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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 ¹⁵N-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: ¹⁵N-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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20 poles (Fay et al., 2015; LeBauer & Treseder, 2008; Reich & Oleksyn, 2004; Vitousek
21 & Howarth, 1991). The litter decomposition process consists of fragmentation, depoly-
22 merization and mineralization occurring across the litter–soil organic matter continuum
23 (Schimel & Bennett, 2004). Soil physico-chemical properties, biological activity, and wa-
24 ter fluxes determine the pathways of the litter-derived N transfer, mineralization and/or
25 stabilization in the soil (Berg & McLaugherty, 2014; Bingham & Cotrufo, 2016; Cotrufo
26 et al., 2015; Lehmann & Kleber, 2015; von Lützow et al., 2006; Schmidt et al., 2011). It
27 remains to be seen how these decomposition mechanisms modulate N cycling rates with
28 the highly variable pedo-climatic conditions that occur with the pronounced seasonality
29 of SW Siberia.

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

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

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

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

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

72 **2. Materials and methods**

73 *2.1. Site description*

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

80 As according to the updated world map of the Koeppen-Geiger climate classification
81 (Peel et al., 2007), the southern taiga is located in the very southern part of Dfc zone
82 (cold - without dry season - cold summer) and the forest-steppe is located inside Dfb
83 zone (cold - without dry season - warm Summer) in direction to BSk (arid - steppe - cold
84 summer). Forest vegetation of southern taiga in West Siberia is mostly represented by the
85 polydominant community with a prevalence of coniferous forest represented mostly by
86 *Abies sibirica* as well as by *Pinus sibirica* and *Populus tremula*. This subzone is also
87 distinguished by the absence of ground moss cover and developed herbaceous layer. All
88 treeless areas within the subzone originated from human activities and occupied by true
89 meadows (Ilina et al., 1985). The vegetation of forest-steppe zone is characterized by the
90 natural combination of “islands” of small-leaved deciduous forest (mostly *Betula pendula*
91 and less *Populus tremula*) and dry meadows in its northern part and meadow steppe in
92 the southern part. The proportion of area under meadow vegetation and the number of
93 xerophytes in its community increases from north to south (Shumilova, 1962; Ilina et al.,
94 1985).

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

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

111 Siberia. All aspen stands had a closed canopy.

112 *2.2. Preparation and installation of ^{15}N -labelled litters*

113 We used a single source of labelled material for all sites and both vegetation types,
114 which allows the assessment of the pedo-climatic effects on its decomposition. ^{15}N -
115 labelled aspen and grass leaf-litters were produced near the village of Chebula (Novosi-
116 birsk region), located in between all our study sites. Two liters of ^{15}N -labelled urea
117 (3 g urea L^{-1}) were sprayed on the foliage of aspen trees and on live grasses in late June
118 2012. This technique allows uniform incorporation of the ^{15}N into the leaves (Zeller et al.,
119 1998). Approximately 2 kg (dry mass) of each labelled vegetation type were collected at
120 the beginning of September 2012, in the late phase of senescence but before brown aspen
121 leaves fell to the ground. The collected material was air-dried to avoid decomposition
122 before its deposition on the experimental field sites. The $\delta^{15}\text{N}$ of the labelled litters
123 ($528\text{ ‰} \pm 103\text{ ‰}$ for the aspen litter, and $3159\text{ ‰} \pm 474\text{ ‰}$ for the grass litter; mean
124 \pm sd for 8 and 6 replicates, respectively) were well above the natural abundances of
125 the litters on site (1.1 ‰ – 3.9 ‰ for aspen litter, and 0.5 ‰ – 2.3 ‰ for the grass litter).
126 The elemental compositions of the labelled litters (C: $446.6\text{ mg C g}^{-1} \pm 5.4\text{ mg C g}^{-1}$, N:
127 $13.2\text{ mg N g}^{-1} \pm 0.8\text{ mg N g}^{-1}$, and a C:N ratio of 33.9 ± 2.2 for the aspen labelled litter;
128 and C: $424.1\text{ mg C g}^{-1} \pm 4.0\text{ mg C g}^{-1}$, N: $9.9\text{ mg N g}^{-1} \pm 1.4\text{ mg N g}^{-1}$, and a C:N ratio
129 of 43.6 ± 6.6 for the grass labelled litter) were within the range of variation observed on
130 sites for litterfall and grass litter (Table S1).

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

141 *2.3. Sample collection and analyses*

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

158 Elemental and isotopic compositions (total C, total N and $\delta^{15}\text{N}$) were determined
159 by an IsoPrime 100 isotope ratio mass-spectrometer (IsoPrime Corporation, Cheadle,
160 UK) and vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH,
161 Hanau, Germany) using international reference materials USGS 24 (IAEA N1 (0.4 ‰
162 vN2), IAEA N2 (20.3 ‰ vN2)) and USGS 26 (53.7 ‰ vN2). The measurement error of
163 $\delta^{15}\text{N}$ was approximately 0.2 ‰.

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

167 *2.4. Isotopic calculations*

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

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

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

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

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

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

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

175 where At.% $^{15}\text{N}_{\text{sample}}$ is the ^{15}N abundance in the sampled layer, At.% $^{15}\text{N}_{\text{control}}$ is the
176 ^{15}N natural abundance of the layer (without labelling), At.% $^{15}\text{N}_{\text{lab litter}}$ is the ^{15}N abun-
177 dant in the labelled litter, At.% $^{15}\text{N}_{\text{unlab litter}}$ is the ^{15}N natural abundance in the litter,
178 $M_{\text{N sample}}$ is the mass of N in the layer sampled (in g N m^{-2}), and $M_{\text{N litter dep}}$ is the mass
179 of N deposited with the labelled litter (in g N m^{-2}).

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

185 2.5. Statistical analyses

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

191 2.6. Modelling

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

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

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

$$\frac{dN_L}{dt} = -k_L N_L \quad (4)$$

$$\frac{dN_1}{dt} = k_L N_L \times a_{L \rightarrow 1} - k_1 N_1 \quad (5)$$

$$\frac{dN_2}{dt} = k_1 N_1 \times a_{1 \rightarrow 2} - k_2 N_2 \quad (6)$$

200 where: N_L , N_1 and N_2 are the N recovered in the litter, the first (0–5 cm) and the second
 201 (5–10 cm) soil compartments, respectively ; k_L , k_1 and k_2 are the decomposition rates
 202 of these compartments and $a_{L \rightarrow 1}$ and $a_{1 \rightarrow 2}$ are allocation constants, i.e. the proportion
 203 of the output from the litter compartment and the first soil compartment that reach the
 204 first and the second soil compartment, respectively. The inverse of the decomposition
 205 rate (k) is the mean residence time (*MRT*) of N in a given compartment:

$$MRT = \frac{1}{k} \quad (7)$$

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

208 The analytic solutions of these differential equations are:

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

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

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

209 The parameters k_L , k_1 , k_2 , $a_{L \rightarrow 1}$ and $a_{1 \rightarrow 2}$ were fitted simultaneously by minimizing
 210 the following fitness, which is the sum of the normalized mean square errors in the three
 211 compartments:

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

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

216 The optimization was performed with a genetic algorithm (population size 50, proba-
 217 bility of crossover between pairs of chromosomes 0.8, probability of mutation in a parent
 218 chromosome 0.1, maximum number of iterations 1000, with local search by “L-BFGS-
 219 B” method) with the following constraints on the parameters: $0.00055 < k_L < 0.0055$,
 220 $0.00014 < k_{soil} < 0.0055$ and $0 < a < 1$. In summary, the genetic algorithm helps to
 221 search the best set of model parameters giving the smallest fitness (the global minimum).

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

224 3. Results

225 3.1. N recovery observations

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

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

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

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

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

245 In the grassland plots, N loss from the litter layer below the netting tended to be faster
246 than for the forest plots at all the sites (Fig. 3); however, there were no statistically de-
247 tectable differences in loss rates between the sites (Tables S6 and S7). Uncertainties
248 inherent to the sampling of such material might have altered the precision of our mea-
249 surements (see the possible outliers for spring and autumn 2013 at BAR). In June 2013,
250 almost all the labelled N was recovered in the litter layer below the netting at BAR (al-
251 most 100 %) and SAE (91 %) while only 50 % was recovered in TOM. In October 2014,
252 only 19 and 16 % of N were recovered in this litter layer at SAE and TOM (19 and 16 %,
253 respectively) but 40 % were still recovered at BAR. Generally, in the 0–2.5 cm soil layer,
254 large amounts of litter-derived N were recovered (often > 40 %), which was significantly
255 greater than in forest. Only up to 10 % of the deposited N was recovered in the soil
256 between 2.5 and 10 cm, except in SAE where the recovery reached 20 % in the 2.5–5 cm
257 layer in October 2014. At SAE, a peak N recovery in the 0–2.5 cm soil layer was observed
258 in October 2014 (83 %), while at BAR and TOM the N recovery measured in October
259 2015 was the highest (64 and 55 %, respectively). At each sampling, live vegetation was
260 enriched in litter-derived N. Interestingly, the highest N recovery in the vegetation was
261 measured in June 2013 (8, 3 and 6 % in BAR, SAE and TOM, respectively). The N
262 recovery in the litter above the netting increased with time, reaching about 2.5 % in
263 October 2014.

264 *3.2. N recovery modelling*

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

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

269 In the forest plots, the *MRT* of N in aspen litter was estimated to be 2.9 and 4.6 years
270 in the forest-steppe sites BAR and SAE, respectively, and 1.5 and 0.9 years in the southern
271 taiga sites SAW and TOM, respectively (Table 3). The *MRT* of N in the 0–5 cm soil
272 compartment was shorter than its *MRT* in the litter layer. SAW had the shortest *MRT*
273 (1.5 years) and TOM the longest (2.1 years). In the 5–10 cm soil compartment, all the
274 *MRT* but one ranged between 0.6 and 1.1 years. The allocation factor, which is the
275 proportion of the output from one compartment that reaches the compartment below,
276 ranged from 62 (SAE) to 94 % (SAW) in the 0–5 cm soil compartment and from 42 (SAW)
277 to 100 % (BAR) in the 5–10 cm soil compartment (Table 3). The parameters obtained
278 for the 5–10 cm soil compartment must be interpreted with caution because of the short
279 duration of the experiment and the dilution of the ^{15}N signal in the ecosystem.

280 For the grassland plots, TOM also exhibited the shortest *MRT* in the litter (1.2 years)
281 but the difference with the two other sites was less than one year (*MRT* of 1.6 and
282 1.4 years for BAR and SAE, respectively; Table 3). The *MRT* range (4.9 years at TOM
283 to 9.4 years at SAE) in the 0–5 cm soil compartment was much larger than in the litter.
284 The *MRT*'s were also greater than forest estimates at the same compartment. In the
285 5–10 cm soil compartment, the *MRT* were close to 1 year in SAE and TOM, and around
286 2.6 years in BAR. However, the latter might be an over-estimate since the available
287 data do not permit to constrain the curvature of the fit in the deepest layer of BAR
288 grassland. Allocation from the litter to the 0–5 cm soil compartment and from the 0–5
289 to the 5–10 cm soil compartment was greater than 85 % for all sites.

290 We simulated the average N recoveries over 3000 days (which is about twice as long
291 as the time frame of this study) in the three compartments of the model (Fig. 6). The
292 simulations resulted in specific patterns related to site position and vegetation types. In
293 forests, we distinguished 2 categories of sites. SAW and TOM presented a fast release of
294 N from the litter and transfer to the 0–5 cm soil, but also a fast N loss out of the system.
295 According to the model, 50 % of litter N was lost before 1000 days in those sites. In BAR
296 and SAE, the release of N from the litter was slower and 50 % of the N remained in the
297 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 mg C g⁻¹) and N (10–13 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

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

364 *4.2. N dynamics in the soil layers: role of climate, vegetation type and soil properties*

365 *4.2.1. Vertical transfer*

366 Across all sites, there were distinct periods over the year where N transfers occurred
367 within the soil, as revealed by the specific “build-up and release” pattern observed in the
368 0–2.5 cm and 2.5–5 cm soil layers: a net increase in N recovery was observed from the
369 autumn samplings while a net decrease was observed from the spring samplings (Fig. 2
370 and 3).

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

389 has been estimated to be almost five times higher in TOM ($262 \pm 73 \text{ mm year}^{-1}$, 49 years
390 mean \pm standard deviation) than in BAR ($60 \pm 43 \text{ mm year}^{-1}$), for example (Brédoire,
391 2016).

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

402 4.2.2. N retention in soil

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

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

420 woody sites (Booth et al., 2005) and, since ammonium is usually taken up more efficiently
421 by vegetation and micro-organisms (Kuzyakov & Xu, 2013), this could explain the shallow
422 transfer of N in grasslands. In addition, grasslands in SW Siberia tend to have a greater
423 net primary production than nearby forests (Monserud et al., 1995) and they have a
424 dense root mat found in the first centimeters of the soil (Table 2 and Brédoire et al.
425 (2016b)), both of which facilitate N retention and cycling in the topsoils of grasslands.

426 Soil organic C has a faster turnover in southern taiga than in forest-steppe in these
427 Siberian ecosystems (Kayler et al., 2018); however, we did not find such a pattern for the
428 *MRT* of N within the first ten centimeters of the soil. Besides pedo-climatic conditions
429 which control the transfer and immobilization of N, texture and mineralogy also control
430 the fate of N within the soil as N is mainly associated with clay and silt fractions (Moni
431 et al., 2012; Mueller et al., 2009; Kayler et al., 2011), and N protection increases with
432 their increasing amounts (Bingham & Cotrufo, 2016; Dignac et al., 2017; Kleber et al.,
433 2015; von Lützow et al., 2006) as well as metallic (hydr)oxides (Bingham & Cotrufo, 2016;
434 Duiker et al., 2003; Porras et al., 2017; Torn et al., 1997). By extending our experiment
435 on a longer period of time, we may strengthen our estimations of *MRT* and seek to
436 verify how soil texture and mineralogy control the stabilization of N in these Siberian
437 ecosystems.

438 *4.3. Summary and future outlook*

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

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

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

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

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

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480 **Author contributions**

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

486 **Competing interests statement**

487 The authors have no competing interests to declare.

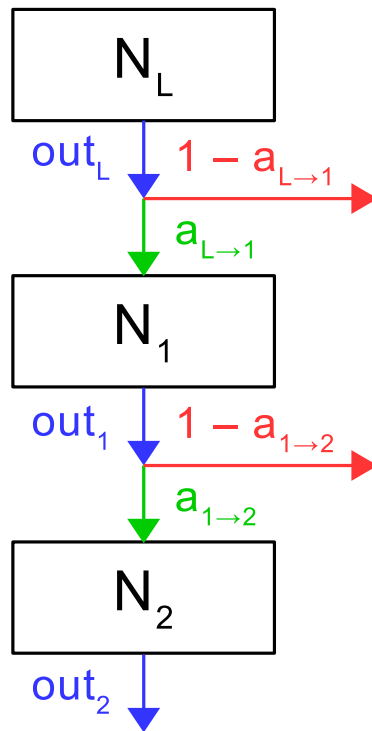


Figure 1: Model diagram. N_L , N_1 and N_2 are the litter-derived N contents of the litter layer, the first (0–5 cm) and the second (5–10 cm) soil layers, respectively. N_x is the N content in the compartment x , $a_{x \rightarrow y}$ is the proportion of the output from x (out_x) that reaches y , and the difference “ $1 - a_{x \rightarrow y}$ ” 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).

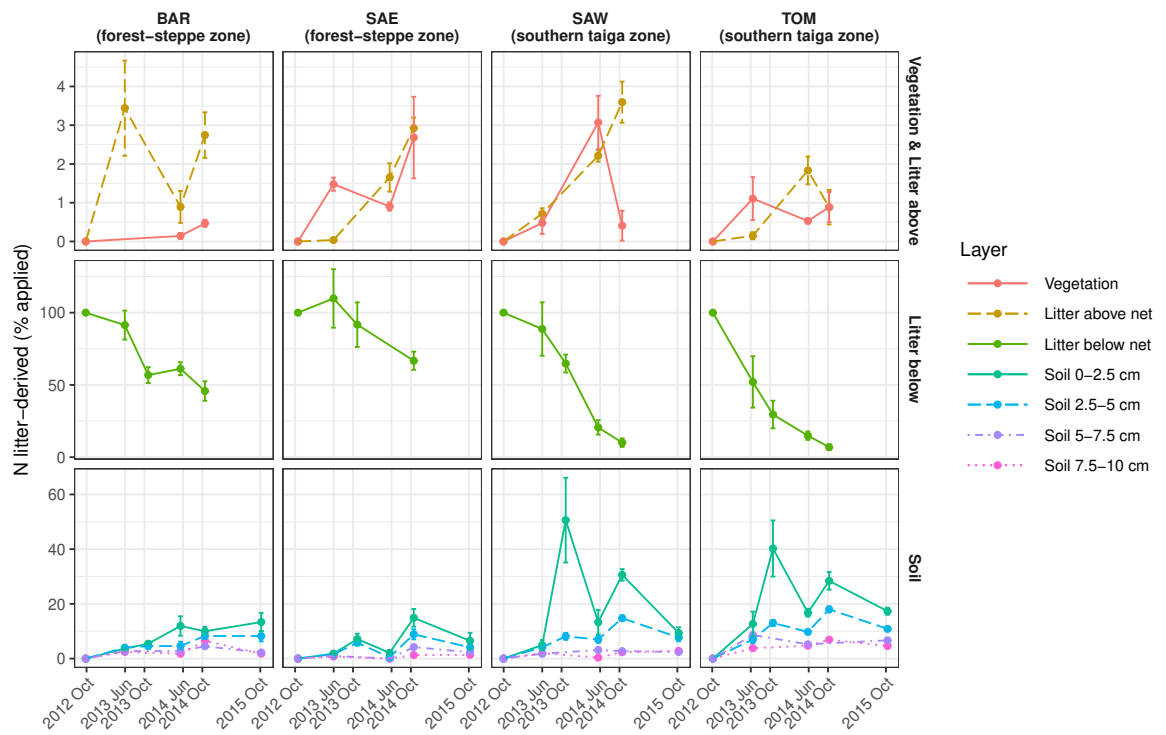


Figure 2: Proportion of litter-derived N recovered in each layer in forest. Mean value \pm standard deviation (number of replicates given in Table S7). Vegetation refers to live undertorey vegetation. The terms “above” and “below” refer to the netting which protects the ^{15}N -labelled litter.

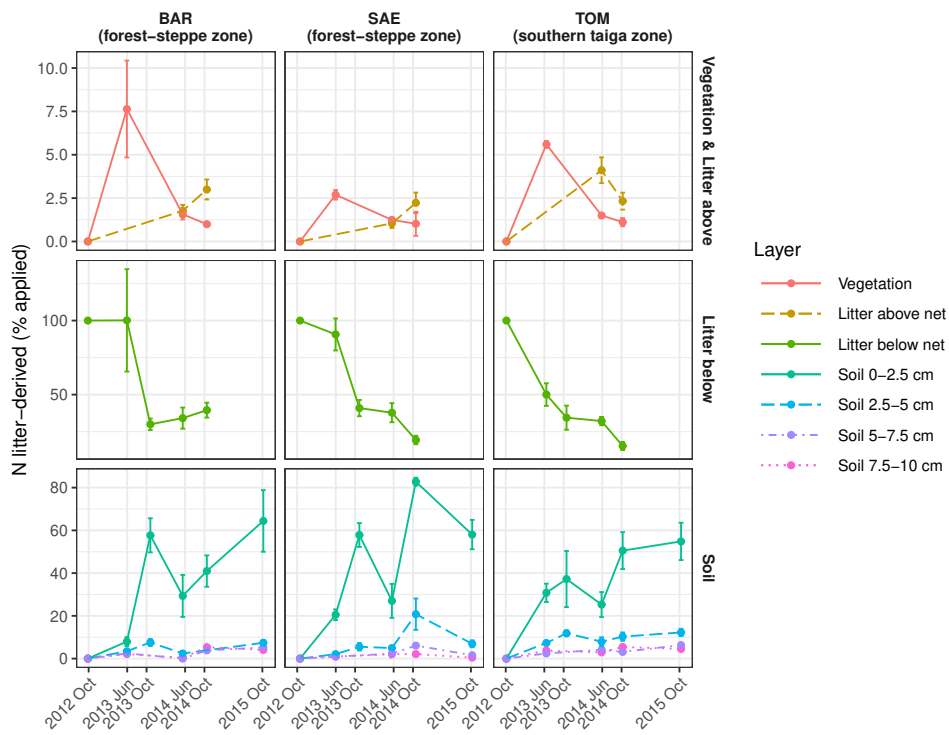


Figure 3: Proportion of litter-derived N recovered in each layer in grassland. Mean value \pm standard deviation (number of replicates given in Table S7). The terms “above” and “below” refer to the netting which protects the ^{15}N -labelled litter.

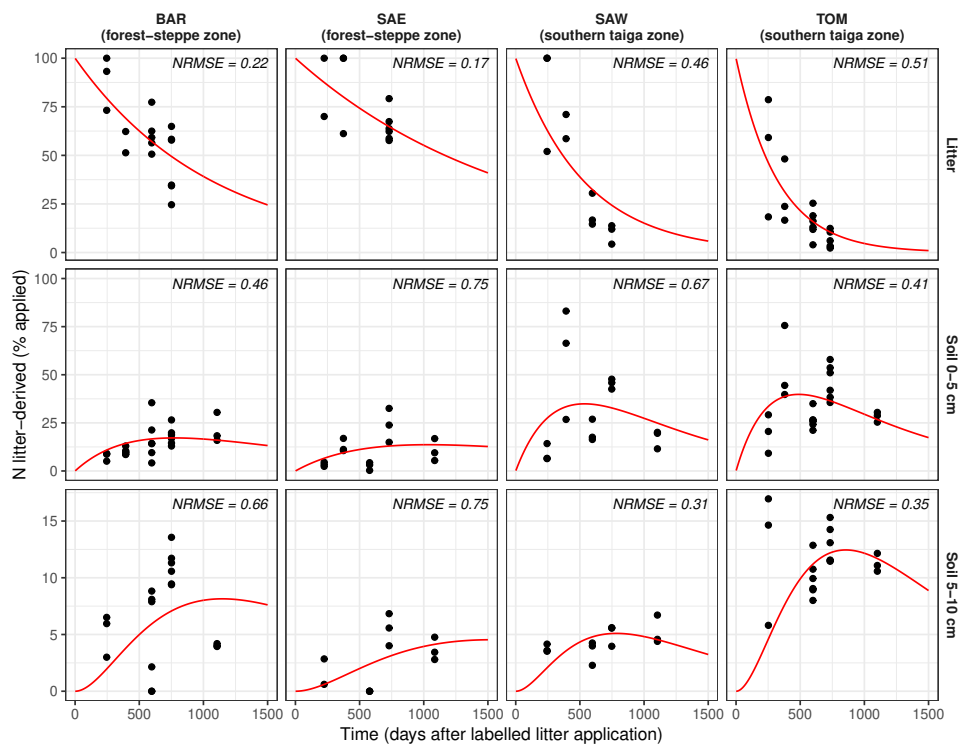


Figure 4: Fit of the N decomposition and transfer model in forest with indication of the normalized root mean square error ($NRMSE = RMSE/\bar{O}$ where \bar{O} is the mean of the mean observation per date).

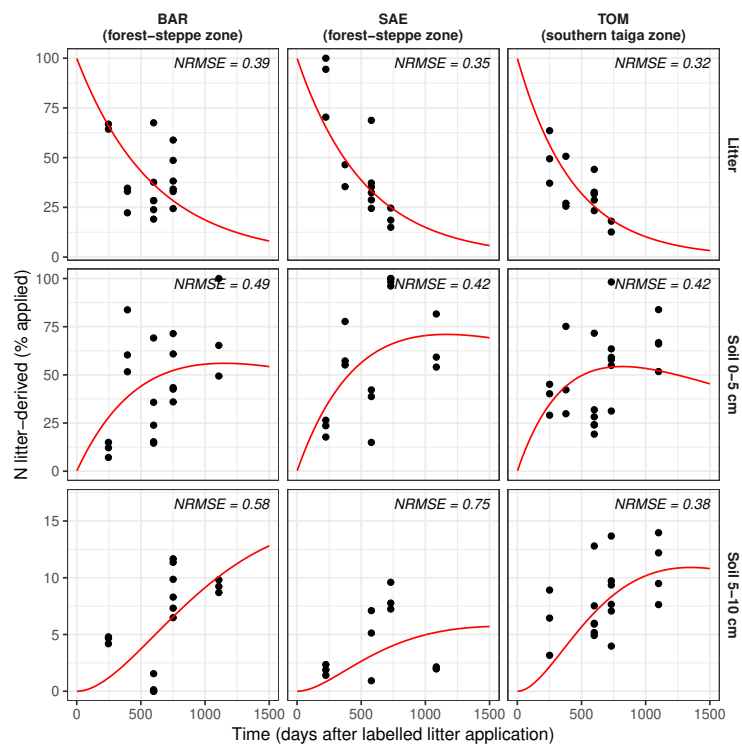


Figure 5: Fit of the N decomposition and transfer model in grassland with indication of the normalized root mean square error ($NRMSE = RMSE/\bar{O}$ where \bar{O} is the mean of the mean observation per date).

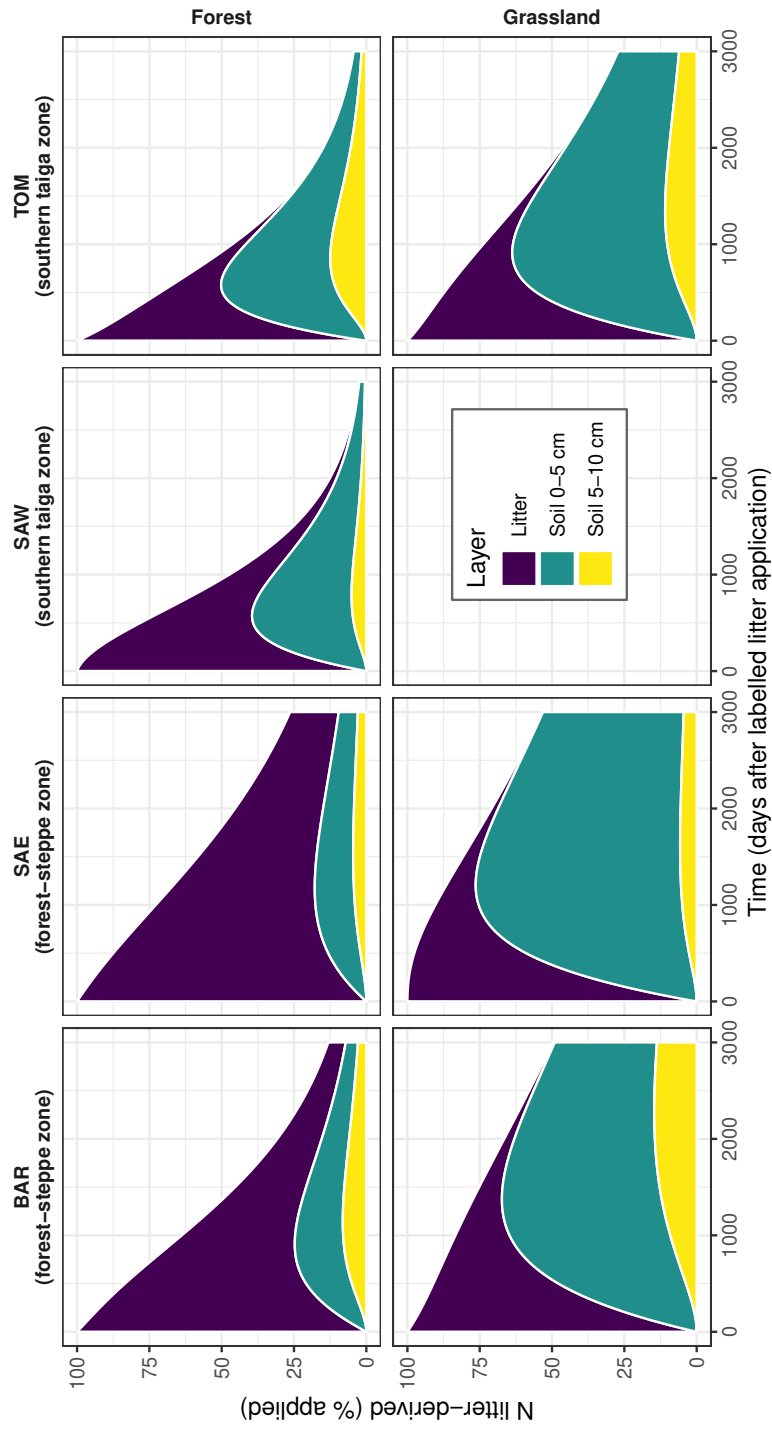


Figure 6: Simulation of N recovery over time.

Table 1: Main characteristics of the study sites.

Site ID	BAR	SAE	SAW	TOM
<i>General</i>				
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
<i>Climatic features (mean annual values over the period 1981–2010)</i>				
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
<i>Field measurements of the snow height: mean (min–max)^{ef}</i>				
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

^aaccording to the name of the closest city or of the geographical area; ^bWorld Meteorological Organization

(WMO) index of the closest weather station; ^cdistance site–weather station; ^ddue 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; ^esnow height at climax (usually between mid-February

and mid-March); ^fsnow was measured on the experimental sites every meter with the help of a rigid ruler on

a transect of 20 m; ^g22/02/2014; ^h15/02/2014; ⁱ24/02/2015; ^j25/02/2015; ^k27/02/2015

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 (cm)	Forest				Grassland		
		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 (mg N g^{-1} dry soil)	0–2.5	5.51	8.76	5.83	5.70	4.81	7.78	3.77
	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 (mg C g^{-1} dry soil)	0–2.5	73.59	115.53	78.45	76.21	56.86	95.06	49.02
	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 (g kg^{-1})	5	< 1	< 1	< 1	< 1	< 1	< 1	< 1
	15	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Al oxides* (mmol kg^{-1})	5	63.4	101.6	77.1	86.7	58.6	101.2	90.4
	15	64.9	126.0	88.9	95.3	59.3	104.9	91.2
Fe oxides* (mmol kg^{-1})	5	31.3	56.0	68.0	75.2	25.2	48.5	93.7
	15	33.3	67.2	75.6	79.0	26.3	49.6	95.6
Fine root length density (cm roots cm^{-3} soil)	5	1.44	2.16	0.92	0.77	2.35	2.82	2.79
	15	0.77	0.94	0.37	0.82	1.30	1.03	1.06
Fine root mass density (mg roots cm^{-3} soil)	5	1.47	1.88	0.86	0.87	1.49	2.04	1.06
	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 ($a_{L \rightarrow 1}$) and from the 0–5 to the 5–10 cm soil layer ($a_{1 \rightarrow 2}$). 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	$a_{L \rightarrow 1}$	$a_{1 \rightarrow 2}$	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

