (N), which is essential for plant growth and photosynthesis, is generally considered the most limiting nutrient in arctic and subarctic ecosystems (Shaver et al. 1992, Sjögersten and Wookey 2005). The slow rate of litter decomposition at high

latitudes, and the large proportion of N that is bound in complex organic matter, has traditionally been seen as driving the rate of N supply and causing N limitation (Shaver et al. 1992, Jonasson et al. 1999). N limitation may further be maintained through strong N retention by microorganisms, which keeps levels of available N very low (Fernandez and Kennedy 2016, Högberg et al. 2017). Indeed, the tundra biome has some of the highest root:shoot ratios (Mokany et al. 2006), an adaptation to N limitation (through high resource allocation to N uptake tissues) and harsh winter conditions (Bliss 1962, Shaver and Billings 1975).

Interspecific competition and acquisition of soil N is an important control on plant community composition and distribution (McKane et al. 2002). Differing N acquisition strategies and efficiency between species within treeline ecotones may determine the speed and species diversity of the climate driven expansion of treelines above or north of current ranges (Rees et al. 2020, Dial et al. 2022). This predicted expansion is likely to affect carbon (C) cycling through changes to primary productivity (Hudson and Henry 2009, Epstein et al. 2012), as well as alterations in mycorrhizosphere (roots and mycorrhizal mycelia) processes and soil organic matter dynamics) (Street et al. 2020, Parker et al. 2021). Therefore, it is important to further our understanding of N and C cycling and how the acquisition of limited resources shapes plant communities at high-latitudes. Specifically, in this context, mountain birch forests are undergoing rapid and dynamic changes in primary productivity and species shifts driven by climate change (Rees et al. 2020, Dial et al. 2022).

Nitrogen uptake by plants is frequently facilitated by mycorrhizal mycelium which forage for N, using extracellular enzymes to decay complex organic material (Schimel and Bennett 2004, Talbot et al. 2008, Lindahl and Tunlid 2015, Lindahl et al. 2021). In subarctic treeline forests, extracellular enzymes are utilised by both ecto-mycorrhizal (ECM) fungi, which associate with a range of important tall deciduous and treeline genera such as *Betula* (Read and Perez-Moreno 2003, Lin et al. 2017), and ericoid mycorrhizal (ERM) fungi, which associate with ericaceous shrubs (Emmerton et al. 2001).

Tree root and mycorrhizal production of the canopy forming mountain birch (*Betula pubescens* ssp. *czerepanovii*) in the treeline forest of subarctic Sweden are consistently high up to 3 m away from the base of individual trees, well beyond the crown width, and potentially spanning large forest gaps (Friggens et al. 2020a). Hence, both roots and ECM mycelia may explore forest floors extensively for nutrient and water uptake in relatively open treeline stands.

The understorey of treeline forests is made up of both ECM shrubs (*Betula nana*) and ERM shrubs (*Vaccinium vitis-idaea*, *Vaccinium myrtillus* and *Empetrum nigrum*). ERM fungal associations produce single hyphae which rarely extend further than 1 cm from the root (Perotto et al. 1996, Mitchell and Gibson 2006). By contrast, many ECM fungi are capable of producing dense mats or rhizomorphs that facilitate long-distance exploration up to ~10 cm from root tips (Agerer 2001, Weigt et al. 2012). Due to this co-occurrence of ECM and ERM fungal species within the forest, and the variation in exploration types formed by the two contrasting mycorrhizal types, there may be a difference in the range of nutrient foraging and the extent of mycelial exploration (Tedersoo and Bahram 2019) between canopy and understorey species, as well as between ECM and ERM shrubs within the understorey. As well as having extensive root and associated mycorrhizal mycelial coverage beyond crown width (Friggens et al. 2020a), mountain birch trees are adapted for greater productivity and faster growth than understorey shrubs, particularly in response to herbivory (Karlsson et al. 2004). As a consequence they may not only have the potential for more expansive nutrient foraging ranges but also have greater N demand and uptake than the understorey plants. Combined, the differences in expected nutrient foraging range and N demand may result in canopy forming trees accessing a greater proportion of available soil N than understorey shrubs.

As N is a limited resource in these forests, a difference in N acquisition capacity between canopy and understorey species may be important in modulating predicted tree and shrub expansion in this region. A larger foraging range and nutrient uptake capacity may confer a competitive advantage to canopy species within the forest and facilitate rapid expansion into ERM shrub dominated tundra heaths with N immobilised by soil microbes (Jonasson and Michelsen 1996). Recent evidence suggests that mycorrhizal N 'mining' strategies can affect organic matter turnover, soil C stocks (Sulman et al. 2017, Clemmensen et al. 2021) and ecosystem responses to elevated CO_2 (Terrer et al. 2018). In these rapidly changing northern ecosystems, with globally important soil C stores (Köchy et al. 2015), it is important to understand the controls on tree and shrub expansion and how these might affect C and N cycling (Wookey et al. 2009, Street et al. 2018, 2020).

Labelling techniques, using the stable isotope ^{15}N, have been used to measure available N and N flow through soil and plant pools (Schimel and Bennett 2004). Indeed, Göttlicher et al. (2008) applied a ^{15}N label to examine N transfer in 10 m radius plots of boreal pine forest, revealing transport to distances up to 9.5 m from sources. To our knowledge, however, ^{15}N has not been used to investigate lateral inorganic N transfer and community partitioning within subarctic treeline mountain birch forest ecosystems. To test the spatial reach of nutrient foraging and N partitioning in a subarctic treeline forest, we conducted a ^{15}N pulse-chase field experiment, where ^{15}N was injected into the soil and traced into surrounding tree foliage 1–50 m away, and shrub foliage 0.5–11.0 m away. As roots and mycorrhizal fungi explore extensively within open mountain birch forests, we hypothesise that:

1) Mountain birch trees can access soil nitrogen at least 3 m from a nitrogen source (Friggens et al. 2020b).
2) Canopy-forming mountain birch trees access a greater proportion of soil nitrogen than would be expected based on their contribution to total community leaf area.
3) Ectomycorrhizal shrubs have 1) a larger foraging range and 2) can access a greater proportion of soil nitrogen than ericoid mycorrhizal shrubs.

Material and methods

Site description and plot set-up

All five studied plots were set up within a permafrost-free area (approx. 1 km^2) in the subarctic treeline ecotone region, ca 4 km south of Abisko, Sweden (68°18′56.2″N, 18°49′18.2″E), at ~600 m a.s.l. The treeline forest is formed by mountain birch *Betula pubescens* ssp. *czerepanovii*) and has an open canopy structure with an ericaceous understorey consisting of *Betula nana*, *Vaccinium vitis-idaea*, *V. myrtillus* and *Empetrum nigrum* ssp. *hermaphroditum*. Forest soils are microspodosols with a thin O horizon (< 5 cm) underlain by glacial till on a bedrock typically of hard-shale (Sjögersten and Wookey 2002); soil pH in the organic horizon is 4.3 ± 0.1 (Parker et al. 2015). Within the open mountain birch forest, five plots with 50 m radius were selected. Care was taken to ensure a relatively homogeneous tree density and mixture of tree sizes within the plots. As polycormic growth form is common in these forests; the average number of stems per tree was 4.3 ± 2.8 (mean ± SD) and the average combined DBH (diameter at breast height) for all stems per tree was 34.6 ± 21.1 cm (mean ± SD). All plots were ≥ 50 m apart.

Soil isotope labelling

A 1 × 1 m square of ground was measured out at the centre of each plot for the ^{15}N label to be applied (Fig. 1). The size of the labelled area was chosen to avoid stochastic effects resulting from applying label to too small an area, whilst maintaining a scale spatially explicit enough to determine the distances over which trees/shrubs access N. 50 g of $^{15}NH_4Cl$ ≥ 98 atom% ^{15}N was dissolved in 5 l of deionised water resulting in a 10 g l^{-1} $^{15}NH_4Cl$ solution. $^{15}NH_4Cl$ was chosen because ECM communities have been shown to discriminate against NO_3^- (Clemmensen et al. 2008). One litre of the solution was dispensed in the 1-m^2 central labelling area of each of the five plots (equivalent to 1 mm rainfall) as 100 × 10 ml soil injections. Soil injections were conducted as per Clemmensen et al. (2008), using a syringe inserted at 5 cm soil depth and steadily pulling it up as the solution was dispensed so that this was applied evenly within the top 5 cm of soil. The ^{15}N label was applied to all plots on 10 June-2018.

Foliar sampling

Twelve trees at varying compass directions up to 20 m from the plot centre, and three trees 20–50 m away from the plot centre, were selected for sampling and their distances from the centre measured (Fig. 1, Supporting information). Ten to fifteen leaves from different parts of the tree crown were sampled. This was conducted before any ^{15}N label was added to the plots (10 June-2018) and on days 5, 25, 55 and 417 post soil labelling. Samples were taken from the same marked trees on each of the sampling days. All foliar samples were transported to the lab within 4 h of sampling and oven dried at 60°C for 72 h, then milled for homogenisation.

On day 53 and 421 post soil labelling, foliar samples were taken from dominant understorey species *Betula nana*, *Vaccinium vitis-idaea* and *Empetrum nigrum*. Foliar samples of each species were taken at four different distances (0.5–11.0 m) from the labelling area. Each of the four samples were taken at ordinal compass directions. Samples were not taken from the same individual plants on days 53 and 421 but from patches of each shrub species at similar distances from the labelled area on both sampling occasions. Reference samples of each understorey species with natural abundance levels of ^{15}N were sampled ≥ 100 m from all ^{15}N labelling plots. Understorey samples were oven dried at 60°C for 72 h and milled for homogenisation.

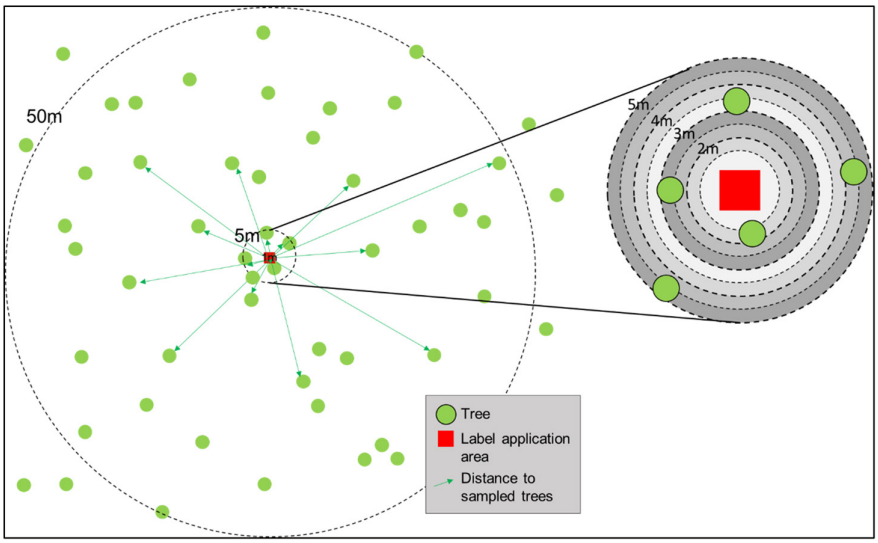

Figure 1. Plan view schematic diagram of plot set-up. The $^{15}NH_4Cl$ label was injected into the soil in a 1-m^2 area at the centre of each plot (red square). Foliar samples from 15 trees between 1 and 50 m away from the labelled area were harvested and analysed for their isotopic composition. Concentric circles of 0.5 m width were used to calculate pulse-derived forest N uptake. Diagram not to scale.

Ground cover surveys of the understorey were carried out in four 1 × 1 m quadrats spaced contiguously between 1 and 5 m away from each plot centre. This was repeated at four ordinal compass directions at each plot. Standard curves converting percent cover to leaf biomass per m^2 (Supporting information) were generated by harvesting, drying and weighing all leaf biomass of a given species from seven 20 × 20 cm quadrats with varying species cover adjacent to the ^{15}N addition plots.

Stable isotope analysis

Milled canopy samples (*Betula pubescens*) from days 0 to 55 were analysed at the NERC (Natural Environment Research Council) Life Science Mass Spectrometry Facility at the Centre for Ecology and Hydrology (CEH) in Lancaster, UK, by EA–IRMS (elemental analysis–isotope ratio mass spectrometry). Samples and standards were dried at 105°C for one hour in an oven, then cooled and stored in a desiccator prior to analysis. A varying amount of each sample (enough to yield 100 µg N) was weighed using a high-precision microbalance and sealed into 6 × 4 mm tin capsules. Samples were then combusted using an automated elemental analyser coupled to an isotope ratio mass-spectrometer. Working standards of either natural abundance wheat flour or ^{15}N-enriched flour were analysed after every twelfth sample, resulting in a maximum analytical precision of 0.32‰ (0.366 atom %) for the natural abundance standard, and 3.10‰ (0.377 atom %) for the ^{15}N-enriched flour (current mean value of 133.58‰ (0.415 atom %)). These standards are calibrated against the certified reference material IAEA-N1 (NIST number 8547, National Inst. of Standards and Technology, Gaithersburg, USA). For duplicates analysed, standard deviation was a maximum of 0.33‰ (0.366 atom %). Results are expressed in atom percent; i.e.

$$\text{Atom percent}\left(A\%\right) = \frac{R_{\text{sample}}}{\left(R_{\text{sample}} + 1\right)} \times 100 \quad (1)$$

where R is the ratio of ^{15}N to ^{14}N in the sample.

Milled canopy samples from day 417 as well as all understorey samples (*Betula nana*, *Vaccinium vitis-idaea*, *Empetrum nigrum*) were analysed at the UC Davis Stable Isotope Facility in California, USA. Samples were analysed for ^{13}C and ^{15}N isotopes using an Elementar Micro Cube elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer. During analysis, samples were interspersed with several replicates of at least four different laboratory reference materials. These reference materials have been previously calibrated against international reference materials, including: IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64 and USGS-65. A sample's provisional isotope ratio was measured relative to a reference gas peak analysed with each sample. These provisional values were finalised by correcting the values for the entire batch based on the known values of the included laboratory reference materials.

Data analyses

All statistical analyses were carried out using R ver. 4.0.2 (www.r-project.org).

Pulse-derived N was calculated as sample ^{15}N Atom percent excess (APE) using the following equation:

$$\text{Atom \% excess}\left(\text{APE}\right) = x_i\left(A\%\right) - \bar{a}_{\text{natural abundance}}\left(A\%\right) \quad (2)$$

where x_i is sample A% and $\bar{a}_{\text{natural abundance}}$ is mean A% of natural abundance samples (day 0 for *B. pubescens* (n = 25) and control samples for *B. nana* (n = 5), *E. nigrum* (n = 5) and *V. vitis-idaea* (n = 5)). Samples were considered enriched if A% exceeded the mean A% of natural abundance/control samples plus one standard deviation of the mean.

Total pulse-derived N was calculated using concentric circles radiating from the central labelled area each 0.5 m wide (Fig. 1) and the following equation:

$$\text{Total pulse derived } N\left(\text{g}\right) = \sum\left(A_{\text{con}}\left(\text{m}^2\right) \times \text{FLB}\left(\text{g m}^{-2}\right)\right) \times \left(\frac{\overline{\%N}}{100}\right) \times \left(\overline{\text{APE}_{\text{con}}} \times 100\right) \quad (3)$$

where A_{con} is the area within each concentric circle, FLB is the forest leaf biomass for each species. *Betula pubescens* FLB was derived from leaf area index and specific leaf area data from Parker et al. (2020). *Betula nana*, *E. nigrum* and *V. vitis-idaea* FLB was derived from percent cover data for each plot and percent cover to leaf biomass standard curves (Supporting information) generated from the forest floor adjacent to the ^{15}N addition plots. $\overline{\%N}$ is the mean leaf N content for each sampling day and $\overline{\text{APE}_{\text{con}}}$ is the ^{15}N atom percent excess at the midpoint of each concentric circle as modelled by an exponential regression of concentric circle mean enrichment with distance for each species.

The change in APE of mountain birch leaves over distance was modelled using the self-starting 5-parameter logistic function in the dose–response curve package drc::drm (Ritz et al. 2015) which includes a fifth parameter that models the asymmetry of the curve as well as upper and lower asymptotes. Alternative dose–response models were compared and selected using drc::mselect with AIC (Akaike information criterion) values and drc::mr.test for fit using the Mizon–Richard test. The difference between sampling days was compared using least-squares means (Lenth 2018). The exponential decay of leaf N content over time in mountain birch trees was modelled using a self-starting non-linear asymptotic regression (stats::SSasymp, www.r-project.org). APE of the understorey over distance from the label was modelled using a self-starting non-linear asymptotic regression (stats::SSasymp, www.r-project.org) or polynomial fit (NLS.Poly2::aomisc, Onofri 2020).

Results

Enrichment of ^{15}N in mountain birch tree foliage was detected in trees between 1.0 and 4.9 m away from the labelled soil area (Fig. 2). No ^{15}N enrichment was detected in the foliage of mountain birch trees between 4.9 and 50.0 m (Fig. 2). The slope of the curve fitted to the APE data between 1.0 and 4.9 m is not significant ($p > 0.1$) for any sampling day (Fig. 2). The differences between the fitted curves compared using least squares means for each sampling day are not significant between days 0 and 5. However, days 0 and 5 are significantly different to days 25, 55 and 417 (Table 1).

The N content of sampled *B. pubescens* leaves declined throughout the growing season, following an exponential decay pattern with an asymptote at 2.03% leaf N (Fig. 3).

Enrichment of ^{15}N in *B. nana* foliage was detected up to 1.1 m away from the labelled soil area on day 53 post soil labelling and up to 1.2 m away from the label on day 421 (Fig. 4). The mean ^{15}N enrichment in *B. nana* foliage was 18.2 times higher on day 421 compared to foliage on day 53. Enrichment of ^{15}N in *E. nigrum* foliage was detected up to 1.8 m away from the labelled soil area on day 53 post soil labelling and up to 1.2 m away from the label on day 421, however not all samples up to 1.8 m or 1.2 m, respectively, were enriched (Fig. 4). Enrichment of ^{15}N in *V. vitis-idaea* foliage was detected in plants up to 1.9 m away from the labelled soil area on day 53 post soil labelling and up to 1.3 m away from the label on day 421, however not all samples up to 1.9 m or 1.3 m, respectively, were enriched (Fig. 4). The mean ^{15}N enrichment for all three understorey species on day 421 (Fig. 4) was more than three times as high as that found in mountain birch trees on day 417 (Fig. 2).

The largest fraction of pulse-derived N was found in mountain birch tree *B. pubescens* foliage (1.27%) followed by *E. nigrum* (0.59%) then *V. vitis-idaea* (0.44%) and finally *B. nana* (0.085%) (Table 2). This pattern integrates the levels of enrichment, the distance over which the enrichment was detected, leaf biomass per unit area and leaf N content for each species. All four species sampled had higher levels of enrichment and total pulse-derived N incorporated into biomass in year 2 sampling (days 417 and 421 post soil labelling) compared to year 1 sampling (days 5–55 post soil labelling). ECM species had significantly higher leaf N content on days 417/421 of sampling than ERM species LAI estimates for *B. pubescens* are relatively low compared to closed canopy broadleaf forests (Lee et al. 2004) reflecting the open canopy structure and low tree density in these forests (see Fig. 1b in Parker et al. 2020).

Discussion

Nitrogen foraging distances – birch trees out-forage understorey shrubs

Using a ^{15}N stable isotope label, the uptake of N from the soil into mountain birch tree foliage was detectable up to 5 m from the source (Fig. 2). This finding supports hypothesis 1, that mountain birch trees can access N at least 3 m away from the source, a distance within which the growth of mountain birch tree roots and mycorrhizal fungi remains high (Friggens et al. 2020b).

It has previously been demonstrated in mountain birch forests that both root and mycorrhizal mycelial production remain consistently high between 0.25 and 3.50 m from the nearest tree (Friggens et al. 2020a). The current results provide new evidence of nutrient uptake and transfer by the mycorrhizosphere (roots and mycorrhizas) to mountain birch tree hosts

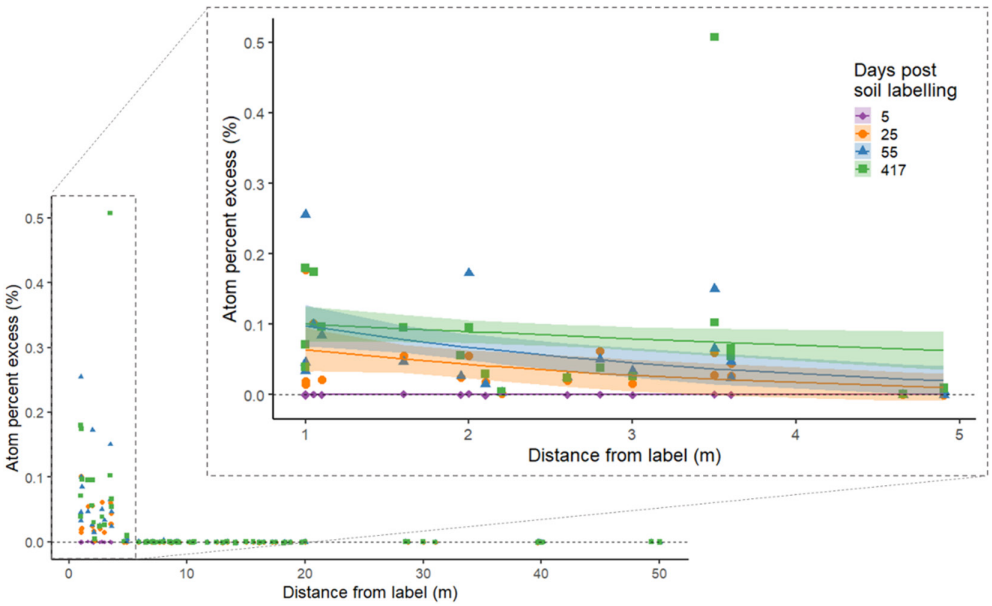

Figure 2. ^{15}N atom percent excess (APE) in mountain birch tree foliage samples on days 5–417 post soil labelling. Inset shows range of enrichment < 5 m with change in APE with distance modelled using a 5-parameter logistic function. Error ribbon is ± 1 standard error.

Table 1. p-values for the difference between sampling days compared using least-squares means.

Day	0	5	25	55	417
0		0.98	0.00080	0.00076	0.0034
5			0.037	0.0072	0.0002
25				0.31	0.032
55					0.25
417					

up to 5 m away. Beyond 5 m from the plot centre, there was no detectable ^{15}N label in mountain birch tree foliage, suggesting that the radius within which mountain birch tree roots and mycorrhizal mycelia forage is limited to ~5 m in these forests. Alternatively, it is possible that foraging may occur beyond 5 m but that N uptake and transport across greater distances becomes increasingly diluted and may be below the detection limits of the method. The 5 m foraging distance found here is less than the distance of 9.0–9.5 m away from the soil injection point at which Göttlicher et al. (2008) detected ^{15}N in tree foliage of two 48–120 year old boreal Scots pine *Pinus sylvestris* forest plots in northern Sweden. This difference may be due to the contrasting species and size of trees studied, with 48–120 year old pine forests likely to include significantly larger trees and more extensive root systems than the 3–4 m tall subarctic mountain birch trees studied here. With N uptake detected in trees located up to 5 m from the N source, we can speculate that individual mountain birch trees have the potential to exploit N at similar distances in all directions from the tree base, thus over ~75 m^2, although in competition with other plants and soil organisms. The spatial conservation of key mineral nutrients such as N is likely to be driven partly by high N retention by mycorrhizal fungi at low N levels, and greater fungus-to-plant N transfer at high N levels (Näsholm et al. 2013, Franklin et al. 2014), as well as low levels of lateral transfer within the soil in this region of low precipitation (304 mm $year^{-1}$ (Sjögersten and Wookey 2005)) and freely-draining soils.

By contrast, the maximum distance over which the ^{15}N label was detectable in understorey foliage varied from 1.2 to 2 m, which is therefore shorter than that observed for mountain birch trees (Fig. 4). Within the understorey, the ERM shrubs *E. nigrum* and *V. vitis-idaea* had a larger N foraging range than the ECM shrub *B. nana*, contrary to hypothesis 3(i). It is noteworthy that, for each of the two ericoid understorey shrub species, not all samples within the maximum distance of uptake were enriched, and the majority of plants did not show any uptake of the ^{15}N label, even at short distances from the source (Fig. 4). This result indicates that the roots and mycorrhizal mycelia associated with ericaceous understorey shrubs in these forests are not evenly distributed, radially, from a given shrub. This may be due to microtopography, hydrological barriers, rocks or stochastic exploration patterns by roots and mycelia. Our observations support those of Göttlicher et al. (2008), who observed that root and mycorrhizal systems of ericoid shrubs are highly directional and asymmetric. The ECM understorey shrub *B. nana* did not show this stochastic pattern, as all samples within the maximum distance of uptake were enriched, as was the case with mountain birch trees. The distance over which the *B. nana* accessed N was more similar to the ERM understorey shrubs than the ECM canopy birch trees, suggesting that the range within which treeline forest species can access N may be determined by growth form (i.e. woody shrub versus canopy forming tree) and rooting patterns, in addition to mycorrhizal exploration type. For example, rhizomorph-forming species (*Leccinum* spp.) or mat-forming species (*Cortinarius* spp.) (Trappe and Cromack 2012) found in these forests (Parker et al. 2017, Clemmensen et al. 2021)

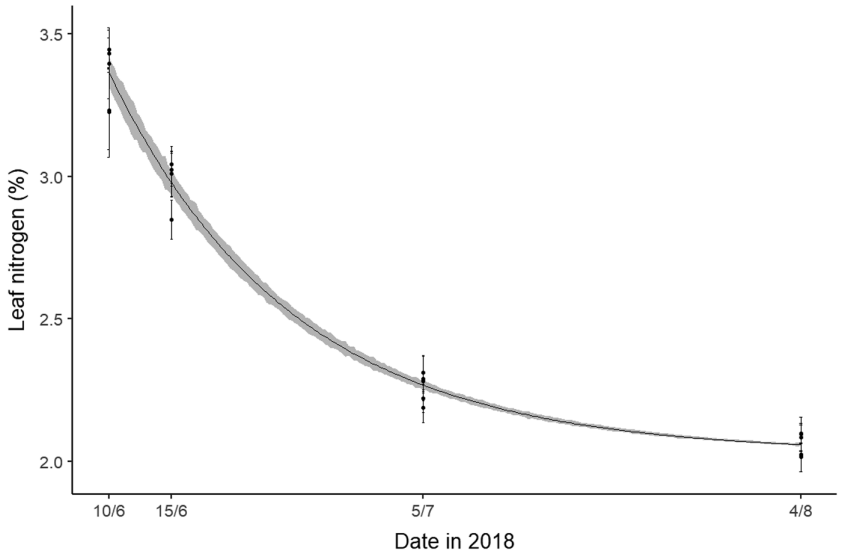

Figure 3. Nitrogen content (%) of mountain birch leaves sampled in the growing season of 2018. Points indicate plot averages (n = 15). Line predicted from a nonlinear least squares model of exponential decay, error ribbon is ± 1 standard error. Note the y-axis does not start at 0, to aid data visualisation.

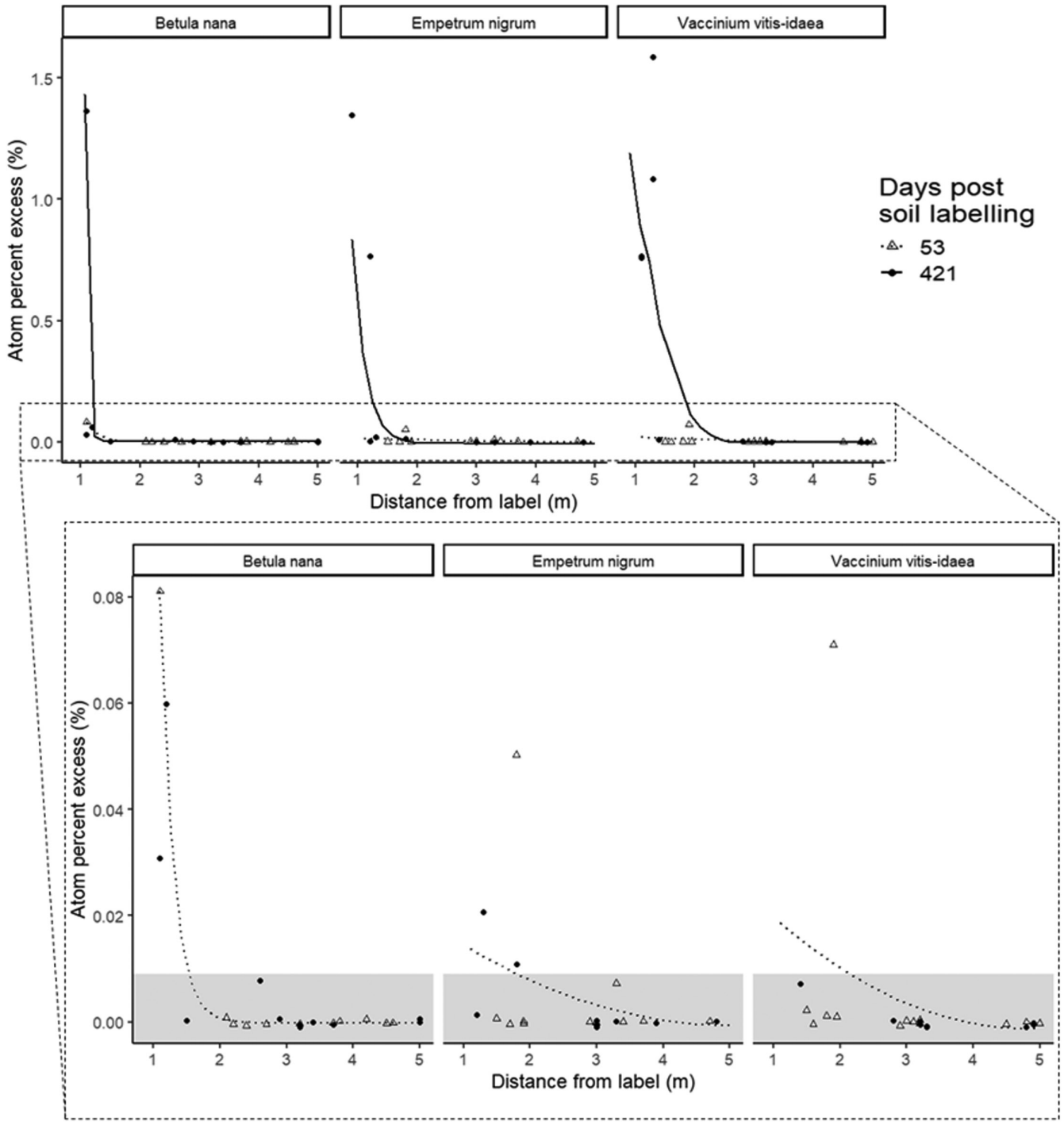

Figure 4. ^{15}N atom percent excess (APE) in understorey shrub foliage samples on days 53 (open triangles and dotted regression line) and 421 (filled circles, solid regression line) post soil labelling. Change in APE with distance modelled using an exponential decay function for all species on day 421, and *B. nana* on day 53, and polynomial distributions for *E. nigrum* and *V. vitis-idaea* on day 53. Lower 'zoomed' plot shows APE < 0.8% to aid data visualisation of clustered points in upper plot with all data. Greyed area indicates APE range of control samples within which samples are not considered enriched.

may enable 'long distance' nutrient foraging (Agerer 2001). Furthermore, the root-to-shoot ratios of the tree and shrub species examined here may vary significantly, and although not measured here, may play a role in determining the range over which a given species can access N as well as the extent to which foliar ^{15}N enrichment accurately indicates the level of N uptake (e.g. in cases where acquired N may remain stored in root tissues).

Table 2. Total pulse derived N (mg) (SD) in canopy forming mountain birch tree and understorey shrub foliage[a] 1–5 m away from soil labelling area (n = 5) and forest leaf variables used to calculate total pulse derived N. % of N added is the proportion (%) of labelled N (mg) added to plots recovered as pulse derived N in foliage on day 417/421. [a] Data from adjacent plots measured in Parker et al. (2020). [b] Average from literature values, see the Supporting information.

	Species			
sampling day	*Betula pubescens*	*Betula nana*	*Empetrum nigrum*	*Vaccinium vitis-idaea*
5	0.046 (0.041)			
25	18 (1.2)			
53/55	24 (1.6)	0.97 (0.19)	1.8 (0.56)	7.3 (2.7)
417/421	34 (4.6)	2.3 (0.68)	16 (1.0)	12 (5.0)
% of N added	1.27	0.085	0.59	0.44
Plot leaf biomass (g m^{-2})	52	5.1 (13)	170 (62)	46 (28)
Species ground cover (%)		3.4 (8.9)	56.9 (18.5)	19.1 (12.2)
Leaf N content (day 417/421) (%)	1.97 (0.26)	1.54 (0.17)	0.85 (0.12)	0.76 (0.076)
Leaf mass area (g m^{-2})	82 (10)[a]	88.9[b]	159.6[b]	169.9[b]
LAI (m^2 m^{-2})	0.63 (0.41)[a]	0.058	1.07	0.27

The mean foliar enrichment of all three understorey species sampled was many-fold higher than mean enrichment in canopy foliage > 1 year post soil labelling (Fig. 2, 4). This pattern occurred in both deciduous (*B. nana*) and evergreen (*V. vitis-idaea* and *E. nigrum*) species, the latter of which may immobilise N within live tissues for several years (Fletcher et al. 2010). This assimilation and retention of N in understorey tissues and their associated mycorrhizas near to the N source may have prevented translocation of N into trees and shrubs further away from the source, and illustrates the intensity of demand for N in these N limited forests.

Nitrogen partitioning within the community – disproportionate levels of N are assimilated by the canopy compared to the understorey

Within the range that trees and understorey shrubs accessed the injected ^{15}N, only an estimated 2.43% of the ^{15}N added was retrieved in foliage of sampled species (Table 2). In a system where N is a limited resource, an abundance of N injected into the upper soil layer may have multiple fates, for example 1) assimilation and retention by free-living soil microbes (Näsholm et al. 2013), 2) assimilation and retention in mycorrhizal mycelium (Clemmensen et al. 2008), 3) translocation to understorey shrubs (Fig. 4), 4) translocation to canopy species (Fig. 2), 5) hydrology-driven vertical leaching through the soil (Yano et al. 2010) or 6) potential losses, in gaseous form, via denitrification. Further work is needed to trace the fate of soil N into other pools not covered here, such as bacterial and fungal biomass as well as other plant tissues.

The largest proportion of pulse-derived N in any one species sampled was found in mountain birch tree foliage (1.27%), with whole tree pulse-derived N likely to be higher, given that pulse-derived N will be found in stem and root tissues as well. The three dominant understorey shrub species (*B. nana*, *E. nigrum* and *V. vitis-idaea*) cumulatively assimilated 1.16% of pulse-derived N in foliage (Table 2). Therefore, a slightly larger proportion of pulse-derived N was found in the forest canopy than in the sampled understorey. In our specific plots, we found that understorey LAI was 1.40 m^2 m^{-2} and canopy LAI 0.63 m^2 m^{-2} (Table 2). This means that the mountain birch canopy assimilated just over half the total pulse-derived N in foliage despite contributing only 31% of community leaf area. Thus, there was a disproportionate allocation of the added ^{15}N label to the birch canopy compared with the contribution of mountain birch trees to ecosystem LAI. We therefore accept our hypothesis 2; that mountain birch trees access a greater proportion of soil N than expected based on their contribution to community leaf area, as, despite similar absolute amounts of pulse-derived N assimilated by the canopy and understorey, inorganic N partitioning was not determined by the contribution to total community leaf area in this case.

The three understorey shrub species sampled were dominant in the community (Wookey et al. 1993), cumulatively representing 90% of ground cover (data from nearby plots surveyed in 2015 and 2021), however the full understorey consists of further vascular plant species not sampled here, which are likely to have acquired a small proportion of the label N added.

A similar pattern of tree influence in mountain birch forests has recently been found in C cycling, with birch trees making a larger than expected contribution to soil CO_2 fluxes and driving most of the hyphae production (Parker et al. 2020). As mountain birch trees in these forests access the largest fraction of available N from discrete patches (Table 2) and disproportionately control C dynamics (Parker et al. 2020), there is mounting evidence that mountain birch trees may act as ecosystem engineers (Mitchell et al. 2007) controlling C and N cycling. Indeed it has recently been suggested that the presence of birch trees and associated biota, and not the abundance of ECM plants per se, mediates high rates of belowground C turnover driven by specific mycorrhizal N 'mining' strategies (Clemmensen et al. 2021). It should be noted that, due to the spatial foraging aspect of this experiment, N was made available in discrete patches which may be likened to an animal carcass or dead tree, but may not reflect responses to community wide N availability. The availability of N in discrete patches may have induced a foraging response

by the mountain birch trees. Birch trees are likely to have greater C resource availability than understorey shrubs which can be mobilised to facilitate root proliferation within nutrient patches, as well as their greater foraging range (Fig. 2) increasing the probability of encountering such a nutrient patch. Therefore, whilst we find that mountain birch trees out-forage understorey shrubs for discrete nutrient patches this may not apply to competition for mineral N available across larger areas.

Within the understorey, the ECM shrub *B. nana* assimilated significantly less of the ^{15}N label (0.085%) than either of the two ERM shrubs, *E. nigrum* and *V. vitis-idaea* (0.59 and 0.44%, respectively, Table 2). However, it is notable that all *B. nana* samples up to 1.2 m from the labelled area were ^{15}N-enriched, suggesting more homogeneous exploration of the soil matrix by this ECM shrub, compared with the ERM shrubs *E. nigrum* and *V. vitis-idaea* (discussed above). These data do not support our hypothesis 3(ii), that ECM shrubs access a greater proportion of available soil N. This difference between understorey shrubs may be due to the difference in mycorrhizal type, ECM versus ERM fungi, or growth form, but is likely to be driven primarily by the low *B. nana* cover within the plots (3.4%) compared to *E. nigrum* and *V. vitis-idaea* (57 and 19 %, respectively). This contrast in understorey species cover complicates direct N budget comparisons between sampled species, and these data should therefore be interpreted cautiously. Even though *B. nana* had low levels of pulse-derived N uptake within the plot, maximum levels of enrichment of *B. nana* were similar to those of *E. nigrum* and *V. vitis-idaea* (Fig. 4) suggesting that all three understorey species had similar levels of N acquisition capacity but varied in cover, leaf biomass and LAI (Table 2).

The wider foraging range and greater assimilation of available N in discrete patches, compared with the contribution to ecosystem LAI of ECM mountain birch trees, may confer a competitive advantage for canopy forming trees over understorey shrubs in these forests. This is particularly important in light of tree and tall shrub expansion in the subarctic (Myers-Smith et al. 2011, Rees et al. 2020), with consequences for both above- and belowground C cycling (Parker et al. 2021), which may in part be controlled by N foraging strategies and competition. Competition for a limited resource such as N is likely an important control on plant demography, community composition and distribution (McKane et al. 2002). Treeline advance may also have implications for plant diversity as treeline forests are less species rich than the open tundra heath (Supplementary material of Clemmensen et al. 2021). Previous studies on the nitrogen economy of mountain birch seedlings (Weih and Karlsson 1999) demonstrate that both relative growth rate and the rate of N accumulation during the 12-week growing season were closely related to subsequent winter survival. They noted that nutrient supply, soil temperature, vegetation shade and, potentially, allelopathy (caused by *Empetrum nigrum*, specifically) affect the N acquisition of first-year mountain birch seedlings, with implications for winter survival. Together with our results, it is an intriguing possibility that the 'open' structure of the mountain birch treeline forests is strongly modulated by N availability, intense competition for nutrients as well as potentially space, light and moisture in the understorey, and associated constraints on mountain birch seedling recruitment.

Understanding the net consequences of shrub and tree community dynamics for both N and C cycling is becoming increasingly urgent in subarctic treeline forests undergoing rapid climate driven change. Indeed, the relative abundance of ECM and ERM plant functional types could be critical for determining the stoichiometry of C and N in these systems, and their net potential to either sequester atmospheric CO_2, or emit it to the atmosphere, under global change.

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Author contributions

Nina L. Friggens: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Iain P. Hartley**: Writing – review and editing (supporting). **Thomas C. Parker**: Conceptualization (supporting); Writing – review and editing (supporting). **Jens-Arne Subke**: Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (supporting). **Philip P. Wookey**: Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j0zpc86j6 (Friggens et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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