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Wildfire effects on the fate of deposited nitrogen in a boreal larch forest

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Abstract The effects of nitrogen (N) deposition on forests largely depend on the ecosystem N status and the fates of deposited N. Boreal forests are typically N-limited ecosystems and are considered to be more efficient in retaining deposited N relative to temperate and tropical forests. As a primary disturbance in boreal forests, wildfires may alleviate N limitation in the burned ecosystem and increase mineralization, resulting in the altered outcomes of the N deposition. In order to explore the effects of a severe wildfire on the retention of deposited N, we investigated the fates of newly deposited N in burned and unburned boreal larch forests by applying $^{15}NH_4NO_3$ tracers to the forest floors. Results showed that total ecosystem retention for the deposited N was 60% in the forest recovering from a severe wildfire burned five years ago, significantly lower than in the unburned mature forest (89%). The difference was mainly attributed to the substantially lower retention in vegetation (8.3%) in the burned site than in the unburned forest (32.4%), as tracer recoveries in soil were similar (51.2 and 56.6%, respectively). Although most ^{15}N tracer was immobilized in organic soil in both burned and unburned forests (33 and 47%, respectively), a noticeably higher amount of ^{15}N was found in mineral soil in the burned forest (19%) than in the unburned forest (10%), suggesting mineral soil as a significant sink for N deposition in the burned forest. A higher total ^{15}N retention in the unburned forest implies that more new N input may stimulate C sequestration and promote the productivity of the Eurasian boreal forest under the background of atmospheric N deposition. However, a considerable amount of deposited N may be lost from the disturbed boreal larch forest ecosystem after a severe wildfire.

Keywords Wildfire · Nitrogen deposition · Nitrogen fate · Nitrogen retention · Nitrogen saturation · Boreal larch forest

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Introduction

Global nitrogen (N) deposition has increased considerably due to human activities, such as fossil fuel combustion and the intensive use of agricultural fertilizers (Galloway et al. 2008). There is widespread concern about elevated N deposition as it could alter ecosystem processes and properties (Vitousek et al. 1997; Matson et al. 2002; LeBauer and Treseder 2008). A growing body of research has been conducted to investigate ecosystem responses to deposited N and concluded that the effects of N deposition in forest ecosystems largely depend on the ecosystem's existing N status (Aber et al. 2003; Xia and Wan 2008). For example, the elevated N may cause nitrate leaching and denitrification in N-saturated forests, leading to soil acidification, aquatic eutrophication, and forest decline (Gundersen et al. 1998; Aber et al. 2003; Lovett and Goodale 2011). In contrast, a large amount of the deposited N may be retained in the soil to stimulate plant growth in N-limited forests, enhancing plant growth and carbon (C) sequestration (LeBauer and Treseder 2008; Quinn Thomas et al. 2009; Niu et al. 2016). Therefore, understanding the fate of the deposited N is critical to predicting ecosystem responses to N deposition and the changes in the global C cycle.

Temperate and boreal forests are often reported as N-limited ecosystems with low N availability (Vitousek and Howarth 1991). However, human activity has increased N deposition substantially over much of these areas (Aber et al. 2003; Galloway et al. 2004, 2011). Despite a recent declining trend in some regions due to clean air regulations, the atmospheric N deposition remains five to ten times higher than preindustrial levels (Borer and Stevens 2022). Studies suggested that a large portion of the deposited N is retained in ecosystems and stimulates carbon uptake and storage in temperate forests (Tietema et al. 1998; Magill et al. 2000; MacDonald et al. 2002; Holland et al. 2005; Liu et al. 2017; Li et al. 2019). Boreal forests are considered to retain the deposited N more efficiently due to a low N mineralization rate at a low temperature relative to temperate forests (Schulte-Uebbing and de Vries 2017). However, limited studies investigated the fate of N deposition in boreal forests (Weber and Cleve 1981; Melin and Nômmik 1983, 1988; Preston et al. 1990; Gundale et al. 2014; Sheng et al. 2014; Goodale et al. 2016).

Boreal forests in North America, Asia and Europe are increasingly impacted by severe wildfires (Turner and Romme 1994; Turner et al. 2007). Wildfires could reduce N storage through burning vegetation and litter but may increase inorganic N and mineralization rates through ash deposition and decomposition of remaining organic matter (Popova et al. 2013; Kong et al. 2014). Due to reduced plant biomass, the increased inorganic N may be lost through leaching or gaseous emission in burned forests (Högberg 1997; Bladon et al. 2008).

The Great Xing'an Mountains of Northeast China are situated at the southern extension of the Eurasian boreal forest. This region was historically characterized by frequent, mixed-severity surface fires intermingled with infrequent, stand-replacing crown fires, with fire-free intervals ranging from 30 to 120 years (Xu et al. 1997; Liu et al. 2012). As a result of climate change, this region is experiencing more frequent high-severity wildfires (Fang et al. 2015). However, knowledge is still lacking on the fate of N deposition and the distribution of deposited N in different ecosystem compartments of the boreal larch forests in the Great Xing'an Mountains.

In this study, we applied ^{15}N tracers to a recently burned boreal forest and an adjacent mature larch forest located in the Great Xing'an Mountains of northeastern China. Our main objective was to determine the retention and partitioning of deposited N in various ecosystem compartments in both the unburned and burned boreal larch forests. Then, by comparing the retention and partitioning patterns of ^{15}N tracers in the burned and unburned forests, we could explore the mechanisms affecting the fates of deposited N on plant and soil compartments in the context of wildfire. Based on the current literature about fire ecology, we proposed the following specific hypotheses:

(1) Vegetation retains a lower proportion of the deposited N in the burned forest than in the unburned forest due to plant biomass removal by burning.
(2) Organic soil retains a lower proportion of N deposition in the burned forest than in the unburned forest because of the smaller O horizon due to burning, but the ^{15}N retention rate in mineral soil may be similar between burned and unburned forests.

(3) The total ecosystem ^{15}N retention is lower in the burned forest than in the unburned forest.

Materials and methods

Study site

The study was conducted at Huzhong National Nature Reserve (HNNR), located in the Great Xing'an Mountains (50°10′ N to 53°33′N, 121°12′E to 127°00′E) of northeastern China, with a total area of 8.46×10^4 km^2. This region experienced a terrestrial monsoon climate with a long and cold winter. The climate characteristics combined with the poorly decomposable plant litter and waterlogged soil contribute to a very low decomposition rate and N availability. The mean annual precipitation is approximately 500 mm, and the mean annual temperature is − 4.7 °C (Zhou 1991; Liu et al. 2012). The average monthly precipitation was 41 mm over the first year after the ^{15}N was applied (from June 2014 to July 2015). The amount of N deposition in this region was modest, only 1.8 kg ha^{-1} yr^{-1} (Schulte-Uebbing and de Vries 2017). The soil is classified as brown coniferous forest soil (Kong et al. 2019). The vegetation of this area is dominated by larch (*Larix gmelini*) with mixtures of pine (*Pinus sylvestris* var. *mongolica*), spruce (*Picea koraiensis*), birch (*Betula platyphylla*), and two species of aspen (*Populus davidiana* and *Populus suaveolens*). *Vaccinium vitis-idaea* and *Ledum palustre* are the most abundant understory species. Due to close proximity, the watersheds within the burned and unburned areas are characterized by the same geology and landform. In addition, these watersheds belong to the same natural reserve, where the forests have been protected from human exploitation since the 1950s. Therefore, the burned sites may be considered to possess similar pre-fire vegetation structure and soil properties with the corresponding unburned sites that share almost identical topographic characteristics such as altitude, aspect, and topographic position (Fig. 1).

Experimental design

Wildfire is a principal disturbance agent in the Great Xing'an Mountains. The area was characterized by frequent, mixed-intensity surface fires intermingled with infrequent stand-replacing fires. A severe wildfire burned 600 ha of Huzhong National Natural Reserve on June 26th, 2010. This fire provided an ideal opportunity to study wildfire effects on the fates of N deposition in this ecosystem. In May 2014, we selected three headwater-level watersheds in the above-mentioned burned area and randomly set four plots (10 m^2) with two plots at north-facing and south-facing slopes in each watershed. Six unburned plots (10×10 m^2 to account for mature tree's canopy) were established in three watersheds near the burned area, with one plot at each aspect

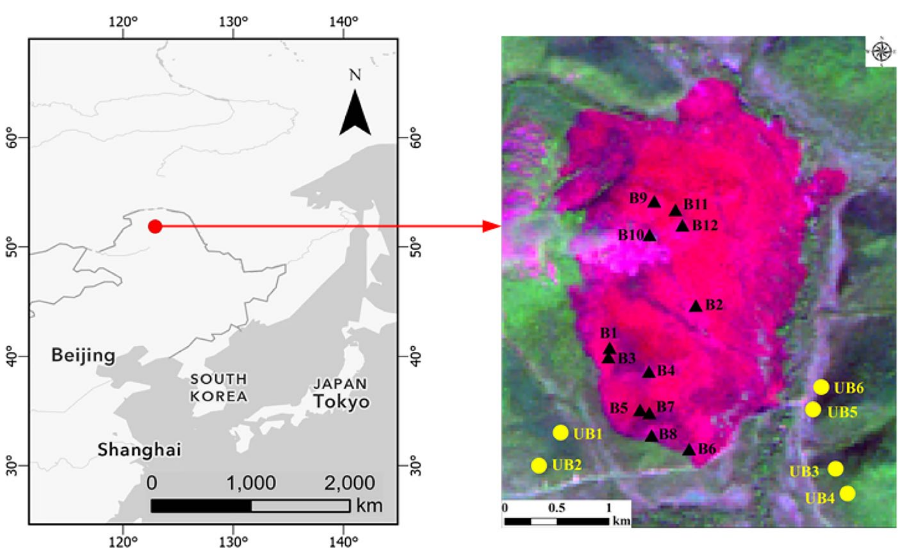

Fig. 1 Map of the study area. The red area represents the burned forest. The green area represents the unburned boreal larch forest. The black triangles represent sample plots in the burned forest, and the yellow circles represent unburned plots

within each watershed, as shown in Fig. 1. Despite the inherent limitations, pairing the unburned with the burned sites provides an opportunity to observe effects of large-scale natural disturbances on forests ecosystems. We located the plots at least 200 m from the roads to avoid edge effects. To minimize spatial autocorrelation, we set the plots at least 200 m away from each other. We applied 1.3636 g 99.14 atom% $^{15}NH_4NO_3$ salt dissolved in 2 L purified water in each burned plot, and 13.6364 g 99.14 atom% $^{15}NH_4NO_3$ salt dissolved in 20 L purified water was applied in each unburned plot. The quantity of the ^{15}N tracer per unit area applied to each plot was calculated to be 25 mg $^{15}N \cdot m^{-2}$. Compared to the bulky soil N pool, such a small amount of N input would not elevate soil N concentrations. After ^{15}N addition, the concentration of ^{15}N increased significantly above its natural abundance in almost all of the major ecosystem compartments without a noticeable impact on ecosystem N pools and fluxes.

Field sampling

Major ecosystem compartments were sampled before and 13 months after the ^{15}N labeling. At the beginning of labeling (June 2015), plant and soil samples from the burned and unburned plots were collected. In the burned plots, no live mature trees were observed. We harvested all the shrubs and herbs within 1/3 of the area of each plot and collected plant and soil samples. Larch is the dominant (often the single) tree species in the unburned plots. We recorded the DBH of each larch tree and collected their foliage and branches. Cores and bark samples were collected ~ 1.3 m above the soil surface using an increment borer. In order to calculate the foliage and branch biomass of tall shrubs in unburned plots, such as *Pinus pumila* and *Rhododendron dauricum*, we measured certain allometric indexes, such as the diameter at the rising portion of the top stem and the length of the top stem for *P. pumila* (Kajimono 1992) and height, branch number and crown breadth for *R. dauricum*. We selected four 1 m × 1 m subplots along the plot's border and recorded the shrub species. Then, the foliage and branches of both tall and dwarf shrubs were sampled. Mosses were collected from three 10 cm × 10 cm templates in each plot.

Three 20 cm × 20 cm subplots were randomly set to collect organic soil in each plot. The organic soil was separated into Oi Layer (slightly decomposed) and Oa + e Layer (moderately and highly decomposed). Mineral soil samples from three layers (M1: 0–10 cm, M2: 10–20 cm, and M3: 20–30 cm) were taken in the same subplots. Three soil samples were collected at each soil layer and mixed into one composite sample per plot. Live roots were hand-sorted from Oa + e and 0–30 cm mineral soil. Roots were divided into fine roots (diameter ≤ 2 mm) and coarse roots (diameter > 2 mm). Each mineral soil layer was collected with a 100 cm^3 cutting ring to measure the bulk density. Cones, large twigs and roots were removed from the soil samples.

Laboratory analysis

Samples of organic and mineral soils were air-dried, crushed, and sieved through 5 mm and 2 mm mesh, respectively. Plant and soil samples were dried at 60 °C to constant weight and were ground to fine powder in a ball mill to pass through a 0.15 mm mesh sieve before analyzing $\delta^{15}N$, N, and C concentrations using an elemental analyzer (EA1112) coupled with an isotope ratio mass spectrometry (Delta XP; Thermo Fisher Scientific and Yokohama, Japan). Calibrated DL-alanine ($\delta^{15}N = -1.7‰$), glycine ($\delta^{15}N = 10.0‰$), and histidine ($\delta^{15}N = -8.0‰$) were used as the internal standards. Stable isotope abundance was expressed as:

$$\delta^{15}N(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

where R_{sample} and R_{standard} are the ratios between ^{15}N and ^{14}N of the sample and standard, respectively. The standard is atmospheric N_2, with a ^{15}N:^{14}N ratio of 0.0036765 (Högberg 1997). The analytical precision for $\delta^{15}N$ was, in general, better than 0.3‰.

Calculations and statistical analyses

Ecosystem biomass and N pools

In the burned plots, litter and plant samples were oven-dried to constant weight at 60 °C to calculate their biomass. In the unburned plots, all the dwarf shrubs and herbs within the four 1 × 1 m subplots were harvested and weighted to estimate the biomass. Tree biomass for the species *larix*, *P. pumila* and *R. dauricum* was calculated based on the allometric relationships developed by previous studies (Kajimoto 1992; Wang 2006), with separate equations for leaf, branch, trunk, and root. The mass for each of the three mineral soil horizons (0–10, 10–20, 20–30 cm) was estimated according to each soil horizon's bulk density and soil bulk. Subsequently, the N content was estimated as the product of the mean N concentration and the biomass or mass for each ecosystem compartment.

Percent ^{15}N tracer recovery ($^{15}N_{rec}$) in each ecosystem compartment was estimated by ^{15}N tracer mass balance according to the following equation (Providoli et al. 2005):

$$^{15}N_{\mathrm{rec}}(\%) = \frac{\left(\mathrm{at.\%}\,^{15}N_{\mathrm{sample}} - \mathrm{at.\%}\,^{15}N_{\mathrm{ref}}\right) \times N_{\mathrm{s}}\% \times M_{\mathrm{pool}}}{\left(\mathrm{at.\%}\,^{15}N_{\mathrm{tracer}} - \mathrm{at.\%}\,^{15}N_{\mathrm{ref}}\right) \times M_{\mathrm{tracer}}} \times 100\% \quad (2)$$

$$\mathrm{atom\%} = \frac{^{15}N}{^{14}N + {}^{15}N} \times 100\% \quad (3)$$

where atom% is used to express the atomic percentage of ^{15}N; at.% $^{15}N_{sample}$,at.% $^{15}N_{ref}$ and at.% $^{15}N_{tracer}$ are the atom% of ^{15}N in the labeled samples, non-labeled samples and applied N tracer, respectively; N_s% is the N concentration of N samples from the labeled plots; M_{pool} is the dry mass of the labeled N pool; M_{tracer} is the total mass of ^{15}N of the applied tracer. We used ^{15}N tracer recoveries to estimate net N retention in burned and unburned forests. In our study, total ecosystem retention of applied ^{15}N was calculated as the sum of ^{15}N tracer recoveries within different horizons of soil, moss, and plant tissues (foliage, branch, and root).

We used Welch's t-test, which allows for the comparison of two groups with unequal sample sizes and unequal variances, to examine the wildfire effects on total ecosystem N retention in burned and unburned sites and the differences in the proportion of ^{15}N tracer recoveries of different ecosystem compartments in burned and unburned forests. All statistical analyses were conducted using R software v. 3.6.1 (R Core Team 2019).

Results

Basic soil and plant properties

The TN, TC, and C:N were lower in the burned soil, but only the reduction of TC in the organic soil layer reached a significant level (Table 1). The significant increases in soil inorganic N concentrations in response to the wildfire were only observed in the mineral soil. Compared to unburned sites, the amount of NH_4^+ was increased from 1.6 to 5.0 mg N·kg^{-1} in the mineral soil of the burned sites. As shown in Table 2, the plant biomass in burned and unburned forests was 9 and 77 t ha^{-1}, respectively. There was no significant difference in mineral soil mass between burned and unburned forests. The C:N of the various ecosystem compartments in the burned forest was significantly lower than that of the unburned forest, except for the fine root at the Oa + e horizon, the organic soil at the Oa + e layer, and mineral soil. The N% decreased with soil depth. In the burned forest, the N% of shrub, moss and mineral soil at the depth of 0–10 cm and 10–20 cm were significantly higher than that in the unburned forest, whereas the values of N% in organic soil (Oi and Oa + e) in the burned forest were higher than in the unburned forest.

Ecosystem N pools

The total ecosystem N pool in the burned forest was about 2528 kg N ha^{-1}, which was substantially lower than that in the unburned forest (3370 kg N ha^{-1}, Table 2). A significantly decreased N pool was observed in the Oi layer in the burned (23 kg N ha^{-1}) when compared to the unburned forest (126 kg N ha^{-1}). However, no significant difference was found in the Oa + e layer ($p = 0.14$) or the mineral soil at the depth of 0–10 cm ($p = 0.09$) and 10–20 cm ($p = 0.16$) between the burned and unburned forest (Table 2). The N pool in 20–30 cm mineral soil was significantly higher in the burned sites than in the unburned sites.

N pool of shrub leaf and shrub branch in the burned forest were 21 kg ha^{-1} and 13 kg ha^{-1}, respectively, which were significantly lower than those in the unburned forest (157 kg N ha^{-1} and 167 kg N ha^{-1}, respectively) (Table 2). The N pool of

Table 1 Basic soil properties in the unburned (n = 6) and burned forests (n = 12) sampled prior to ^{15}N labeling

Layer	pH		NH_4^+ (mg N·kg^{-1})		NO_3^- (mg N·kg^{-1})		TN (%)		TC (%)		C:N	
	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Organic layer	4.4 (0.5)	5.2 (0.5)	8.1 (2.6)	7.2 (2.1)	3.3 (1.2)	3.0 (1.2)	0.8 (0.5)	0.4 (0.2)	**29.2 (10.2)**	**9.2 (4.0)**	27.5 (5.0)	20.8 (5.4)
Mineral layer (0–20 cm)	5.2 (0.4)	5.3 (0.3)	**1.6 (0.2)**	**5.0 (1.5)**	0.6 (0.3)	0.5 (0.3)	0.2 (0.0)	0.2 (0.0)	4.3 (1.1)	3.1 (0.5)	24.1 (4.1)	20.3 (2.4)

Values presented are means with the standard error in parentheses. Bold values indicate a significant difference ($p < 0.05$) between the burned site and unburned forest

underground plant materials in the burned area (78 kg N ha^{-1}) was significantly lower than in the unburned area (428 kg N ha^{-1}).

δ^{15}N of plants and soil before and after the ^{15}N tracer addition

The δ^{15}N values of plants and organic soil in burned sites before ^{15}N addition (natural abundance) were significantly higher compared to the δ^{15}N values in unburned forests (Fig. 2a). The shrub foliar and branch δ^{15}N were, on average, 2.2 and 1.7‰, respectively, in the burned forest, which were significantly greater than those in the unburned forest (both − 3.5‰). The moss average δ^{15}N was 0.7‰ in the burned forest, which was significantly higher than the mean in the unburned forest (− 4.1‰). Fine roots mean δ^{15}N in three soil layers (Oa + e, M1 and M2) were 1.0, 0.7 and 0.5‰, respectively, in burned forest and were significantly higher than those in unburned forest (− 1.6, − 0.6 and − 0.7‰, respectively). The wildfire also significantly increased the δ^{15}N of Oa + e and Oi soil layers but did not significantly affect mineral soil layers ($p = 0.23$, 0.25 and 0.19 for mineral soil at the depth of 0–10, 10–20 and 20–30 cm, respectively).

In the 13 months after adding ^{15}N tracer, δ^{15}N in shrub branches and moss in the burned forest were significantly lower than in the unburned forest (Fig. 2b). There is no significant difference in δ^{15}N for the other ecosystem compartments above the ground. The significantly higher values of δ^{15}N in fine roots were observed in Oa + e in the burned sites compared to those values in unburned forests. Mean δ^{15}N in Oa + e from the burned forest reached 95.3‰ and was significantly higher than that in the unburned forest (21.0‰). A significant difference of δ^{15}N between the burned and unburned forests was also found in each of the three mineral soil horizons.

^{15}N tracer recovery in plants and soil

In the 13 months after adding $^{15}NH_4NO_3$ tracer, the average total ^{15}N recovery was 60 and 89% in the burned and unburned forests, respectively (Fig. 3). In both forests, most ^{15}N was recovered in soil (burned: 51.2 ± 5%, unburned: 56.6 ± 9%, Fig. 3a), particularly in organic soil (burned: 34%, unburned: 47%, Fig. 3b). Among various soil compartments,

Table 2 Mean and standard error of C:N, N concentration, mass, and N content of major ecosystem compartments in unburned and burned forests sampled 13 months after N15 labeling

Ecosystem compartments	C:N		N%		Mass (t ha^{-1})		N(kg ha^{-1})	
	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Tree								
Leaf	**23.77 (0.21)**	**18.13 (0.84)**	2.09 (0.08)	2.48 (0.17)	**2.40 (0.95)**	**0.28 (0.17)**	**58.44 (20.79)**	**1.67 (1.11)**
Branch	**62.13 (0.57)**	**41.21 (3.81)**	0.78 (0.04)	1.02 (0.02)	**22.24 (7.52)**	**0.00 (0.00)**	**171.19 (66.36)**	**0.20 (0.08)**
Coarse root	62.1 (1.1)		0.56 (0.01)		20.37 (0.98)		102.61 (32.38)	
Shrub								
Leaf	**32.98 (3.08)**	**18.11 (2.43)**	**1.69 (0.16)**	**2.78 (0.20)**	**0.40 (0.10)**	**0.05 (0.02)**	**157.34 (52.51)**	**21.39 (6.75)**
Branch	**51.23 (1.12)**	**36.11 (1.89)**	**0.98 (0.09)**	**1.34 (0.05)**	**4.71 (2.01)**	**0.04 (0.01)**	**167.35 (60.86)**	**12.63 (4.14)**
Herb		13.03 (0.95)		3.16 (0.16)		0.07 (0.01)		3.69 (0.61)
Moss	**39.17 (1.85)**	**28.38 (0.87)**	**1.28 (0.07)**	**1.52 (0.05)**	1.17 (0.24)	0.99 (0.21)	14.54 (2.78)	15.18 (3.25)
Fine roots								
Oa + e	37.92 (3.05)	36.40 (1.86)	1.06 (0.07)	1.07 (0.05)	**24.40 (5.51)**	**1. 05 (0.53)**	**245.90 (52.19)**	**11.35 (5.82)**
0–10 cm	**44.93 (3.02)**	**36.77 (1.08)**	1.16 (0.06)	1.18 (0.06)	4.75 (3.69)	0.47 (0.32)	47.68 (35.32)	5.12 (3.40)
10–20 cm	**49.33 (1.30)**	**39.56 (1.68)**	1.00 (0.07)	1.06 (0.08)	0.08 (0.06)	5.81 (4.63)	0.65 (0.50)	61.44 (51.54)
Organic								
Oi	**25.85 (2.47)**	**17.97 (1.11)**	**1.33 (0.06)**	**0.96 (0.05)**	**9.37 (1.35)**	**2.56 (0.37)**	**125.89 (19.87)**	**23.36 (3.01)**
Oa + e	**27.51 (1.51)**	**36.40 (1.86)**	**1.14 (0.07)**	**0.72 (0.07)**	37.34 (9.74)	43.21 (4.26)	452.75 (132.83)	289.16 (23.83)
Mineral								
0–10 cm	21.12 (1.61)	19.51 (0.81)	0.19 (0.02)	0.15 (0.01)	566.38 (66.11)	531.08 (35.95)	1042.69 (164.78)	782.92 (36.03)
10–20 cm	18.35 (1.65)	18.44 (0.88)	**0.11 (0.01)**	**0.13 (0.01)**	579.84 (52.76)	575. 28 (43.31)	634.97 (66.56)	727.13 (58.01)
20–30 cm	17.74 (1.56)	16.94 (0.97)	**0.08 (0.01)**	**0.11 (0.01)**	566.10 (70.04)	566. 15 (42.70)	**439.96 (14.99)**	**606.07 (56.48)**

Bold values indicate a significant difference ($p < 0.05$) between the burned site and unburned forest

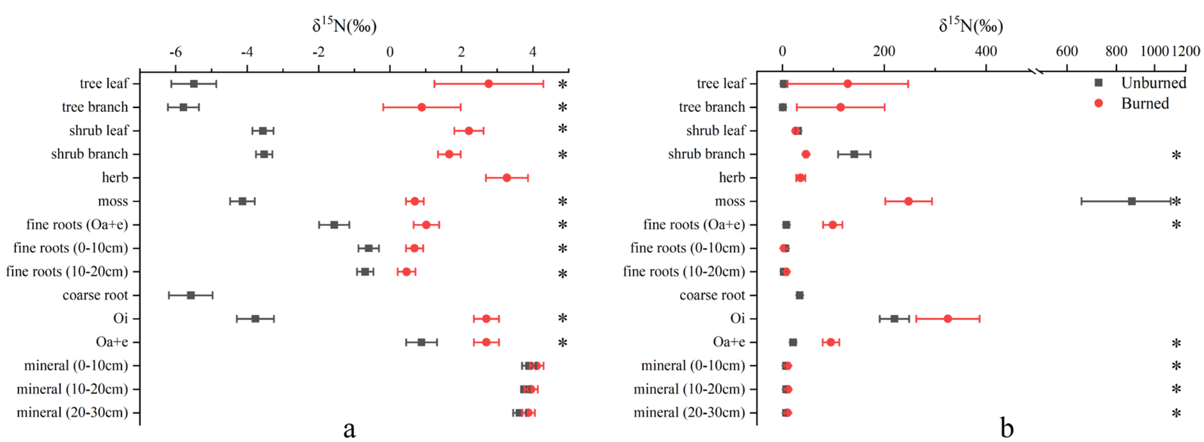

Fig. 2 The δ^{15}N (‰) for plant and soil compartments before (**a**) and after (**b**) adding $^{15}NH_4NO_3$ in the burned forest and unburned forest. Solid red circles represent burned plots, and solid black squares represent unburned plots. Error bars represent the standard error of the mean (n = 6 for unburned treatment and 12 for burned treatment). One asterisk indicates a significant difference between the burned and unburned forests at $p < 0.05$

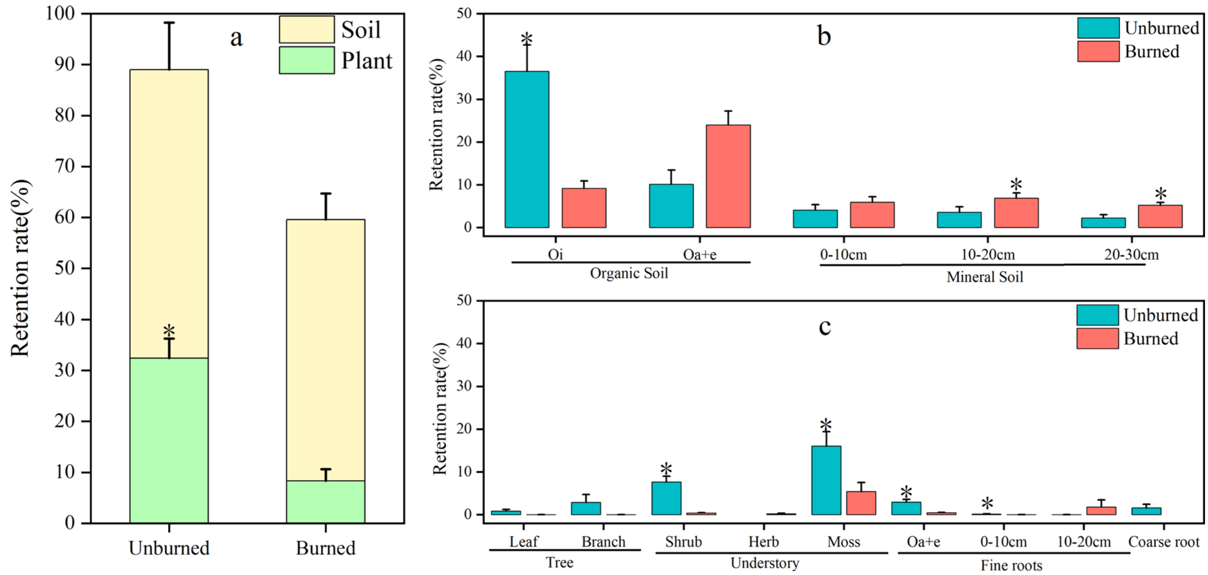

Fig. 3 Tracer ($^{15}NH_4NO_3$) recovery in the plant and soil (**a**), in various ecosystem compartments of soil (**b**) and plants (**c**) after ^{15}N tracer addition between the unburned and burned boreal larch forests. Error bars represent SE. One asterisk indicates a significant difference between the burned and unburned forests at $p < 0.05$

Oi contained the largest percentage (37%) of the tracer ^{15}N in the unburned forest, followed by Oa + e (10%, Fig. 3). In contrast, the Oa + e layer was the most important sink of ^{15}N (24%), whereas Oi (10%) was the second important sink in the burned forest (Fig. 3). ^{15}N recovery with the mineral soil constituents was higher in the burned forest than the unburned forest and decreased with depth in both forests (Fig. 3). The differences in ^{15}N recovery in the 10–20 cm and 20–30 cm mineral soil layers were statistically significant between burned and unburned sites.

A significantly higher ^{15}N recovery by plants was observed in unburned forests than in burned sites. Plants accounted for 32.4% of the added ^{15}N in the unburned sites but only 8.3% in the unburned forest. The ^{15}N recovery in shrub branches and leaves was less than 1% in the burned forest, significantly lower than those (6 ± 1 and 2 ± 1%, respectively) in the unburned forest. The ^{15}N recovery in moss was significantly higher in the unburned forest (16 ± 3%) than in the burned sites (5 ± 2%). The recoveries for fine roots in Oa + e and 0–10 cm mineral soil were less than 1% in the burned sites. In the unburned forests, their corresponding mean and standard error values were 2.9 ± 0.6 and 0.4 ± 0.1%, respectively.

Discussion

^{15}N tracer distribution in plants

Plants play an essential role in retaining the deposited N in a mature boreal larch forest, accounting for 32% of the added $^{15}NH_4NO_3$ tracer. However, the importance of plants in N retention was weakened in the burned forest, with only an average of 8% of the ^{15}N tracer incorporated into the plant. These results fully supported our first hypothesis. The significantly reduced biomass and declined N pool in the burned sites probably led to the lower ^{15}N tracer recovery in the plant. The higher ^{15}N recovery in the unburned forest may be attributed to the large biomass of plants, especially trees and understory shrubs. In the 5-year post-fire burned sites, the trees and shrubs were mostly removed, with some dwarf shrubs, herbs, and moss remaining, and very few larch seedlings regenerated. A higher ^{15}N retention of plants in the unburned forest than in burned sites indicates that although the deposited N could be incorporated into plants to stimulate the productivity of the boreal larch forest, a considerable amount of new N input could be lost from the ecosystem after a wildfire.

The mean ^{15}N recoveries in moss were 16 and 5% in unburned and burned forests, respectively, and accounted for more than half of the added ^{15}N tracer in plant N pool, indicating moss was a significant sink for the deposited N in boreal forests. Applications of ^{15}N to boreal forests generally showed a considerable amount of ^{15}N tracer in the moss layer (Weber and Cleve 1981; Preston et al. 1990; Gundale et al. 2014; Rousk et al. 2014). A study conducted in the Alaskan *Picea mariana* forest showed that 90% of the ^{15}N tracer was retained in the feathermoss (Weber and Cleve 1981). This differs from temperate forests, where the understory vegetation only accounts for 2–15% of the new N inputs (Preston et al. 1990; Buchmann et al. 1996; Tietema et al. 1998). For example, the observed ^{15}N recoveries in understories (both shrub and herb) were approximately 2% and 9% in two temperate forests (Qingyuan Forest and Changbai Mountain Forest) in northeastern China (Liu et al. 2017; Li et al. 2019), respectively.

The significantly higher ^{15}N recovery of fine roots in the Oa + e layer and the 0–10 cm mineral soil layer in the unburned forest may be attributed to the higher fine root biomass in the unburned forest than in the burned forest. However, the higher ^{15}N retention of fine root in the 10–20 cm mineral soil layer was observed in the burned forest. The following two reasons may explain this phenomenon. The first was that fine roots were mainly distributed in the burned forest's 0–20 cm mineral soil. While in the unburned sites, fine roots were mainly distributed in the organic soil layer. The other one was that the higher $\delta^{15}N$ of fine roots in 10–20 mineral soil in the burned forest might result from inorganic N being transported into the deep soil layer. The wildfire consumed surface litter layers, forcing plants to take up N from deeper soil horizons, where ^{15}N tracer recovery was higher in the burned sites than in the unburned sites (Fig. 3b). Part of $^{15}NH_4^+$ infiltrated into the deeper mineral soil with rainfall from the surface soil layer, leading to the mineral soil N pool being enriched in ^{15}N.

^{15}N tracer retention and redistribution in the soil

A higher ^{15}N retention in organic soil was observed in the burned forest than in the unburned forest, in accordance with the first half of our hypothesis 2. However, our results did not support the second half of hypothesis 2, "^{15}N retention captured in mineral soil may be similar in burned and unburned forests". This suggests that mineral soil plays a more important role in deposited N retention in the burned forest than in the unburned forest after the reduction of organic soil.

The recovery of added ^{15}N tracer in soil was similar in the burned sites and unburned forest, respectively. This finding was consistent with previous studies conducted elsewhere (Nadelhoffer et al. 1999; Zak et al. 2004; Liu et al. 2017). Our study further showed that the NH_4^+ tracer was predominantly captured in organic soil layers. This phenomenon could be attributed to these two mechanisms: (1) the preference for immobilizing NH_4^+ by microbes in temperate and boreal forests (Perakis and Hedin 2001; Zhu and Wang 2010), and (2) the thick litter layer (about 20 cm) in the unburned forest, which served as a buffer to prevent the deposited N from being lost from ecosystems through leaching or denitrification (Liu et al. 2017). Consequently, the thinner organic layer after the severe wildfire was the main reason for the significantly lower ^{15}N retention rate observed in the burned Oi layer. A study conducted in tropical forests also showed that a thin organic layer resulted in a low ^{15}N retention rate (Wang et al. 2018). Additionally, a higher soil C:N ratio is generally associated with higher microbial N immobilization, which could lead to greater N retention (Templer et al. 2012). Thus, a lower C:N of Oi layer in the burned forest leads to a lower ^{15}N retention when compared to the unburned forest. Vise verse, a higher ^{15}N retention in Oa + e was observed in the burned forest than in the unburned forest because of the higher C:N of Oa + e in the burned forest. Our study showed that the Oi layer is a dominant sink for the deposited N in the mature boreal larch forest. However, the Oa + e layer was the main sink for the added ^{15}N in the burned sites. The less hindrance to transfer $^{15}NH_4^+$ from the Oi layer to the deeper Oa + e layer, resulting from the declined thickness of the Oi layer by the wildfire, could explain the higher retention of ^{15}N tracer in the Oa + e layer in the burned sites. A higher ^{15}N tracer recovery was observed in the mineral soil layer at 20–30 cm depth in the burned sites, indicating that the added ^{15}N tracer transported to deeper soil horizons.

Total ecosystem ^{15}N tracer recovery

Compared to the unburned forest, the decreased ^{15}N tracer recovery in the burned sites suggested a lower retention capacity in the boreal forest after a severe wildfire. These results supported our hypothesis 3. NH_4^+ is reported as the primary form of deposited N in Chinese boreal forests (Sheng et al. 2014). The significantly declined ecosystem ^{15}N recovery at the burned sites indicated that a considerable amount of the deposited N is not incorporated into plant and soil pools in this ecosystem. The declined N recovery in the burned sites may be attributed to lower N immobilization because of the smaller O horizon due to burning. The different N retention patterns in plants and the organic soil layer are probably the principal drivers of the difference in total N retention capacity between the burned and unburned boreal larch forests.

Although there is limited knowledge on the effects of wildfire disturbance on the fates of deposited N, studies in which tracers have been applied to other disturbances, like agriculture conversion (Compton and Boone 2000) and deforestation (Lewis et al. 2014), also suggest the total ecosystem ^{15}N tracer recovery would decline after a disturbance. The changed N status might explain this pattern. The higher values of ^{15}N natural abundance in soil and plants generally indicate ecosystems with a more open N cycle (Robinson 2001; Matsushima et al. 2012; Houle et al. 2014) and less N retention (Templer et al. 2012). In this study, the N-limited status of boreal forest may have been alleviated after the severe wildfire. The foliar ^{15}N natural abundance from the same species of tree (larch) and shrubs (*Rhododendron dauricum* and *Ledum palustre*) showed a significantly higher value in the burned area than those in the unburned area, indicating a more N saturation status in the burned sites and less ^{15}N retention. Furthermore, studies across the forest ecosystems of Europe and North America indicate that the total ecosystem ^{15}N tracer recovery positively correlates with soil C:N ratio (Templer et al. 2012). Thus, a lower mineral soil C:N in the burned forest (shown in Tables 1, 2) could be another reason for a lower ^{15}N retention rate in the burned forest.

Our result showed that the undisturbed boreal larch forest in northeastern China has a high (89%) ^{15}N tracer recovery rate after 13 months of tracer addition. This finding is corroborated by another field experiment conducted in a boreal larch forest in Great Xing'an Mountain by Sheng et al. (2014), whose results showed a high $(^{15}NH_4)_2SO_4$ tracer retention (90.5%) with a majority of ^{15}N tracer in the organic soil. The ^{15}N tracer recovery in our experiment was higher than in a similar experiment conducted in two temperate forests (a larch plantation forest and a mixed broadleaved and Korean pine forest) also located in northeastern China (Qingyuan Forest Research Station), which had a mean ^{15}N tracer recovery of 57 and 67% one year after the tracer addition, respectively (Li et al. 2019). Compared to Qingyuan Forest, Chinese boreal larch forests are located in the northernmost part of northeastern China, where the extremely low mean annual temperature could inhibit microbial activities, leading to lower rates of N cycling and less N availability. Thus, the new input N could be more steadily incorporated into plants and soil of the boreal larch forests. Additionally, high N retention rates are often associated with low atmospheric N deposition rates (Templer et al. 2012). Atmospheric N deposition in the Qingyuan Forest area is reported at the level of 15–21 kg N ha^{-1} yr^{-1} (Li et al. 2019). In contrast, the boreal larch forest had a much lower atmospheric N deposition (1.8 kg N ha^{-1} yr^{-1}), which may lead to a high capacity for retaining the deposited N.

Conclusions

In order to explore the impacts of a severe wildfire on the fates of deposited N, we measured the ^{15}N retention rates in different ecosystem compartments in a burned Chinese boreal forest and a mature boreal larch forest by applying $^{15}NH_4NO_3$ tracers to the forest floors. In the unburned mature larch boreal forest, moss and understory are major plant sinks for ^{15}N in this ecosystem. The added $^{15}NH_4^+$ tracers were primarily stored in the organic soil horizon (Oi and Oa + e layers). Compared to temperate forests in northeastern China, the Chinese boreal larch forest has a high capacity for retaining the deposited N. The wildfire reduced the boreal larch forest's capacity to capture the new N input and altered its partitioning patterns in different ecosystem compartments. The declined N recovery in plants likely resulted from combustion and N removal during burning. The capacities of retaining ^{15}N in Oa + e and deeper mineral soils were enhanced after a severe wildfire. Our results implied that anthropogenic N input might stimulate C sequestration and promote productivity in an undisturbed boreal larch forest. In contrast, a considerable amount of deposited N could be lost from the ecosystem after a wildfire.

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Author contributions All authors contributed to the conception and design. Sample collection was carried out by WL, JZ and BL. WL, LQ and WH performed the analyses and result interpretation. WL wrote the manuscript with input from other authors. YF and JY contributed significantly to the analyses with constructive discussion and critical revision of this article. All authors reviewed, edited, and approved the final manuscript.

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Data availability All data generated or analyzed during this study are available as supplementary after the paper is published.

Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

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