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The fate of leaf-litter N under contrasting pedo-climatic conditions in south-western Siberia

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Abstract

Nitrogen (N) made available through the decomposition of organic matter is a major source for plants in terrestrial ecosystems. N cycling in Siberia is however poorly documented despite the region representing a substantial surface area of the globe.

We studied the influence of pedo-climate (using two forest-steppe and two southern taiga sites) and vegetation type (aspen forest and grassland) on the redistribution of N released from decomposing ^{15}N-labelled leaf-litter in south-western (SW) Siberia. A model of N dynamics was fit to field measurements that yielded estimates of N mean residence time (*MRT*) within litter and soil layers, as well as the proportion of N transferred from one layer to another.

The release of N from the aspen litter was slower in the forest-steppe (*MRT* in litter: 2.9–4.6 years) than in the southern taiga (0.9–1.5 years), likely because winter soil freezing and summer drought slowed decomposition in the forest-steppe. In contrast, no difference between the bioclimatic zones was observed for the grass litter (*MRT* 1.2–1.6 years), suggesting litter chemistry outweighs pedo-climate in these zones. While most of the vertical transfer of N down the soil profile occurred during the vegetative season, important losses were observed after snow-melt. Over three years, the transfer of N within the soil profile was deeper in the southern taiga sites than in the forest-steppe, and in forest than in grassland. In the topsoil, the *MRT* of N was longer in grassland

(4.9–9.4 years) than in forest (1.5–2.1 years) but there were no pronounced differences between bioclimatic zones.

The detailed and quantitative view of current N cycling in SW Siberia provided in this study may serve as the basis for informing ecosystem models that anticipate future climate and land-use changes.

Keywords: ^{15}N-Labelled Litter, Nitrogen Cycling, Nitrogen Flow Model, Leaf-Litter Decomposition, Pedo-Climate, South-Western Siberia

1. Introduction

Siberia covers over 10 million km^{-2} (6.7 % of terrestrial land globally) and, given its northern proximity, it is one of the largest landmasses to be affected by climate change (Groisman et al., 2012). For instance, the bioclimatic zones of south-western (SW) Siberia (steppe, forest-steppe, and southern taiga), which encompasses the transition from cold desert in the south to dense boreal forest in the north, are predicted to spread northwards at the expense of taiga zones (Jiang et al., 2012; Lucht et al., 2006; Soja et al., 2007; Shuman et al., 2015; Tchebakova et al., 2009). With climate change, shifts in temperature and precipitation regimes directly affect microbial enzymatic activities related to nitrogen (N) transformations (Borken & Matzner, 2009; Rustad et al., 2001) as well as indirectly by influencing transport of enzymes and N substrates through the soil profile (Greaver et al., 2016). How these effects manifest in SW Siberia's different bioclimatic zones is not well characterized and, given the potential of these lands as candidates for agricultural conversion (Tchebakova et al., 2011; Kicklighter et al., 2014), there is a pressing need to understand the soil nutrient cycling of this region.

In northern ecosystems, litter decomposition is a pivotal process for N cycling. In those regions, atmospheric N deposition is generally low (Dentener et al., 2006) and non-symbiotic plants depend mostly on litter N recycling to fulfil their nutrient requirements (Högberg et al., 2017). Furthermore, N limitation is reported to increase towards the

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poles (Fay et al., 2015; LeBauer & Treseder, 2008; Reich & Oleksyn, 2004; Vitousek & Howarth, 1991). The litter decomposition process consists of fragmentation, depolymerization and mineralization occurring across the litter–soil organic matter continuum (Schimel & Bennett, 2004). Soil physico-chemical properties, biological activity, and water fluxes determine the pathways of the litter-derived N transfer, mineralization and/or stabilization in the soil (Berg & McClaugherty, 2014; Bingham & Cotrufo, 2016; Cotrufo et al., 2015; Lehmann & Kleber, 2015; von Lützow et al., 2006; Schmidt et al., 2011). It remains to be seen how these decomposition mechanisms modulate N cycling rates with the highly variable pedo-climatic conditions that occur with the pronounced seasonality of SW Siberia.

The SW Siberia region has long cold and snowy winters with temperate summers. It is positioned on a gradient of climatic conditions with decreasing air temperature and increasing precipitation from south (forest-steppe) to north (southern taiga). During winter, the thick snow-pack in the southern taiga prevents soil from freezing while soil freezes under the shallow snow-pack in the forest-steppe. As a consequence, soil moisture availability is the most contrasting in summer and winter, when the soils of forest-steppe are particularly dry because of drought and freezing, while soil moisture remains available in the soils of southern taiga. Those pedo-climatic conditions can have a major impact on N pool sizes and process rates through the modulation of microbial processes, which generally require soil temperatures above zero and sufficient moisture availability (Brooks et al., 2011; Groffman et al., 2001; Matzner & Borken, 2008; Shibata, 2016). Finally, the soil hydrology is consistently different between the two regions. In the forest-steppe, water reserves are recharged by spring snow-melt, while in the southern taiga the soils are mostly refilled by autumn precipitation and the snow melt leads to raised groundwater levels and overland flow (Brédoire, 2016). Thus, in the southern taiga, snow-melt induces drainage and runoff and is followed by the retreat of the water-table from the soil surface at the beginning of summer. Such water fluxes could influence the vertical transfer of N within the soil.

Plants have adapted to these contrasting pedo-climatic conditions and exhibit specific strategies to access water and nutrients. Notably, fine roots grow deeper and at higher densities in forest-steppe than in southern taiga (Brédoire et al., 2016b). As such, differ-

ent uptake patterns may also participate in contrasting rates of N cycling, and vertical N transfer within the soil profile. The type of vegetation also affects the rate of N release from litter decomposition and the time during which N stays in the soil prior to plant uptake. In SW Siberia, grasslands interspersed with aspen-birch forests are typical. Grass litters generally decompose faster than forest leaf-litters given their lower lignin content (Berg & McClaugherty, 2014); thus they may also release N more rapidly (d'Annunzio et al., 2008).

We set out to quantify N cycling in relation to the pedo-climate, and vegetation type in remote sites of SW Siberia. Over three years, we traced the ^{15}N released from labelled leaf-litter during decomposition in aspen forests and grasslands located in the southern taiga and forest-steppe zones. From the collected data, we developed a N transport model that provides quantitative values of the time N resides in the different soil layers and transfer coefficient between the litter and soil layers. We checked the following hypotheses:

1. rates of aspen and grass litter decomposition at the northern southern taiga sites are faster than rates at the forest-steppe sites (based on soil temperature and moisture regimes);
2. N transfer within the soil profile is deeper in the southern taiga than in the forest-steppe (based on soil hydrology); and
3. the time between litterfall and the recycling of litter-derived N by vegetation uptake is shorter in grassland than in forest (based on litter chemistry).

2. Materials and methods

2.1. Site description

We selected four sites in SW Siberia that span across a transition from the forest-steppe to the southern taiga bioclimatic zones (Fig. S1). Barnaul (BAR) is located in the southern part of forest-steppe, Salair East (SAE) in the forest-steppe of the foothills of the Salair mountains range, Salair West (SAW) in the southern taiga belt of Salair mountains, and Tomsk (TOM) in southern taiga. The main geographic and climate characteristics are provided in Table 1.

As according to the updated world map of the Koeppen-Geiger climate classification (Peel et al., 2007), the southern taiga is located in the very southern part of Dfc zone (cold - without dry season - cold summer) and the forest-steppe is located inside Dfb zone (cold - without dry season - warm Summer) in direction to BSk (arid - steppe - cold summer). Forest vegetation of southern taiga in West Siberia is mostly represented by the polydominant community with a prevalence of coniferous forest represented mostly by *Abies sibirica* as well as by *Pinus sibirica* and *Populus tremula*. This subzone is also distinguished by the absence of ground moss cover and developed herbaceous layer. All treeless areas within the subzone originated from human activities and occupied by true meadows (Ilina et al., 1985). The vegetation of forest-steppe zone is characterized by the natural combination of "islands" of small-leaved deciduous forest (mostly *Betula pendula* and less *Populus tremula*) and dry meadows in its northern part and meadow steppe in the southern part. The proportion of area under meadow vegetation and the number of xerophytes in its community increases from north to south (Shumilova, 1962; Ilina et al., 1985).

The soils in SW Siberia have undergone different development from their common origin as loess deposits. At the BAR and SAE forest-steppe sites, the main soil-forming processes are the formation and accumulation of organic matter, leaching of carbonates in the topsoil and formation of secondary carbonates in deep soil layers. Soils in the forest-steppe belong to the groups of Chernozems and Phaeozems (Table 1). At the SAW and TOM southern taiga sites, the main soil-forming processes are related to the periodic movements of the water table, clays are washed from the topsoil and accumulate in the deeper layers and carbonates have disappeared from the first meter of the soil profile. In these two southern taiga sites, soils belong to the group of Luvisols (Table 1). Physico-chemical characteristics (data from Brédoire et al. (2016a)) as well as fine root densities (data from Brédoire et al. (2016b)) of the topsoil are provided in Table 2.

All the study sites presented share comparable features in terms of dominant species composition and stand characteristics (Brédoire et al. (2016b). The main figures are reported in Tables S1 and S2). They had almost pure aspen (*Populus tremula* L.) forest stands (Table S1) along with nearby grassland areas. SAW did not present grassland areas, yielding four sites with forest and three with grassland in our data set for SW

Siberia. All aspen stands had a closed canopy.

2.2. Preparation and installation of ^{15}N-labelled litters

We used a single source of labelled material for all sites and both vegetation types, which allows the assessment of the pedo-climatic effects on its decomposition. ^{15}N-labelled aspen and grass leaf-litters were produced near the village of Chebula (Novosibirsk region), located in between all our study sites. Two liters of ^{15}N-labelled urea ($3\,\mathrm{g\,urea\,L^{-1}}$) were sprayed on the foliage of aspen trees and on live grasses in late June 2012. This technique allows uniform incorporation of the ^{15}N into the leaves (Zeller et al., 1998). Approximately 2 kg (dry mass) of each labelled vegetation type were collected at the beginning of September 2012, in the late phase of senescence but before brown aspen leaves fell to the ground. The collected material was air-dried to avoid decomposition before its deposition on the experimental field sites. The δ^{15}N of the labelled litters (528 ‰ ± 103 ‰ for the aspen litter, and 3159 ‰ ± 474 ‰ for the grass litter; mean ± sd for 8 and 6 replicates, respectively) were well above the natural abundances of the litters on site (1.1 ‰–3.9 ‰ for aspen litter, and 0.5 ‰–2.3 ‰ for the grass litter). The elemental compositions of the labelled litters (C: $446.6\,\mathrm{mg\,C\,g^{-1}} \pm 5.4\,\mathrm{mg\,C\,g^{-1}}$, N: $13.2\,\mathrm{mg\,N\,g^{-1}} \pm 0.8\,\mathrm{mg\,N\,g^{-1}}$, and a C:N ratio of 33.9 ± 2.2 for the aspen labelled litter; and C: $424.1\,\mathrm{mg\,C\,g^{-1}} \pm 4.0\,\mathrm{mg\,C\,g^{-1}}$, N: $9.9\,\mathrm{mg\,N\,g^{-1}} \pm 1.4\,\mathrm{mg\,N\,g^{-1}}$, and a C:N ratio of 43.6 ± 6.6 for the grass labelled litter) were within the range of variation observed on sites for litterfall and grass litter (Table S1).

In late September of 2012, we deposited at each site the ^{15}N-labelled litter on six replicate 1.4×1.4 m plots. The distance between two plots ranged from 3 to 15 m. In forest plots, we carefully removed recently fallen litter (leaves and a few branches) over the area of the experimental plot and replaced it by $255\,\mathrm{g\,m^{-2}}$ of dry ^{15}N-labelled aspen litter, which is similar to the natural production estimated in a preliminary study (litter traps, Barsukov unpublished data). In grassland plots, we cut and removed dead grass and deposited a similar amount of ^{15}N-labelled grass litter (204, 306 and $357\,\mathrm{g\,m^{-2}}$ of dry ^{15}N-labelled litter at BAR, SAE and TOM, respectively). The labelled litter was evenly distributed over the plot area, and then fixed to the soil surface with a nylon net (mesh size of 1.5 cm) to avoid wind dispersal and contamination by non-labelled litter.

2.3. Sample collection and analyses

From May 2013 to October 2015, we sampled vegetation (herbaceous species), litter and soil twice a year, at the end of Spring and in Autumn within our plots. We sampled vegetation and litter layers within a defined area of 30 by 40 cm delimited by a rigid plastic frame. Above the netting, we collected live vegetation (understorey in forest) when available (this depended on the sampling date and plant phenology) and dead plant material, or litter that was deposited after the labelled litter was installed. We refer to the "litter layer" as the organic layers that have accumulated on the top of the mineral soil (often called "forest floor"), which contains the following sub-layers: the Ol layer that contains litter above the net used to keep the litter spatially fixed, ^{15}N-labelled litter below the net (only in Spring 2013, when it still could be distinguished from older litter), litter Of layer, and litter Oh layer if present (Of and Oh layers were distinguished only at SAE forest). Four mineral soil layers were sampled within the same area: 0–2.5 cm, 2.5–5 cm, 5–7.5 cm, and 7.5–10 cm. Vegetation and litter samples were oven-dried at 60 °C and soil samples were air dried, all to a constant mass. The soil was then sieved at 2 mm to remove roots (the topsoils studied do not contain gravel). The samples were homogenized and an aliquot was finely ground before isotope analyses.

Elemental and isotopic compositions (total C, total N and δ^{15}N) were determined by an IsoPrime 100 isotope ratio mass-spectrometer (IsoPrime Corporation, Cheadle, UK) and vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) using international reference materials USGS 24 (IAEA N1 (0.4 ‰ vN2), IAEA N2 (20.3 ‰ vN2)) and USGS 26 (53.7 ‰ vN2). The measurement error of δ^{15}N was approximately 0.2 ‰.

The natural abundance of ^{15}N in vegetation, litter and of the five soil layers defined from 0 to 15 cm were measured at each site on material sampled in July 2013 and prepared following the same methods.

2.4. Isotopic calculations

The isotopic composition of the samples was expressed in delta units (δ^{15}N, in ‰):

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

where R is the mass ratio of ^{15}N to ^{14}N and $R_{standard}$ equals 0.0036765. Summaries of the $\delta^{15}N$ values are provided in the Table S3 and S4.

The proportion of ^{15}N in the total amount of N measured in a sample (N_{tot}), the ^{15}N abundance (At.%^{15}N), was computed as following:

$$\text{At.}\%^{15}\text{N} = 100 \times \frac{^{15}\text{N}}{^{15}\text{N} + ^{14}\text{N}} \tag{2}$$

The recovery of the N derived from the litter applied to plots within a sampled layer (N_{LD}) was calculated, for each sampling date, as follows:

$$\text{N}_{\text{LD}} = \frac{(\text{At.}\%^{15}\text{N}_{\text{sample}} - \text{At.}\%^{15}\text{N}_{\text{control}}) \times M_{\text{N sample}}}{(\text{At.}\%^{15}\text{N}_{\text{lab litter}} - \text{At.}\%^{15}\text{N}_{\text{unlab litter}}) \times M_{\text{N litter dep}}} \tag{3}$$

where At.%$^{15}N_{sample}$ is the ^{15}N abundance in the sampled layer, At.%$^{15}N_{control}$ is the ^{15}N natural abundance of the layer (without labelling), At.%$^{15}N_{lab\,litter}$ is the ^{15}N abundance in the labelled litter, At.%$^{15}N_{unlab\,litter}$ is the ^{15}N natural abundance in the litter, $M_{N\,sample}$ is the mass of N in the layer sampled (in $g\,N\,m^{-2}$), and $M_{N\,litter\,dep}$ is the mass of N deposited with the labelled litter (in $g\,N\,m^{-2}$).

For soil samples, $M_{N\,sample}$ was calculated with the mass, volume, and total N concentration of the soil sample after removal of roots. When the sampling volume was unknown (generally for the 7.5–10 cm layer), we used soil density (Brédoire et al., 2016b) corrected for the volume of large tree roots (> 1 cm diameter) that were numerous in the topsoil.

2.5. Statistical analyses

The comparison of N_{LD} between sites (i.e. for a given combination of layer, sampling and vegetation type) and vegetation covers (i.e. for a given combination of layer, sampling and site) were tested using a one-way ANOVA (significance level of $p < 0.05$) followed by a post-hoc Tukey's HSD (Honestly Significant Difference) test. All data management and statistical analyses were performed with R version 3.3.3 (R Core Team, 2017).

2.6. Modelling

We developed a simple N flow model between litter and soil compartments (Fig. 1). In this model, all the N is initially contained in the litter compartment. Along with litter decomposition, N either is transferred downwards to the adjacent compartment or lost

from the system, i.e. leached, denitrified, or taken up by the vegetation. We assumed the return of the initially deposited N to the litter compartment by vegetation senescence was negligible at the timescale of modelling (three years) because the ^{15}N signal is greatly diluted in the growing vegetation in our experiment.

The variation in N recovery with time in each compartment was written as follows:

$$\frac{dN_L}{dt} = -k_L N_L \tag{4}$$

$$\frac{dN_1}{dt} = k_L N_L \times a_{L\to 1} - k_1 N_1 \tag{5}$$

$$\frac{dN_2}{dt} = k_1 N_1 \times a_{1\to 2} - k_2 N_2 \tag{6}$$

where: N_L, N_1 and N_2 are the N recovered in the litter, the first (0–5 cm) and the second (5–10 cm) soil compartments, respectively ; k_L, k_1 and k_2 are the decomposition rates of these compartments and $a_{L\to 1}$ and $a_{1\to 2}$ are allocation constants, i.e. the proportion of the output from the litter compartment and the first soil compartment that reach the first and the second soil compartment, respectively. The inverse of the decomposition rate (k) is the mean residence time (MRT) of N in a given compartment:

$$MRT = \frac{1}{k} \tag{7}$$

The difference "$1 - a_{x\to y}$" is percentage of N from the compartment x that is exported out of the litter–soil system we studied.

The analytic solutions of these differential equations are:

$$N_L(t) = N_L(0) \times e^{-k_L t} \tag{8}$$

$$N_1(t) = N_L(0) \times \frac{a_{L\to 1} \times k_L}{k_1 - k_L} \times (e^{-k_L t} - e^{-k_1 t}) \tag{9}$$

$$N_2(t) = N_L(0) \times a_{L\to 1} \times a_{1\to 2} \times k_L k_1 \times \left[\frac{e^{-k_L t}}{(k_2 - k_L)(k_1 - k_L)} - \frac{e^{-k_1 t}}{(k_2 - k_1)(k_1 - k_L)} + \frac{e^{-k_2 t}}{(k_2 - k_1)(k_2 - k_L)} \right] \tag{10}$$

The parameters k_L, k_1, k_2, $a_{L\to1}$ and $a_{1\to2}$ were fitted simultaneously by minimizing the following fitness, which is the sum of the normalized mean square errors in the three compartments:

$$fitness = \sum_{i=1}^{3}\left[\frac{1}{\bar{O}_i}\times\frac{1}{n_i}\times\sum_{j=1}^{n_i}(S_i(t)-O_{i,j}(t))^2\right] \quad (11)$$

where $\bar{O}_i$ is the mean of the mean observations per date for the compartment i, n_i is the number of observations in the compartment i, $S_i(t)$ is the simulated value of N recovery for the compartment i at the time t and $O_{i,j}(t)$ is the j^{th} observation in the compartment i at the time t.

The optimization was performed with a genetic algorithm (population size 50, probability of crossover between pairs of chromosomes 0.8, probability of mutation in a parent chromosome 0.1, maximum number of iterations 1000, with local search by "L-BFGS-B" method) with the following constraints on the parameters: $0.00055 < k_L < 0.0055$, $0.00014 < k_{soil} < 0.0055$ and $0 < a < 1$. In summary, the genetic algorithm helps to search the best set of model parameters giving the smallest fitness (the global minimum).

The modelling was performed with R version 3.3.3 (R Core Team, 2017) with the package "GA" version 3.0.2 (Scrucca, 2013) for genetic algorithms.

3. Results

3.1. N recovery observations

Over time, the concentration of N derived from the labelled-litter progressively decreased in the litter layer, N was partly transferred to the soil, taken up by the vegetation, or exported out of the system (Fig. 2 and 3).

In the forest plots, N loss from the litter layer was faster in the southern taiga sites TOM and SAW compared to the forest-steppe sites BAR and SAE (Fig. 2). After two years, in October 2014, the N recovery in the litter layer below the netting was significantly lower in the southern taiga sites SAW (10 %) and TOM (7 %) than in the forest-steppe sites BAR (46 %) and SAE (67 %) (Tables S5 and S7).

The amount of N recovered in the soil decreased with soil depth. The N recovery in the 0–2.5 cm soil layer reached a maximum in October 2013 in the southern taiga sites

SAW (51 %) and TOM (40 %) and in October 2014 in the forest-steppe site SAE (15 %). In BAR, there was no clear peak among the observations; the highest value, 15 %, was measured in October 2015.

Live vegetation usually contained a low amount of litter-derived N (up to 3 %) but there was no clear trend in N recovery for this layer. The litter collected above the netting (i.e. naturally deposited on the top of the labelled-litter) was also enriched, even at the first sampling date, where we measured a recovery of about 3 % in BAR. Albeit the exception of BAR, the N recovered in the litter above the netting tended to increase with time.

In the grassland plots, N loss from the litter layer below the netting tended to be faster than for the forest plots at all the sites (Fig. 3); however, there were no statistically detectable differences in loss rates between the sites (Tables S6 and S7). Uncertainties inherent to the sampling of such material might have altered the precision of our measurements (see the possible outliers for spring and autumn 2013 at BAR). In June 2013, almost all the labelled N was recovered in the litter layer below the netting at BAR (almost 100 %) and SAE (91 %) while only 50 % was recovered in TOM. In October 2014, only 19 and 16 % of N were recovered in this litter layer at SAE and TOM (19 and 16 %, respectively) but 40 % were still recovered at BAR. Generally, in the 0–2.5 cm soil layer, large amounts of litter-derived N were recovered (often >40 %), which was significantly greater than in forest. Only up to 10 % of the deposited N was recovered in the soil between 2.5 and 10 cm, except in SAE where the recovery reached 20 % in the 2.5–5 cm layer in October 2014. At SAE, a peak N recovery in the 0–2.5 cm soil layer was observed in October 2014 (83 %), while at BAR and TOM the N recovery measured in October 2015 was the highest (64 and 55 %, respectively). At each sampling, live vegetation was enriched in litter-derived N. Interestingly, the highest N recovery in the vegetation was measured in June 2013 (8, 3 and 6 % in BAR, SAE and TOM, respectively). The N recovery in the litter above the netting increased with time, reaching about 2.5 % in October 2014.

3.2. N recovery modelling

The model we developed allowed us to reproduce the average N dynamics in each compartment and provided quantitative indicators to compare the sites. It was not

designed to capture the seasonal variations which partly explains the relatively high values of *NRMSE* together with the high variability in observations (Fig. 4 and 5).

In the forest plots, the *MRT* of N in aspen litter was estimated to be 2.9 and 4.6 years in the forest-steppe sites BAR and SAE, respectively, and 1.5 and 0.9 years in the southern taiga sites SAW and TOM, respectively (Table 3). The *MRT* of N in the 0–5 cm soil compartment was shorter than its *MRT* in the litter layer. SAW had the shortest *MRT* (1.5 years) and TOM the longest (2.1 years). In the 5–10 cm soil compartment, all the *MRT* but one ranged between 0.6 and 1.1 years. The allocation factor, which is the proportion of the output from one compartment that reaches the compartment below, ranged from 62 (SAE) to 94 % (SAW) in the 0–5 cm soil compartment and from 42 (SAW) to 100 % (BAR) in the 5–10 cm soil compartment (Table 3). The parameters obtained for the 5–10 cm soil compartment must be interpreted with caution because of the short duration of the experiment and the dilution of the ^{15}N signal in the ecosystem.

For the grassland plots, TOM also exhibited the shortest *MRT* in the litter (1.2 years) but the difference with the two other sites was less than one year (*MRT* of 1.6 and 1.4 years for BAR and SAE, respectively; Table 3). The *MRT* range (4.9 years at TOM to 9.4 years at SAE) in the 0–5 cm soil compartment was much larger than in the litter. The *MRT*'s were also greater than forest estimates at the same compartment. In the 5–10 cm soil compartment, the *MRT* were close to 1 year in SAE and TOM, and around 2.6 years in BAR. However, the latter might be an over-estimate since the available data do not permit to constrain the curvature of the fit in the deepest layer of BAR grassland. Allocation from the litter to the 0–5 cm soil compartment and from the 0–5 to the 5–10 cm soil compartment was greater than 85 % for all sites.

We simulated the average N recoveries over 3000 days (which is about twice as long as the time frame of this study) in the three compartments of the model (Fig. 6). The simulations resulted in specific patterns related to site position and vegetation types. In forests, we distinguished 2 categories of sites. SAW and TOM presented a fast release of N from the litter and transfer to the 0–5 cm soil, but also a fast N loss out of the system. According to the model, 50 % of litter N was lost before 1000 days in those sites. In BAR and SAE, the release of N from the litter was slower and 50 % of the N remained in the system after 1300–1700 days. In grassland, the N loss from the litter occurred rapidly on

all the three sites and N was retained quite efficiently in the 0–5 cm soil compartment. Around 50 % of the N remained in the system after 3000 days in BAR and SAE while this 50 % threshold was reached before 2000 days in TOM.

4. Discussion

Understanding seasonal N cycling and ecosystems transfers is critical to predicting the SW Siberian ecosystem response to changes in climate, land use, or other perturbations. Over the three year experiment, we found higher rates of N release from leaf-litter in the southern taiga relative to the forest-steppe and in grassland relative to forest. The transfer of N down the soil profile was deeper in the southern taiga than in the forest-steppe, and in forests than in grasslands. Below, we discuss how these differences can be related to pedo-climatic conditions and vegetation type, but also how other environmental characteristics, such as soil properties and hydrology, interact to control the fate of N in these Siberian ecosystems.

4.1. N release from the litter layer: the role of climate and vegetation type

Consistent with our first hypothesis, we found aspen litter located in the forest-steppe bioclimatic zone (BAR and SAE) to release N at a slower rate than litter in the southern taiga (SAW and TOM; Table 3). These results are consistent with field observations of only a thin organic layer over the mineral soil in the aspen forests of southern taiga and a thick one in forest-steppe (up to 5 cm in summer) since litter mass and N losses generally exhibit a linear positive relationship (d'Annunzio et al., 2008). In the southern taiga, longer periods of microbial activity are likely facilitated by the combination of higher soil moisture content in the summer, and a warmer and wetter winter soil compared to the forest-steppe (Table 1 and Fig. S2), allowing for a more intense litter decomposition and N release at the annual timescale. In particular, litter degradation can persist over winter in snow-covered environments protected from frost (Baptist et al., 2010; Brooks et al., 2011; Saccone et al., 2013; Uchida et al., 2005).

With about 45 % (BAR) and 65 % (SAE) of N remaining after 2 years in the litter layer (Fig. 2), the N losses from the decomposing aspen litter in the forest-steppe were comparable to those reported in various temperate and sub-tropical forests (Zeller et al.,

2001; Fahey et al., 2011; van Huysen et al., 2013; Blumfield et al., 2004). Surprisingly, the only result we found comparable to the southern taiga (about 10 % N remaining in litter after 2 years in SAW and TOM, Fig. 2) concerned tropical eucalyptus plantations on a sandy soil in the Congo (Versini et al., 2013). In these tropical plantations, the amount of available nutrients is quite low and plant growth largely relies on the rapid recycling of plant residues (Versini et al., 2013). A similar observation in the Siberian southern taiga may indicate that large soil N stocks are not available for plants, thus plants in the southern taiga may also rely on the rapid recycling of N from plant residues.

In contrast to the aspen litter, we did not find significant differences in N release from the grass litter between sites. However, partly consistent with our third hypothesis, N release from the grass litter was faster than the release from aspen litter at all forest-steppe sites while we did not detect such a difference between litter types in the southern taiga. Thus, the fast grass litter decomposition might overcome the pedo-climatic controls in the forest-steppe, while in the southern taiga the pedo-climate outweighs the influence of litter chemistry on litter N release.

The rate of N release in the forest-steppe is potentially influenced by not only the chemical traits of the different vegetation types but also the unique decomposing environment, which ranges from the organic matter milieu present in the litter layer to the micro-climate resulting from different vegetative structures. The initial aspen and grass litter used in this study had similar C (424–445 $\mathrm{mg\,C\,g^{-1}}$) and N (10–13 $\mathrm{mg\,N\,g^{-1}}$) contents, but other components, not measured here (e.g. lignin, P, K, Ca, Mg, Mn), may differ between tree leaves and grass shoots and modulate decay rates (Berg, 2014; Cornwell et al., 2008; Keiluweit et al., 2015; Köchy & Wilson, 1997; Melillo et al., 1982; Zhang et al., 2008). In addition to the initial quality of the labelled material we employed, the forest floor is in reality comprised of a mix of dead leaves and other materials (e.g. tree branches, understorey vegetation) that may also modulate the chemical composition of the whole organic layer and its decomposition (Finerty et al., 2016; Gessner et al., 2010; Hättenschwiler et al., 2005; Joly et al., 2017; De Long et al., 2016).

Related to the pedo-climate, the micro-climate of the litter layer also slightly differs between the forest and grassland within our sites. For example, air and soil surface temperatures were generally higher in the grassland than in the forest plots (these differences

reached about 2 and 2.5–4 °C at summertime, respectively; Fig. S2). Accordingly, higher temperature of the grassland litter layer may enhance its decomposition as compared to forest litter, except in summer when grassland litter might be too dry (particularly in the forest-steppe zone). Finally, since solar irradiation of the soil surface is higher under grass than tree vegetation cover, photo-degradation might further enhance litter decomposition in grasslands (King et al., 2012).

4.2. N dynamics in the soil layers: role of climate, vegetation type and soil properties

4.2.1. Vertical transfer

Across all sites, there were distinct periods over the year where N transfers occurred within the soil, as revealed by the specific "build-up and release" pattern observed in the 0–2.5 cm and 2.5–5 cm soil layers: a net increase in N recovery was observed from the autumn samplings while a net decrease was observed from the spring samplings (Fig. 2 and 3).

In these Siberian ecosystems, the vertical transfer of N down the litter–soil system is probably mostly driven by water fluxes. Indeed, we did not observe a high macro-fauna activity while sampling or digging soil pits for all seasons. We suggest that the growing season (late spring–mid autumn) precipitation events contribute to the "build-up", or the accumulation of litter-derived N in the top five centimeters of the soil. During this season, the soil is drying and precipitation mostly refills the upper soil layers. Also, microbial activity is probably the highest at this period, which allows for an efficient N immobilization in the microbial biomass. In the southern taiga, the retreat of the water-table, that reached the topsoil at snow-melt, could also help in driving N downwards. In the forest-steppe soils, however, the relatively shallower transfer of N and lower concentrations corresponds with the slower rate of N release from the litter, coupled with lower intensities of both soil water fluxes and soil microbial activity due to dry summer conditions. On the contrary, at snow-melt, the water fluxes are particularly strong and the immobilization capacity of microbes is lower, which causes the "release", or the loss of N from the top five centimeters of the soil. The larger losses recorded in forest-steppe coincide with higher infiltration rates resulting from greater winter precipitation as well as snow melting on soils which were previously saturated by autumn precipitation (Brédoire (2016); Fig. S3). In fact, yearly drainage in forest, which occurs almost exclusively at snow-melt,

has been estimated to be almost five times higher in TOM ($262 \pm 73\,\mathrm{mm\,year^{-1}}$, 49 years mean $\pm$ standard deviation) than in BAR ($60 \pm 43\,\mathrm{mm\,year^{-1}}$), for example (Brédoire, 2016).

Possibly contradicting our second hypothesis, in aspen forests, the proportions of litter-derived N exported out of the litter–soil system we studied (given by $1 - a_{L\to 1}$) were larger in forest-steppe than in southern taiga (Table 3). These exports are mainly attributed to leaching below 10 cm, denitrification, and/or plant uptake. It is possible that the yearly plant-uptake in forest-steppe is greater than in southern taiga due to the longer vegetation season and the generally higher net primary productivity (Monserud et al., 1995). In the unfrozen soils of the southern taiga, despite stronger water fluxes relatively to the forest-steppe, the leaching of N below 10 cm could be attenuated at snow-melt by microbial immobilization due to the maintenance of a basal activity over winter (Brooks et al., 2011; Brooks & Williams, 1999).

4.2.2. N retention in soil

Another metric provided by our model is the *MRT* of N in the different soil layers, providing a measure of soil N retention capacity. Our labelling approach followed by simple modelling of a single pool of N at each layer makes the implicit assumption that all N is homogeneously distributed in the soil matrix and follows the same pathway of decomposition and transfer. As our model was calibrated on a short-term experiment, our estimates of *MRT* are relatively short (1.5–2.1 years in aspen forests and 4.9–9.4 years in grasslands). Nevertheless, they are similar to those of fast turnover-pools of N from European beech litter (Salleles, 2014). At the timescale of our study, most of the litter-derived N had not reached the slow-turnover pools (Hatton et al., 2012; Hicks Pries et al., 2017), and the contribution of these pools to the N dynamics and the *MRT* of N in soil are then probably under-estimated here (Derrien & Amelung, 2011; Manzoni et al., 2012). This notwithstanding, our model allows for a comparison between sites and vegetation covers at the timescale of several years.

The longer retention of N in the 0–5 cm soil layer in grassland than in forest partly contradicts our third hypothesis, but is consistent with faster soil C turnover in the topsoils of forest vegetation types compared to non-forest vegetation (Mills et al., 2014). Soil organic matter from grasslands potentially produce more ammonium than from

woody sites (Booth et al., 2005) and, since ammonium is usually taken up more efficiently by vegetation and micro-organisms (Kuzyakov & Xu, 2013), this could explain the shallow transfer of N in grasslands. In addition, grasslands in SW Siberia tend to have a greater net primary production than nearby forests (Monserud et al., 1995) and they have a dense root mat found in the first centimeters of the soil (Table 2 and Brédoire et al. (2016b)), both of which facilitate N retention and cycling in the topsoils of grasslands.

Soil organic C has a faster turnover in southern taiga than in forest-steppe in these Siberian ecosystems (Kayler et al., 2018); however, we did not find such a pattern for the *MRT* of N within the first ten centimeters of the soil. Besides pedo-climatic conditions which control the transfer and immobilization of N, texture and mineralogy also control the fate of N within the soil as N is mainly associated with clay and silt fractions (Moni et al., 2012; Mueller et al., 2009; Kayler et al., 2011), and N protection increases with their increasing amounts (Bingham & Cotrufo, 2016; Dignac et al., 2017; Kleber et al., 2015; von Lützow et al., 2006) as well as metallic (hydr)oxides (Bingham & Cotrufo, 2016; Duiker et al., 2003; Porras et al., 2017; Torn et al., 1997). By extending our experiment on a longer period of time, we may strengthen our estimations of *MRT* and seek to verify how soil texture and mineralogy control the stabilization of N in these Siberian ecosystems.

4.3. Summary and future outlook

Our approach combining isotope tracing with modelling allows for a comparison between sites and vegetation by assessing the rate of N release from the litter, the N mean residence time in soil layers, and its vertical transfer down the soil profile.

The rate of decomposition of the leaf-litter at the soil surface is a major determinant for the rate of N cycling in these ecosystems. It is faster in southern taiga (north of the region) than in forest-steppe (south). As most of the litter decomposition occurs in the vegetation growing season, lower moisture conditions in the forest-steppe might hamper decomposer activity. The faster decomposition of the grass than the aspen leaf-litter might be attributable to the initial litter quality and litter and soil micro-climatic conditions.

Once in the soil, the turnover of N was comparable for all sites for a given vegetation cover. Typically, in the topsoil, we observed "build-up and release" dynamics, with N

inputs during the vegetative season and outputs at snow-melt. Different processes operate in the study sites, depending on pedo-climate and soil physico-chemical properties. Notably, winter soil freezing could be determinant for the vertical transfer of N. The retention of N in the grassland topsoils appeared to be rather efficient and substantially higher than in forest, which we interpret as an ecosystem property.

Climate change will certainly impact N cycling in these ecosystems. While increasing snowfall (Bulygina et al., 2009, 2011) may enhance winter decomposition and microbial immobilization of N by preventing soil freezing in the south of SW Siberia, more frequent and intense summer droughts (Groisman et al., 2012; IPCC, 2013) would hamper decomposition processes and slow down N cycling all over the region (Blok et al., 2016). As primary production greatly depends on the synchronization of nutrient availability and plant demand in those ecosystems with a strong seasonality of climate, an increase in inter-annual climate variability may strongly modulate N cycling and occasionally hamper plant nutrition. The southernmost sites are probably the most exposed because of the primary importance of snow-fall for winter soil temperature and soil moisture availability through the year.

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Author contributions

BZ, PAB, DD, FB, OR and MRB conceived the ideas and designed methodology; FB, PN, PAB, OR, DD, AB, ZEK, MRB, SD, AL and BZ conducted the research; FB, DD and BZ analysed the data; FB, DD and JSM performed the modelling; FB led the writing of the manuscript with contributions of DD and ZK. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests statement

The authors have no competing interests to declare.

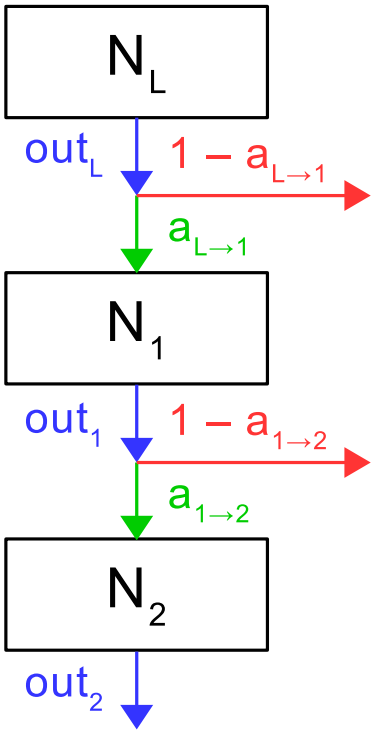

Figure 1: Model diagram. N_L, N_1 and N_2 are the litter-derived N contents of the litter layer, the first (0–5 cm) and the second (5–10 cm) soil layers, respectively. N_x is the N content in the compartment x, $\mathrm{a}_{x\to y}$ is the proportion of the output from x (out_x) that reaches y, and the difference "$1 - \mathrm{a}_{x\to y}$" is the proportion of the output from x that is lost from the litter–soil system before to reach y (e.g. by plant uptake, leaching or denitrification).

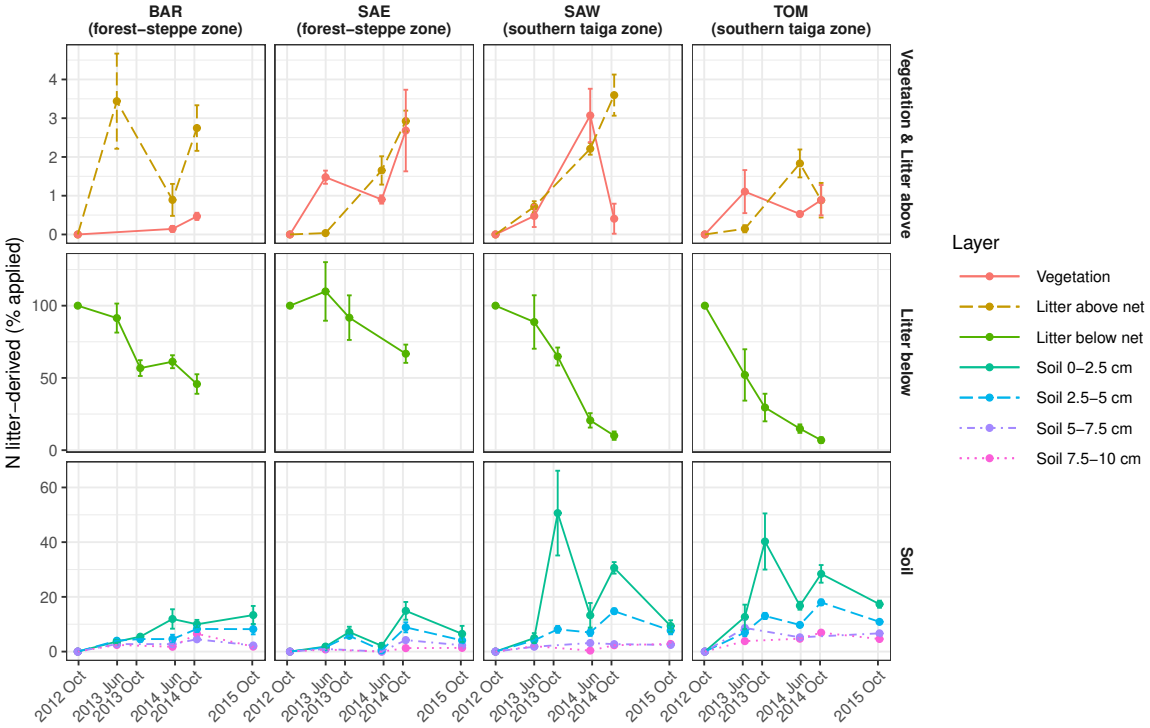

Figure 2: Proportion of litter-derived N recovered in each layer in forest. Mean value ± standard deviation (number of replicates given in Table S7). Vegetation refers to live undertorey vegetation. The terms "above" and "below" refer to the netting which protects the ^{15}N-labelled litter.

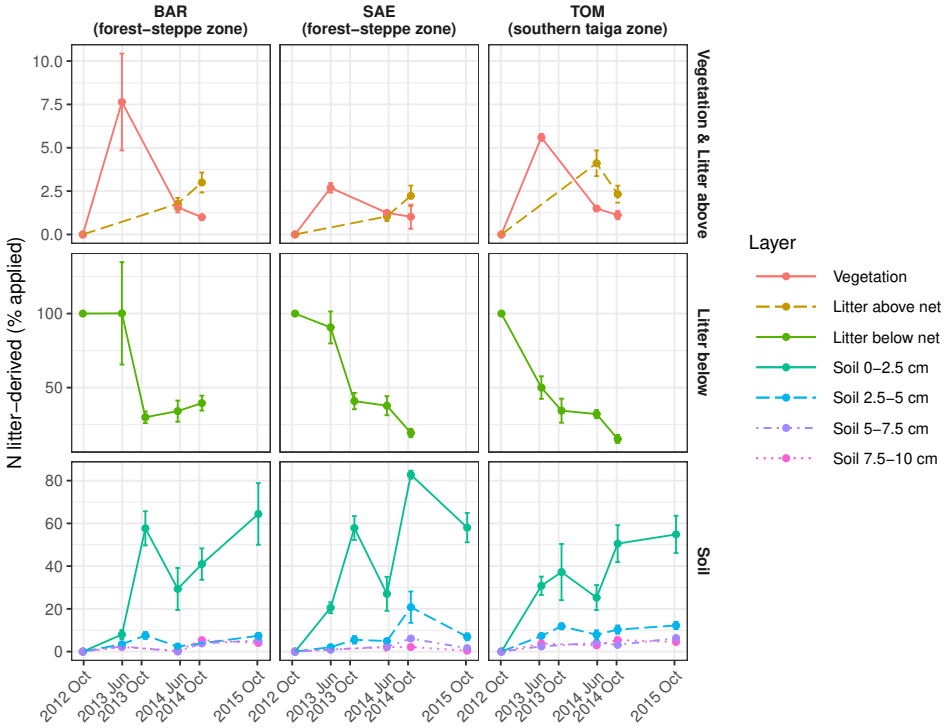

Figure 3: Proportion of litter-derived N recovered in each layer in grassland. Mean value ± standard deviation (number of replicates given in Table S7). The terms "above" and "below" refer to the netting which protects the ^{15}N-labelled litter.

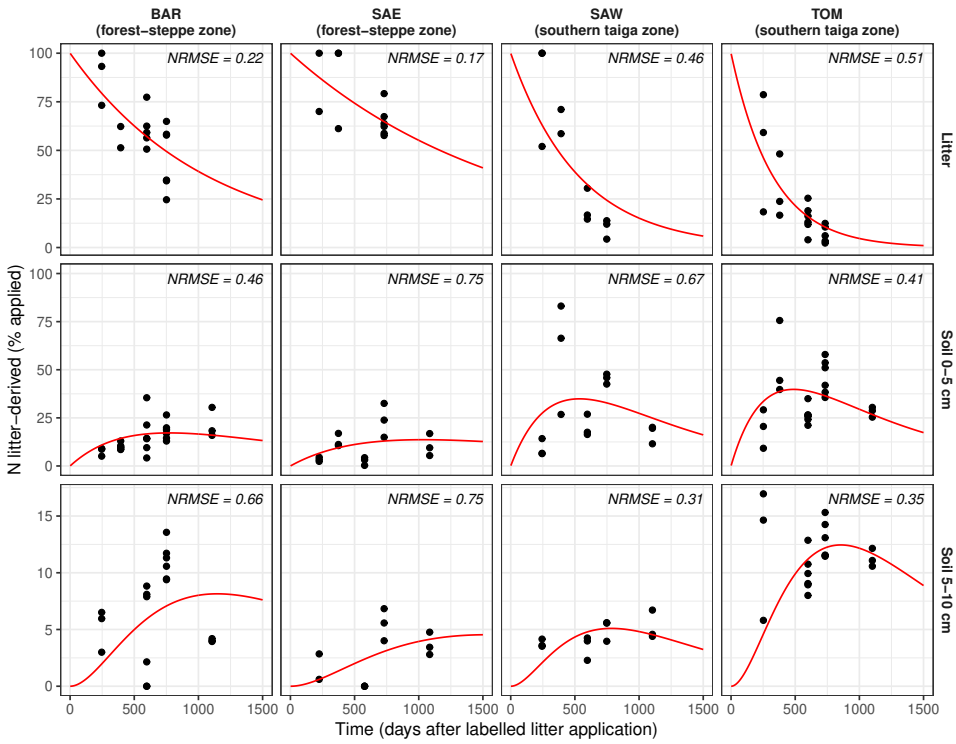

Figure 4: Fit of the N decomposition and transfer model in forest with indication of the normalized root mean square error ($NRMSE = RMSE/\bar{O}$ where $\bar{O}$ is the mean of the mean observation per date).

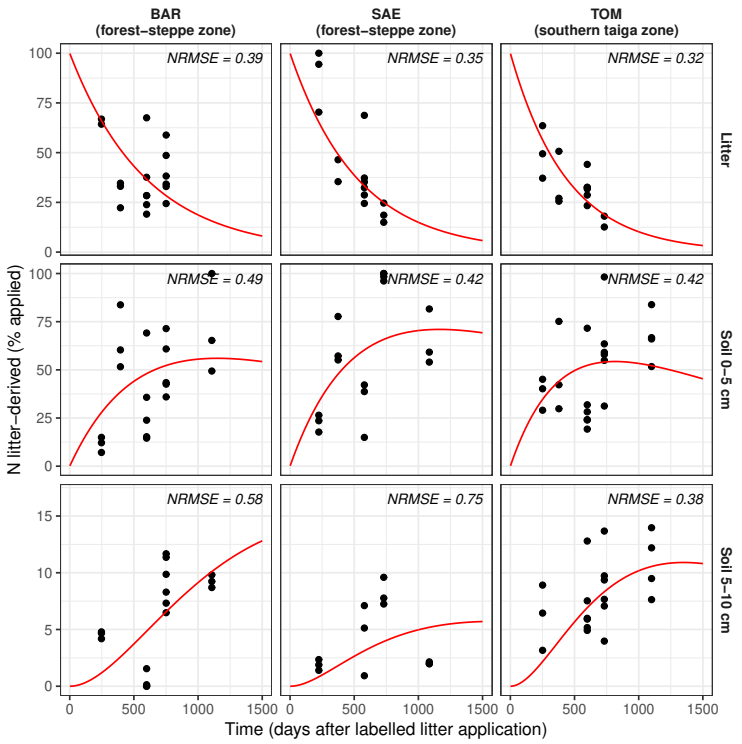

Figure 5: Fit of the N decomposition and transfer model in grassland with indication of the normalized root mean square error ($NRMSE = RMSE/\bar{O}$ where $\bar{O}$ is the mean of the mean observation per date).

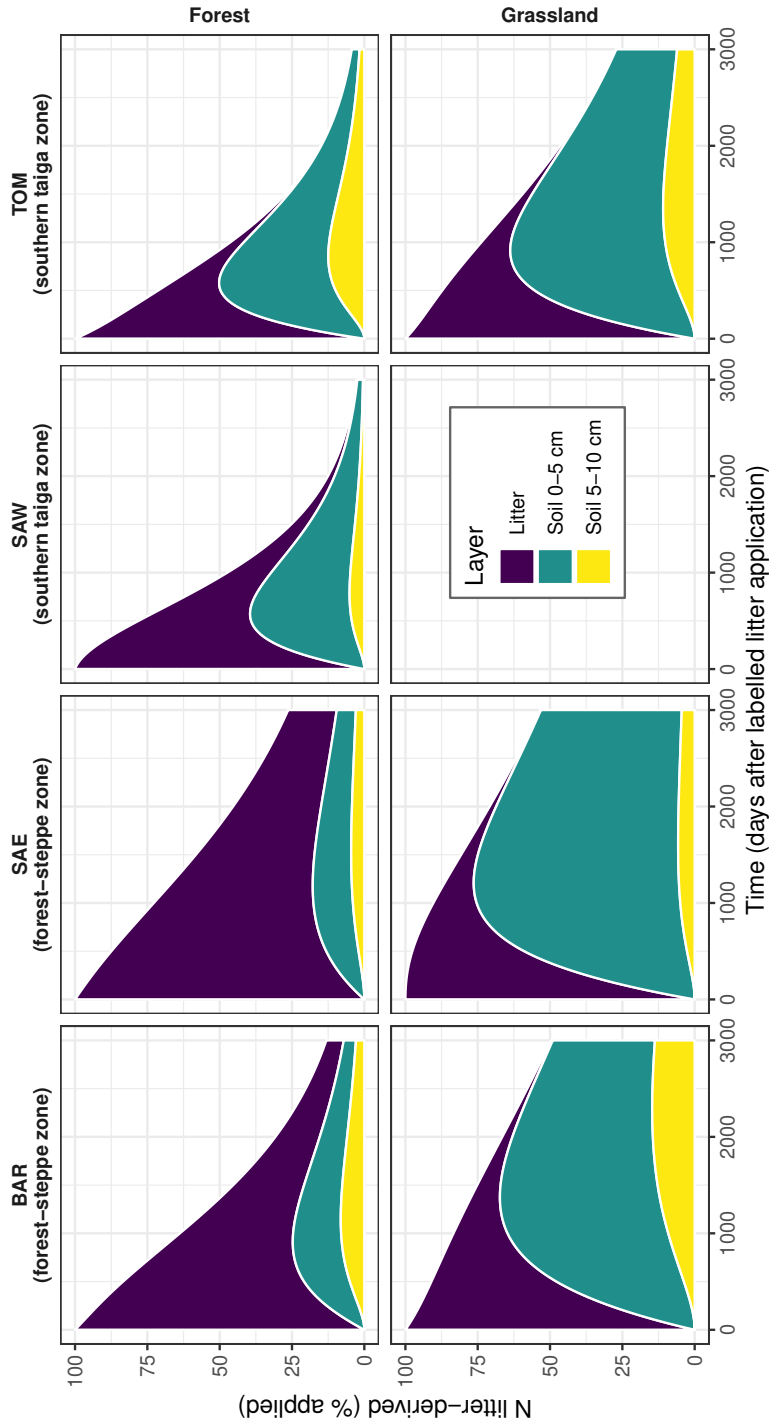

Figure 6: Simulation of N recovery over time.

Table 1: Main characteristics of the study sites.

Site ID	BAR	SAE	SAW	TOM
General				
Site name[a]	Barnaul	Salair East	Salair West	Tomsk
Bioclimatic zone	Forest-steppe	Forest-steppe	southern taiga	southern taiga
Soil in forest	Haplic Phaeozem	Leptic Phaeozem	Haplic Luvisol	Albic Luvisol
Soil in grassland	Calcic Chernozem	Leptic Phaeozem		Albic Luvisol
Latitude N	53.41	54.39	54.18	56.3
Longitude E	83.47	85.75	85.17	85.43
Elevation (m)	221	305	358	232
Climatic features (mean annual values over the period 1981–2010)				
WMO index[b]	29838	29745	29736	29430
Distance[c] (km)	4	18	64[d]	38
Air temperature (°C)	2.7	2.3	1.2[d]	0.9
Precipitation (mm)	432	432	453[d]	567
Snow-pack >1 cm (days)	157	145	149[d]	178
Snow-pack >20 cm (days)	108	88	116[d]	145
Snow height[e] (cm)	49	38	54[d]	71
Field measurements of the snow height: mean (min–max)[ef]				
Winter 2013–2014 forest	35 (20–46)[g]	na	na	64 (50–72)[h]
Winter 2013–2014 grassland	35 (23–47)[g]	na		58 (51–64)[h]
Winter 2014–2015 forest	84 (65–95)[i]	57 (50–70)[j]	112 (110–120)[j]	88 (80–90)[k]
Winter 2014–2015 grassland	58 (50–70)[i]	61 (50–70)[j]		78 (70–86)[k]

[a]according to the name of the closest city or of the geographical area; [b]World Meteorological Organization (WMO) index of the closest weather station; [c]distance site–weather station; [d]due to its position in mountains and to the distance with the weather station, the values are probably over-estimated for temperature and under-estimated for precipitation and snow in SAW; [e]snow height at climax (usually between mid-February and mid-March); [f]snow was measured on the experimental sites every meter with the help of a rigid ruler on a transect of 20 m; [g]22/02/2014; [h]15/02/2014; [i]24/02/2015; [j]25/02/2015; [k]27/02/2015

Table 2: Soil physico-chemical properties. Composite sample from 3 soil pits that were sampled at fixed depths ± 3 cm (data from Brédoire et al. (2016a)), except total C and total N which are means of all the samples analysed for ^{15}N isotopic composition (n = 3–4). Fine root (diameter < 0.8 mm) densities (data from Brédoire et al. (2016b)).

	Depth	Forest				Grassland		
	(cm)	BAR	SAE	SAW	TOM	BAR	SAE	TOM
Apparent density	5	1.0	0.5	0.7	0.9	1.0	0.9	0.9
	15	1.2	0.8	1.0	1.1	1.3	1.1	1.2
Particle size 0–2 µm (%)	5	27.7	40.7	22.2	23.2	27.5	35.3	22.0
	15	27.2	36.8	20.4	21.9	27.7	34.9	21.2
2–20 µm (%)	5	23.2	26.5	37.9	38.8	20.7	23.8	38.9
	15	23.0	25.3	38.2	38.7	21.0	23.9	40.5
20–50 µm (%)	5	35.3	14.9	34.4	30.2	35.5	17.0	30.8
	15	35.7	15.6	36.6	31.0	32.7	17.6	31.7
50–200 µm (%)	5	13.0	4.4	4.6	6.9	14.0	4.7	6.7
	15	13.5	5.2	3.9	7.4	16.0	4.2	4.7
200–2000 µm (%)	5	0.7	13.4	0.8	0.8	2.2	19.1	1.5
	15	0.5	17.0	0.8	0.9	2.5	19.3	1.8
pH H_2O	5	6.10	6.17	6.07	5.37	6.50	6.47	5.45
	15	6.12	5.97	5.45	5.25	7.20	6.58	5.54
Total N	0–2.5	5.51	8.76	5.83	5.70	4.81	7.78	3.77
(mg N g^{-1} dry soil)	2.5–5	4.25	7.41	4.41	5.02	3.07	5.47	3.01
	5–7.5	3.22	5.66	3.40	4.20	2.77	4.80	2.68
	7.5–10	3.02	4.72	2.67	3.73	2.70	4.59	2.35
	10–15	2.75	3.86	2.48	3.36	2.71	4.57	2.06
Total C	0–2.5	73.59	115.53	78.45	76.21	56.86	95.06	49.02
(mg C g^{-1} dry soil)	2.5–5	53.83	93.29	55.23	64.60	33.50	65.91	36.06
	5–7.5	39.66	72.95	39.13	50.91	30.64	57.67	29.37
	7.5–10	37.13	60.97	28.50	43.57	29.72	54.92	24.63
	10–15	33.54	53.01	26.28	38.08	29.55	54.44	21.10
Total $CaCO_3$	5	< 1	< 1	< 1	< 1	< 1	< 1	< 1
(g kg^{-1})	15	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Al oxides*	5	63.4	101.6	77.1	86.7	58.6	101.2	90.4
(mmol kg^{-1})	15	64.9	126.0	88.9	95.3	59.3	104.9	91.2
Fe oxides*	5	31.3	56.0	68.0	75.2	25.2	48.5	93.7
(mmol kg^{-1})	15	33.3	67.2	75.6	79.0	26.3	49.6	95.6
Fine root length density	5	1.44	2.16	0.92	0.77	2.35	2.82	2.79
(cm roots cm^{-3} soil)	15	0.77	0.94	0.37	0.82	1.30	1.03	1.06
Fine root mass density	5	1.47	1.88	0.86	0.87	1.49	2.04	1.06
(mg roots cm^{-3} soil)	15	0.56	0.87	0.52	0.58	0.59	0.49	0.22

*poorly crystalline oxides extracted with an ammonium oxalate solution (McKeague & Day, 1966)

Table 3: Fitted values of the model parameters. Mean residence time ($MRT = 1/k$) of the deposited N in the litter layer (MRT_L), the 0–5 cm soil layer (MRT_1) and the 5–10 cm soil layer (MRT_2). Allocation of the litter-derived N from the litter layer to the 0–5 cm soil layer ($a_{L\to1}$) and from the 0–5 to the 5–10 cm soil layer ($a_{1\to2}$). The MRT are expressed in years. The fitness is the smallest value obtained by model fitting (Equation 11).

Vegetation	Zone	Site	MRT_L	MRT_1	MRT_2	$a_{L\to1}$	$a_{1\to2}$	Fitness
Forest	Forest-steppe	BAR	2.92	1.59	0.82	0.65	1.00	8.6
		SAE	4.61	1.87	1.09	0.62	0.62	9.8
	southern taiga	SAW	1.45	1.49	0.56	0.94	0.42	23.5
		TOM	0.89	2.13	0.86	0.75	0.92	14.0
Grassland	Forest-steppe	BAR	1.63	7.31	2.62	0.86	0.91	19.5
		SAE	1.44	9.37	0.90	1.00	0.88	18.3
	southern taiga	TOM	1.20	4.88	1.15	0.86	0.96	13.3

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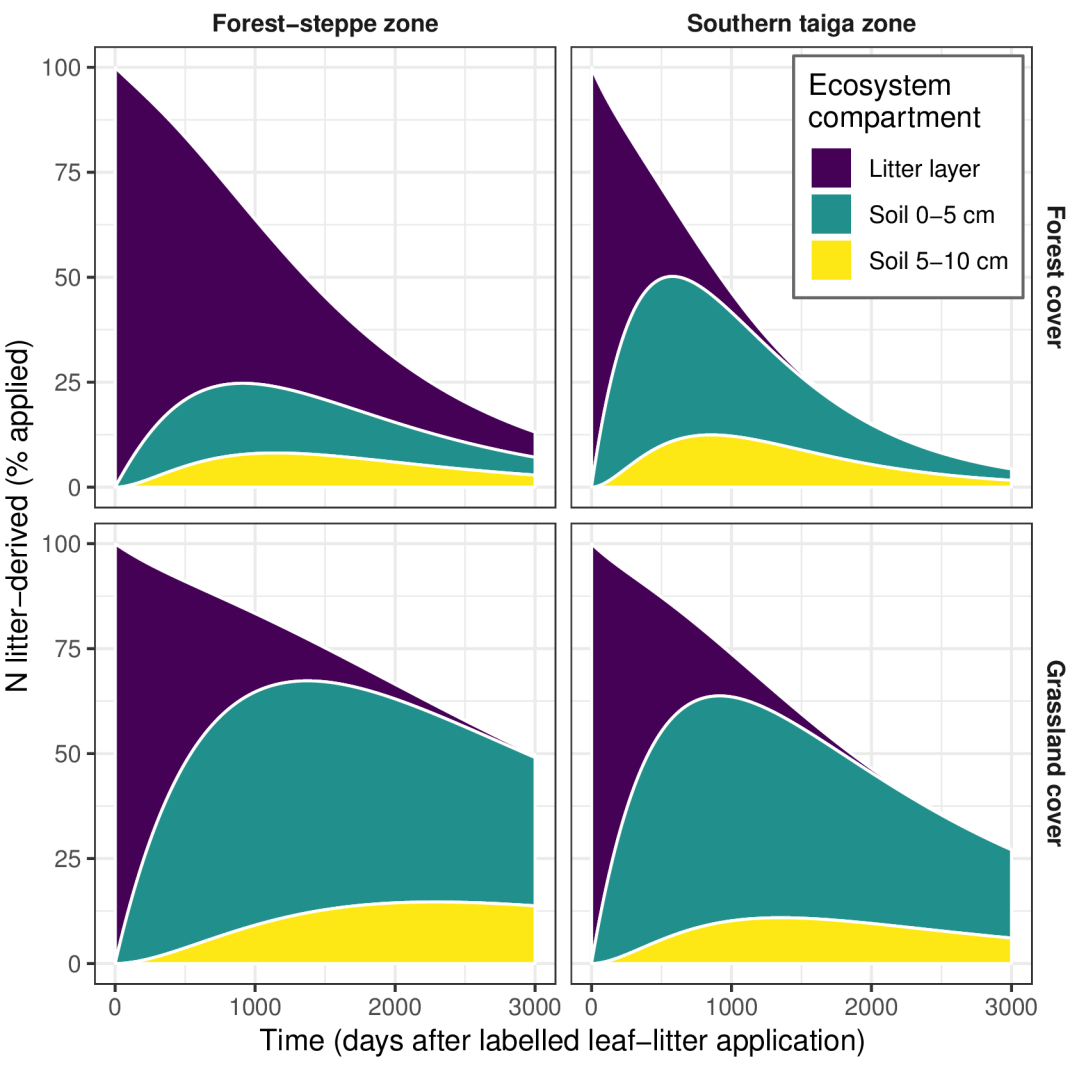
Fate of leaf−litter N in south−western Siberia
Forest−steppe zone
Southern taiga zone
Ecosystem compartment
Litter layer
Soil 0−5 cm
Soil 5−10 cm
Forest cover
Grassland cover
N litter−derived (% applied)
100
75
50
25
0
0
1000
2000
3000
Time (days after labelled leaf−litter application)