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REGULAR ARTICLE

Recovery of nitrogen cycling in riparian zones after stream restoration using $\delta^{15}N$ along a 25-year chronosequence in northern Sweden

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Abstract
Background and aims Swedish boreal streams were modified to transport timber by pushing boulders to stream sides, creating levees that disconnected streams from riparian areas. Many streams have since been restored and our goal was to understand how this affects riparian nitrogen (N) cycling.
Methods We compared the natural abundance of $\delta^{15}N$ isotopes in foliage and roots of *Filipendula ulmaria* plus soils and litter along streams restored 2–25 years ago. We measured sources of N, potential immobilization of N, namely plant diversity and biomass, and the amount and sources of carbon (C) to determine if these were important for describing riparian N cycling.
Results The $\delta^{15}N$ of *F. ulmaria* foliage changed dramatically just after restoration compared to the channelized, disconnected state and then converged over the next 25 years with the steady-state reference.
Conclusions The disturbance and reconnection of the stream with the riparian zone during restoration created a short-term pulse of N availability and gaseous losses of N as a result of enhanced microbial processing of N. With increasing time since restoration, N availability appears to have decreased, and N sources changed to those derived from mycorrhizae, amino acids, or the humus layer, or there was enhanced N-use efficiency by older, more diverse plant communities.

Keywords Boreal · Mycorrhizae · Phytometer · Space-for-time substitution · Succession · Time gradient

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Introduction

As a result of being the interface between land and flowing waters (Naiman and Decamps 1997), riparian zones play an important role in regulating nutrient transport, especially nitrogen (N), from terrestrial to aquatic ecosystems (Hedin et al. 1998; Fig. 1). Given that riparian zones are capable of retaining or removing N entering streams (Peterjohn and Correll 1984), many stream restoration projects aim to reconnect streams to their riparian zones to reduce N from entering streams (Kaushal et al. 2008). Ultimately, the amount and form of N that enters the stream depend on many biotic and abiotic factors (Ocampo et al. 2006; Fig. 1). However, it is unclear how stream restoration activities may affect N-cycling in the riparian zone, especially in N-limited boreal zones and, in general, how long it takes for N-cycling to recover after restoration.

Most streams in northern Sweden were physically modified by humans from the 1850s to the 1960s to

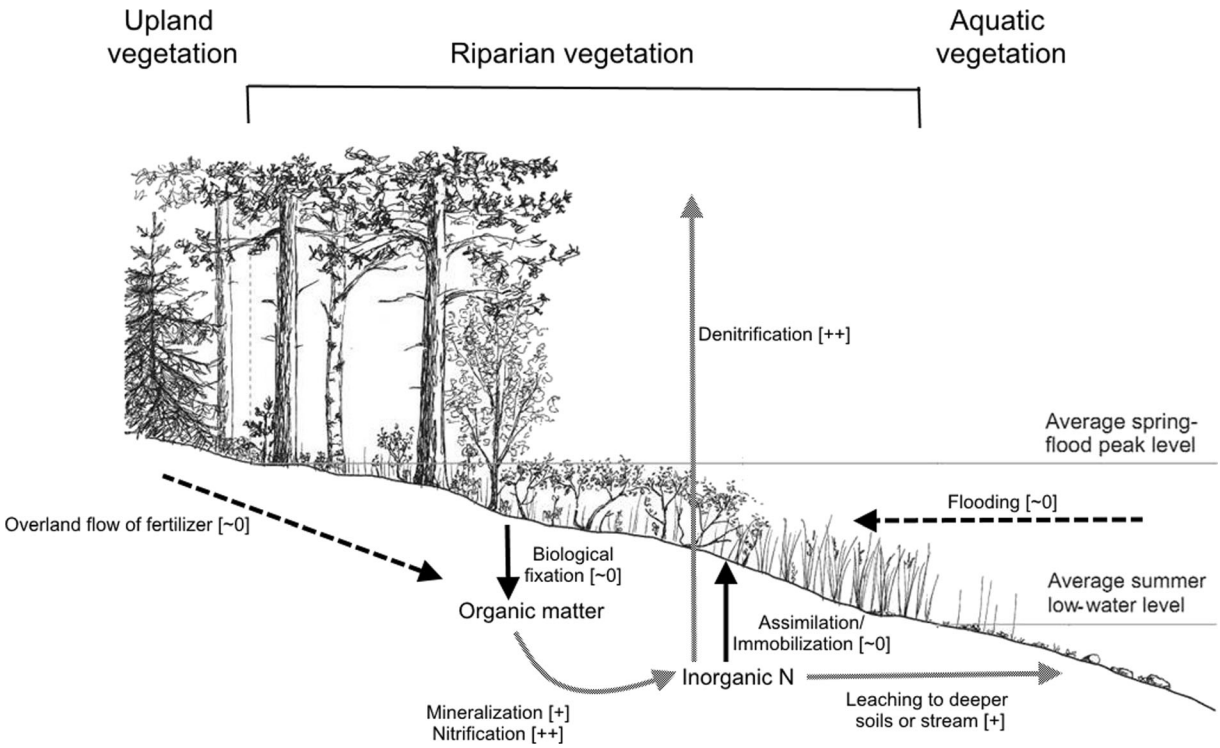

Fig. 1 Processes influencing the N-cycle in riparian zones examined in this study and how they affect fractionation of $\delta^{15}N$ (+ or ++ signs show enrichment or strong enrichment, respectively, or "~ 0" for relatively no effect). We hypothesized these processes would change with time since restoration; black arrows indicate a hypothesized increase, grey arrows represent a hypothesized decrease, and for processes with a dashed arrow we hypothesized that there would be no change with time after restoration. Modified from Ström et al. (2012)

accommodate timber floating, which ceased in the 1970s (Nilsson et al. 2005). Boulders were destroyed with explosives or pushed to the sides of streams creating levee-like structures that disconnected the stream from the riparian zone in order to create narrow and straight channels with faster flow (Nilsson et al. 2005). Beginning in the 1980s, many of these streams were restored to increase habitat complexity (Nilsson et al. 2005; Gardeström et al. 2013), which included reopening closed side channels, dismantling stone levees, and placing boulders and cobbles back into the stream. Although these restoration efforts have primarily focused on improving habitat for local fish populations and other aquatic biota (Nilsson et al. 2015), they have also had the important effect of reconnecting the riparian zone. However, little is known about how stream restoration influences the structure and function of riparian processes, especially in boreal landscapes.

Restoration likely alters N-cycling in boreal riparian forests by (1) physically reconnecting the riparian zone with the stream, (2) initiating plant succession, and (3) physically disturbing the soil and vegetation. The hypothesized effects of these alterations with time since restoration on specific N-cycling processes within the riparian zone are shown in Fig. 1. Reconnection of the stream with the riparian zone likely increases the potential of soil microbes to process N by reestablishing the regular wetting of riparian soils providing the necessary anoxic conditions for denitrification (McClain et al. 2003). However, this initial pulse of microbial activity could decrease over time due to a decrease in N supply in this typically N-limited system (Tamm 1991). In addition, the C stocks that had built up with years of disconnection could be used up to fuel denitrification. The reconnection is also important for delivering nutrients, organic matter, plant propagules (seeds and vegetative parts) in flood waters (Nilsson et al. 2005) and ultimately may lead to the recovery of riparian plant communities (Hasselquist et al. 2015). Plant community succession after restoration can include an increase in species diversity (Hasselquist et al. 2015) that could potentially lead to more efficient use of N with less N leaching (more N assimilated/

immobilized into plant biomass) through niche complementarity (Kleinebecker et al. 2014). Plant succession following restoration could also affect the availability of different N sources through changes in the quantity of species with associative N-fixing bacteria or cyanobacteria, such as *Alnus* spp. (Hobbie et al. 1999) or bryophytes (DeLuca et al. 2002) as well as the extent of mycorrhizal colonization of roots over time because mycorrhizae transfer N directly derived from organic matter (Hobbie et al. 1999). Restoration efforts can destroy riparian plants and disturb the soil through mixing and compaction. Destruction of riparian plants could directly affect the N-cycle by reducing the potential consumption of N by plants leading to more N lost due to leaching (Högberg 1997; Löfgren et al. 2009). Rates of mineralization and nitrification could also initially increase after disturbance (Gundersen et al. 2006) which can lead to more available N. However, like denitrification, these processes would be expected to decrease with time after restoration as carbon stocks decrease and N becomes increasingly immobilized in living biomass. Disturbance could also have an impact by removing the humus layer where plants in older forests typically access N, leaving them to access N from deeper mineral soil layers (LeDuc et al. 2013; Hu et al. 2014) or through a reduction in mycorrhizal colonization that can occur following disturbance (Hobbie et al. 1999). Reconnection of the riparian forest with the stream, initiation of plant succession, and disturbance may all interact to affect N and C sources and plant communities that in turn can influence the recovery of N-cycling in boreal riparian forests after stream restoration.

Because microbes that control N processing discriminate in a systematic way against the heavier stable isotope of N, ^{15}N (represented as the ratio of ^{15}N:^{14}N, or $\delta^{15}N$; Nadelhoffer and Fry 1994; Högberg 1997), $\delta^{15}N$ can provide information on the source, fate, and rates of transformation of N. It is difficult to directly measure N-cycling parameters, and denitrification in particular (Groffman et al. 2006); moreover they vary greatly over time and space (McClain et al. 2003; Pinay et al. 2007). In contrast, $\delta^{15}N$ in plants and soil can provide more integrated measurements over longer timescales and of the entire rhizosphere (Högberg 1997; Robinson 2001; Craine et al. 2015). For example, changes in foliar $\delta^{15}N$ can indicate N sources from different rooting depths (Nadelhoffer and Fry 1994; Hobbie and Högberg 2012), the utilization of organic N (LeDuc and Rothstein 2010; Mayor et al. 2012; Hu et al. 2014), N-fixing plants (Hobbie et al. 1999; DeLuca et al. 2002), industrial fertilizers (Bateman and Kelly 2007), or N transfer from mycorrhizae (Hobbie and Högberg 2012; Mayor et al. 2012; Hu et al. 2014). Enrichment of $\delta^{15}N$ often indicates an increased rate of N lost via gaseous losses during microbial processing (Craine et al. 2015) or leaching (Högberg 1997; Martinelli et al. 1999), whereas depletion of $\delta^{15}N$ is often interpreted as a very closed system where N is cycled tightly and immobilized in plant or microbial biomass (Ometto et al. 2006; Watzka et al. 2006). Further, greater $\Delta\delta^{15}N$ (defined here as the difference between soil and foliage $\delta^{15}N$), has been cited as evidence for greater reliance on mycorrhizal symbionts for N uptake under N-limited conditions (Högberg et al. 2011; Hobbie and Högberg 2012). Although changes in isotopic composition are often difficult to attribute directly to a specific mechanism, the change itself is a robust indication of changes in N source or cycling.

A number of studies have detected distinct phases associated with the initial effects of restoration or natural disturbance and then the subsequent recovery. Studies of boreal forest fire chronosequences have reported high $\delta^{15}N$ values soon after wildfires followed by gradually decreasing values over decades to centuries (Hyodo et al. 2013; Hu et al. 2014). While research on a riparian restoration chronosequence in California has found that while riparian forests strongly resembled remnant forests with respect to plant community composition (Holl and Crone 2004) and biomass (Matzek et al. 2016) after less than 15 years, soil properties and components of nutrient cycling were much slower to change with time (Matzek et al. 2016). Molles et al. (1998) found that the response of riparian forest-floor respiration to the reconnection of the stream with its riparian zone involved three phases that could take from one year to decades to complete: the initial disconnected phase, a reorganization phase initiated by restoration, and a steady-state phase that approximated conditions prior to restoration. Although Molles et al. (1998) work focused only on carbon (C) cycling, we suggest that this reorganization model may apply to other ecosystem processes, such as N-cycling.

To evaluate changes in N-cycling with time since restoration, we measured the N content and the $\delta^{15}N$ of foliage and fine roots of a phytometer species as well as litter, humus, and mineral soil. We did this along a chronosequence of restored sites, ranging in time since restoration from 2 to 25 years, along with disconnected channelized and unchannelized steady-state reference sites. We hypothesized that N-cycling, as estimated by

$\delta^{15}N$ of foliage and roots, would follow the reorganization model of Molles et al. (1998), and would increase after restoration and enter a reorganization phase due to the reconnection of the floodplain and disturbance of the soil and vegetation during the restoration activities that would stimulate N processing. We further hypothesized that the $\delta^{15}N$ of foliage and roots would decrease with time during the reorganization phase reflecting decreased N availability and stabilization of the N-cycle. To explore the mechanisms behind this projected response, we measured or calculated sources of N including mycorrhizal N transfer, rooting depth, N-fixers, N from newly reconnected stream water, and overland flow of industrial fertilizer from uplands. We also explored plant diversity and biomass across the chronosequence to see if changes in plant community dynamics might influence total N immobilization or cycling over time. Finally, we examined the amount and sources of C, particularly amount of soil C and deciduous tree species with high quality C to explore the possibilty that changes in N-cycling was controlled by changing carbon availabilty and quality. Given previous studies of boreal riparian and forest chronosequences, we hypothesized that the N-cycle would be highly perturbed at the point of restoration characterized by fast cycling and large N losses and then over time become similar to reference sites as N availability and immobilization increased. In our conceptual model of N-cycling in the riparian zone (Fig. 1), the effect of fractionation of $\delta^{15}N$ for each of the processes is designated, thus giving its relative contribution to the $\delta^{15}N$.

Methods

Site description

The study reaches were situated along tributaries of the Vindel and Ume Rivers in northern Sweden (64°15′ - 65°36′ N, 16°52′ - 19°50′E). The rivers originate in the Scandes mountains on the border with Norway and flow southeast, parallel to each other before they join about 20 km northwest of Umeå. Downstream of Umeå, the united Ume River flows into the Gulf of Bothnia. These rivers have been classified as “boreal rivers” within the Fennoscandian shield (Petersen et al. 1995), which includes the northern half of Sweden, all of Finland, and the westernmost part of European Russia (Malmqvist et al. 2009). The main soil types are glacial tills and peat; N deposition is low (<2 kg ha^{-1} $year^{-1}$) and similar across sites (Karlsson et al. 2013). The landscape has a fairly low relief (~200–600 m a.s.l.; Fredén 1994), and is the product of many glaciations; large glacial legacy sediment (boulders and cobbles) dominate even low-gradient (<1 %) reaches (Polvi et al. 2014). The tributaries are made up of tranquil reaches interspersed with turbulent reaches (pool-riffle, plane-bed, and cascade); turbulent reaches were typically the target of channelization efforts because these were the places where floated logs would jam.

The upland landscape is characterized by low diversity, managed boreal forests, dominated by *Pinus sylvestris*, *Picea abies*, and *Betula pubescens* with an understory of dwarf shrubs (e.g., *Vaccinium* spp. and *Empetrum hermaphroditum*), mosses, and lichens. Riparian zones are narrow (median width = 24 m), yet are species rich with *Betula* spp., *Alnus incana*, *Salix* spp., and *Juniperus communis* occupying the riparian zone with a diverse understory of indigenous graminoids and forbs. The riparian flora is entirely indigenous. The annual growing season (days with mean temperatures >3 °C) ranges between 140 days at the headwaters to about 165 days at the mouth (Ångström 1974). The highest intensity and duration floods occur during spring after snowmelt, whereas the highest water levels often occur during winter floods, caused by ice dams (Lind et al. 2014). Water levels in these small streams can change rapidly in response to precipitation with summer and autumn floods common. In general, channelized streams have hydrographs that rise and fall rapidly while restored streams rise and recede more slowly.

When streams in northern Sweden were channelized to facilitate timber floating, boulders were usually destroyed with explosives or pushed to the sides of the stream, creating levees that disconnected the stream from the riparian zone and flow velocities that are higher and more spatially homogenous (Törnlund and Östlund 2002; Nilsson et al. 2005). When timber floating ceased in the 1970s, streams were gradually restored by opening up side channels and returning boulders and cobbles from the sides of the streams to the middle of the channel to restore habitat complexity of the stream (described in detail in Lepori et al. 2005; Helfield et al. 2007; Gardeström et al. 2013). Restoration in the study streams was implemented at the reach scale, varying in length from 300 m to 1 km. After 2010, more enhanced restoration techniques added large boulders and large wood that were generally missing from the instream

system because they had been destroyed with explosives since they were too big to move. In all time-periods of restoration, sinuosity was not added because bedrock typically restrains the formation of meanders in this system (Malmqvist et al. 2009). Furthermore, no planting or seeding of the riparian zone was done. The main objective of the restorations was to improve habitat for Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and European grayling (*Thymallus thymallus*), but these instream actions influenced riparian habitats as well. For example, when boulders were moved from the riparian area back into the stream, soil and thus seedling establishment sites were exposed. Furthermore, when boulders from levees were returned to the stream, the stream was widened and water levels increased due to the displacement of water by the boulders (Gardeström et al. 2013). Instream boulders also slowed the flow of water (Gardeström et al. 2013), presumably making conditions better for seed retention and chemical interactions (e.g., denitrification) with the riparian soil (Nilsson et al. 2005; Engström et al. 2009).

A total of 26 riparian study sites were identified in mid-sized tributaries of the Ume and Vindel Rivers, with catchments draining an average of 74 (± 13.9) km^2 (Table 1). Sites were 60-m long, relatively straight and fast-flowing reaches whose riparian zones had not been logged, grazed by cattle, or otherwise disturbed by human activities within the last 50 years. Further, they had similar geology and flow regimes unaffected by dams. Five of the 26 sites were disconnected, channelized stream reaches, and four sites were unchannelized steady-state reference sites. The remaining 17 sites were chosen along a time-after-restoration gradient, ranging from 2 to ca. 25 years after restoration. The restored reaches can be grouped into four categories of different time periods after restoration: (1) three streams that were ca. 25 years old (restored 1987–1988), (2) five streams were ca. 15 years old (restored 1995–1999), (3) five streams were ca. 5 years old (restored 2002–2005) and (4) five streams that were first restored at the same time as the 5-year old streams (2002–2005) but were extensively re-restored in 2010 with enhanced techniques of adding large boulders and large wood to the instream channel (Gardeström et al. 2013). Thus, there are some methodological differences between the older restorations (5–25 year old streams) and the newest restorations, with practitioners having stated that older restorations were "lighter", meaning that fewer boulders and cobbles were returned to the stream. We argue, however, that for this study, the details of the instream work are less important than the removal of the levees that reconnected the stream and the riparian zone. Additionally, our sample size for the 25-year old streams is low because there were not many streams restored at this time and the majority of streams restored 25 years ago have subsequently been re-restored due to perceived lack of success in improving fish habitat. Latitude was the only characteristic that differed among restoration time categories (Table 1).

Understory plant diversity, biomass, and litter cover Along each 60 m reach, plant community composition was measured in 15, ca. 50 × 50 cm quadrats stratified along five transects spaced 10 m apart (see Hasselquist et al. 2015 for details). Percent cover of all vascular plant species, functional groups of bryophytes (including N_2 fixers), as well as substrates such as leaf litter, bare soil, and boulders were visually estimated within each quadrat. Understory biomass (<1 m tall) and litter (Oi horizon) samples were collected in 25 × 25 cm quadrats placed adjacent to each of the larger plots. Biomass and litter samples were dried at 65 °C for 48 h and then weighed. All vegetation surveys were done in August, peak-growing season in northern Sweden; quadrats were sampled in 2011 and reach-scale plant species inventories were done in 2013 (see Hasselquist et al. 2015 for details). Additionally, percent cover of all tree species, including *Alnus incana*, a N_2 fixer, was visually estimated for each stream reach.

Stable isotope and nutrient analyses To control for inter-species differences in plant N isotope values, we used a single phytometer species, *Filipendula ulmaria* that occurred in situ at all sites. This is a tall perennial forb, native to the catchment and grows in damp to wet habitats. It overwinters at or near the soil surface; thus, all aboveground growth is new each year. Within-plant fractionation can also cause variation in isotope values (Högberg 1997), and it has been suggested that the $\delta^{15}N$ in fine roots more closely reflects the $\delta^{15}N$ available to plants in soil solution compared to other plant tissues (Templer et al. 2007). We therefore used a combination of soil, foliage, and fine root $\delta^{15}N$ data to examine patterns of N-cycling and changes in N sources from the riparian zone following restoration.

Samples of *F. ulmaria* were collected over a 2-week period in August 2012. At each site, foliage and fine roots were collected from five individuals located near

Table 1 Mean (± 1SE) characteristics of sites used in this study. The center four columns contain characteristics for the reorganization phase of the restoration chronosequence. $\delta^{15}N$ data for *F. ulmaria* foliage and roots are found in Fig. 2. Litter and mineral soil data were only available for a select set of sites (litter, $N = 21$; mineral soil, $N = 17$). SEs are presented in italics

Site characteristics	Disconnected	Reorganization phase				Steady state
	Channelized	2 year old	5 year old	15 year old	25 year old	Unchannelized
Latitude (decimal degrees)	65.21 ± *0.13*	65.06 ± *0.08*	65.11 ± 0.*09*	65.47 ± *0.05*	64.57 ± *0.02*	64.93 ± *0.27*
Drainage area (km^2)	102.81 ± *53.12*	77.29 ± *24.33*	65.71 ± *30.63*	110.18 ± *32.41*	37.23 ± *2.96*	27.81 ± *6.34*
Alnus incana cover (%)	3.50 ± *3.38*	3.60 ± *1.81*	1.25 ± *0.75*	0.60 ± *0.60*	6.33 ± *4.37*	4.00 ± *2.45*
N-fixing bryophyte cover (%)	8.20 ± *2.38*	21.53 ± *5.02*	15.54 ± *5.27*	14.33 ± *3.28*	13.83 ± *3.29*	12.46 ± *6.07*
$NO_3 + NO_2$ in stream water (μg/l)	5.69 ± *2.28*	5.80 ± *2.08*	3.63 ± *1.49*	2.31 ± *0.33*	4.00 ± *0.58*	8.51 ± *2.73*
Total N in stream water (μg/l)	258.8 ± *27.9*	259.5 ± *16.5*	266.8 ± *23.7*	210.1 ± *6.48*	234.7 ± *11.9*	281.2 ± *26.8*
Open soil (% bare soil)	0.55 ± *0.32*	3.81 ± *1.53*	1.50 ± *0.82*	1.23 ± *0.35*	1.11 ± *1.11*	1.75 ± *0.83*
F. ulmaria foliage N (%)	2.86 ± *0.17*	2.91 ± *2.20*	3.06 ± *0.17*	2.96 ± *0.12*	2.69 ± *0.17*	2.77 ± *0.09*
F. ulmaria root N (%)	0.99 ± *0.05*	1.04 ± *0.10*	1.20 ± *0.15*	1.19 ± *0.05*	0.99 ± *0.10*	0.96 ± *0.04*
Litter $\delta^{15}N$(‰)	-1.33 ± *0.70*	-1.70 ± *0.29*	-2.05 ± *0.13*	-0.81 ± †	-1.80 ± *0.49*	-2.06 ± *0.52*
Litter N (%)	1.24 ± *0.14*	1.15 ± *0.08*	1.29 ± *0.07*	1.61 ± †	1.18 ± *0.05*	1.26 ± *0.14*
Humus - $\delta^{15}N$(‰)	2.09 ± *0.37*	2.12 ± *0.33*	2.28 ± *0.27*	2.35 ± *0.31*	1.56 ± *0.28*	1.60 ± *0.75*
Humus - N (%)	1.20 ± *0.23*	0.89 ± *0.17*	1.22 ± *0.23*	0.99 ± *0.11*	1.18 ± *0.09*	0.69 ± *0.17*
Humus - C	23.40 ± *4.88*	18.22 ± *3.45*	26.56 ± *5.29*	23.18 ± *5.79*	23.19 ± *0.25*	15.37 ± *4.09*
Humus - C:N	19.08 ± *1.46*	19.96 ± *0.27*	21.14 ± *1.21*	24.08 ± *4.78*	19.98 ± *1.71*	21.85 ± *1.02*
Mineral soil - $\delta^{15}N$(‰)	5.22 ± *2.07*	5.43 ± *0.81*	5.96 ± *0.74*	4.62 ± †	3.14 ± *0.94*	4.72 ± *1.65*
Mineral soil - N (%)	0.23 ± *0.07*	0.15 ± *0.04*	0.17 ± *0.04*	0.79 ± †	0.26 ± *0.12*	0.38 ± *0.17*
Upland humus - $\delta^{15}N$(‰)	1.19 ± *0.57*	0.78 ± *0.49*	0.86 ± *0.43*	1.85 ± *0.20*	0.75 ± *0.34*	0.30 ± *0.70*
Upland humus - N (%)	1.49 ± *0.13*	1.19 ± *0.18*	1.33 ± *0.04*	1.57 ± *0.14*	1.27 ± *0.11*	1.25 ± *0.28*
N	5	5	4	5	3	4

† Collected from a reduced set of sites

each of the five transects used for vegetation and biomass sampling if the following criteria were met: (1) the individual was at least 20 cm tall without visible insect damage or infections, and (2) it was located within 1 m (distance) of the summer low water level. Foliage was removed from each individual in the field and placed in a paper bag. After collection of foliage, individual *F. ulmaria* plants were excavated and brought back to the laboratory where roots were washed with deionized water to remove all soil debris.

Coincident with plant sampling in 2012, humus (Oe + A horizon soils) was sampled next to *F. ulmaria* individuals using a soil auger (2-cm diameter) and the depth of the sample varied from <0.2 to 15 cm. To evaluate if N from adjacent land use was affecting riparian N-cycling values (Fig. 1), humus was sampled at the riparian–upland ecotone boundary (~80 cm elevation above summer low-water level) using similar techniques as humus collection adjacent to *F. ulmaria*. At each site, five soil cores were collected and analyzed separately to provide mean values with standard errors. In 2013, mineral soil (B horizon) samples were collected from 13 of the restored sites as well as from all natural and four channelized reference sites. Cores were taken within 1 m distance of the summer low-water level. If mineral soil was present, it was separated from the humus and pooled prior to isotopic analysis. All soils, foliage, and roots were dried (65 °C for 48 h) and soils were sieved (2 mm mesh) before being ground in a ball mill (MM200, Retsch GmbH, Haan, Germany) and weighed into tin capsules for isotopic analyses. Litter samples were pooled by site and the entire sample was homogenized and ground to a fine powder using a Tecator Cyclotec Sample Mill (Model no. 1093, FOSS). A subsample of ground litter was used for isotopic analyses. All isotopic samples (foliage, roots, soils, and litter) were sent to the Stable Isotope Laboratory at Cornell University, Ithaca, NY, USA, where bulk [N] and [C] were measured using a CHN elemental analyzer (NC2500; Thermo Finnigan) and $\delta^{15}N$ was measured using a continuous flow isotope

ratio mass spectrometer (Model Delta V; Thermo Finnigan). All isotope data are expressed in delta notation (‰) relative to the internationally accepted standard.

Stream water was collected in August 2011 and 2012 and samples were frozen until unfiltered samples were analyzed for concentrations of total N, NH_4^+, and NO_3^-+NO_2^- (FIAstar 5000). An average value for each site between the two years was used for analyses.

Data analysis

All data were analyzed using R (R Core Team 2014). To understand how time since restoration affected N-cycling in riparian zones, e.g., how $\delta^{15}N$ and N content of the different N-pools varied during the reorganization phase, we used linear mixed-effect models (LMM) to account for the multiple replicates for each site. Models were fit with time after restoration as a fixed factor and site as a random factor. These models were then compared to models using site within restoration time category as a random factor to determine if differences in latitude among the time categories were important. Time category was included if a likelihood ratio test showed that it had a lower AIC value (Akaike's information criterion); otherwise, this random factor was dropped. The *nlme* package (Pinheiro et al. 2015) was used for LMMs. The overall significance of time since restoration (the fixed factor) was tested by comparing the models with and without time (likelihood ratio test).

To assess the significance of potential N sources, plant diversity, or C sources for explaining the response to time after restoration, we used both LMMs and OLS models. OLS models were tested with *lm* in R. Most of the explanatory variables that were tested were collected at the reach scale. Thus, only the time category was used as a random factor to account for differences in latitude. This random factor was included if a likelihood ratio test showed that it had a lower AIC value than a model without latitude as a random factor. If the latitude did not improve the model, this random factor was dropped and OLS models were used. *L*-ratios are reported if LMMs were used and *F*-statistics are reported if OLS models were used.

Results

The $\delta^{15}N$ in foliage and roots for disconnected, channelized sites was relatively depleted (Fig. 2a, b), whereas shortly after restoration there was an initial increase in $\delta^{15}N$ of 163 % for *F. ulmaria* foliage and of 96 % for *F. ulmaria* roots in newly restored sites over that of disconnected, channelized, sites. Both the $\delta^{15}N$ of *F. ulmaria* foliage and roots later decreased with time since restoration and approached values similar to those observed in the channelized and steady-state, unchannelized, reference sites (foliage, *L*-ratio = 7.76, $p = 0.005$, Fig. 2a; roots, *L*-ratio = 4.99, $p = 0.026$; Fig. 2b). The $\delta^{15}N$ of litter ($F_{1,11} = 0.001$, $p = 0.98$), humus (*L*-ratio = 0.750, $p = 0.386$), and mineral soil ($F_{1,9} = 4.51$, $p = 0.063$) did not have any significant relationships with time since restoration (Table 1). The channelized and unchannelized reaches had similar $\delta^{15}N$ values for *F. ulmaria* foliage, roots, and soils (Fig. 2a, b, Table 1).

Percent N of *F. ulmaria* foliage and roots, as well as litter, humus, and mineral soil did not change with time since restoration ($p > 0.05$; Table 1). Understory biomass had a negative quadratic relationship with time after restoration ($F_{2,14} = 4.34$, $p = 0.034$); with an initial increase in biomass between the second and fifth years followed by a decrease down to reference levels thereafter (Fig. 2c).

To better describe the mechanisms behind the patterns seen in $\delta^{15}N$, we evaluated a number of hypothesized N-source parameters that could affect $\delta^{15}N$ over time. There was evidence of a greater reliance on mycorrhizal fungi for N with increased time after restoration as indicated by an increase in the difference in $\delta^{15}N$ between soil and foliage ($\Delta\ \delta^{15}N$; *L*-ratio = 4.65, $p = 0.031$; Fig. 3). Although open soil patches were not significantly related to $\delta^{15}N$ values ($F_{1,15} = 1.78$, $p = 0.202$), there were less open soil patches as restored sites aged ($F_{1,15} = 5.62$, $p = 0.032$). Stream water nitrate (NO_3^- + NO_2^-) was the only source of N that was significantly related with $\delta^{15}N$ of foliage ($F_{1,12} = 6.70$, $p = 0.024$; Fig. 4a), but did not change significantly with time after restoration ($F_{1,15} = 0.41$, $p = 0.531$). Plant diversity increase with time after restoration ($F_{1,15} = 5.45$, $p = 0.034$), and was also significantly related to $\delta^{15}N$ of restored sites ($F_{1,15} = 4.49$, $p = 0.051$; Fig. 4b). The percent cover of deciduous tree species did not change with time after restoration ($F_{1,15} = 0.002$, $p = 0.962$), but had a positive relationship with $\delta^{15}N$ of restored sites ($F_{1,15} = 4.17$, $p = 0.059$; Fig. 4c). Neither humus C nor humus C:N had any relationships with time after restoration or $\delta^{15}N$ ($F_{1,15} < 0.362$, $p < 0.556$). The abundance of N-fixing plant species did not change over time; *A. incana* did not

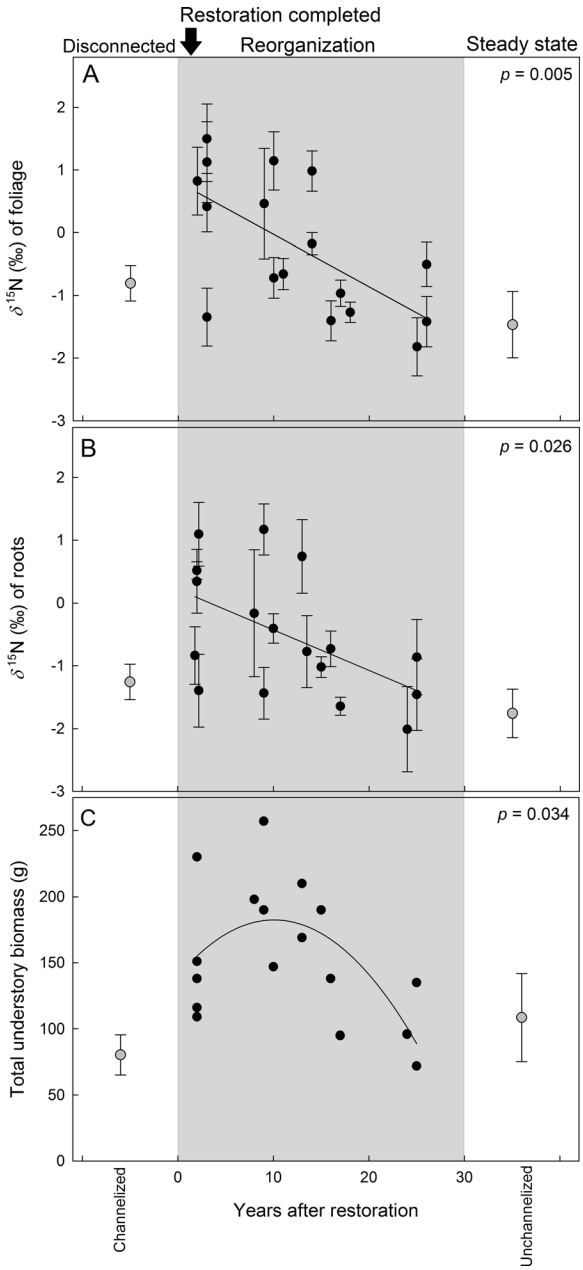

Fig. 2 The mean (± 1SE) δ^{15}N of *F. ulmaria* foliage (A) and roots (B) as well as the total understory biomass (C) for each site along the chronosequence of time since restoration. Panels follow the convention of Molles et al. (1998) reorganization model as indicated at the top of the figure; means (± 1SE) of five disconnected, channelized sites are included on the left to represent disconnected conditions, the shaded region indicates the reorganization phase and includes the restoration chronosequence, and the means (± 1SE) of three unchannelized reaches represent a steady state condition found after reorganization. The *p*-value for the relationship between a given response variable and years after restoration is included each panel

change with time after restoration ($F_{1,15}$ = 0.183, p = 0.675; Table 1), nor did the percent cover of bryophytes with associative N-fixing cyanobacteria ($F_{1,15}$ = 0.013, p = 0.911; Table 1). Overland flow of N from potentially fertilized upland areas as measured by upland soils (taken from the riparian–upland forest ecotone at 80 cm elevation) also did not change with time after restoration ($F_{1,15}$ = 0.263, p = 0.616; Table 1). None of these three variables were correlated with δ^{15}N of foliage ($p > 0.05$). It should be noted that in none of the models was the random factor of latitude significant.

Discussion

As hypothesized, we found that N-cycling, as measured by δ^{15}N of *F. ulmaria* foliage and roots, followed a reorganization model similar to that of Molles et al. (1998); Fig. 2). Shortly after the disconnected, channelized sites were restored, they entered a reorganization phase that was characterized by a short-term pulse of N availability and enhanced microbial N processing as indicated by high understory biomass and enriched foliar and root δ^{15}N values of *F. ulmaria* in newly restored sites. As the reorganization phase progressed, understory biomass and foliar and root δ^{15}N values of *F. ulmaria* became progressively depleted potentially from a change in N source (N derived from mycorrhizae, amino acids, or shallower soil layers) and/or enhanced N-use efficiency by older, more diverse plant communities all of which could indicate increasing N limitation. The recovery of N-cycling was a gradual process, and it took more than 20 years for the restored sites to approach δ^{15}N values similar to those observed in the steady-state, unchannelized, reference sites.

After disturbance, several studies have shown that rates of mineralization and nitrification increase (Gundersen et al. 2006) which can lead to higher rates of N-cycling and more enriched foliar δ^{15}N due to gaseous losses during these two processes (Stenger et al. 1995; DeLuca et al. 2002). Our findings of more enriched foliar δ^{15}N values in the youngest restored sites (Fig. 2a, b), suggest that restoration may act like other disturbances and initally create an N-cycle with greater gaseous losses of N through increased rates of both mineralization and nitrification, and consequently an increase in N availability (i.e., NO_3^-; Kronzucker et al. 1997). Changes in understory biomass support the

notion of increased N availability in the younger sites. Reduced understory biomass in the youngest restored sites is likely a relic of the disturbance caused by the restoration activities (Fig. 2c) that, in turn, decreased the overall plant demand for N at these younger sites and increased the potential for N losses through nitrate leaching (Aber et al. 1989; Högberg and Johannisson 1993; Löfgren et al. 2009). Further, abiotic changes within the riparian zone after restoration may have created favorable conditions for gaseous N losses, resulting in δ^{15}N enrichment of available N for plants. Built stone levees reduced the duration of flooding of riparian zones (Nilsson et al. 2005). After restoration, riparian zones were reconnected with the stream creating a new flooding regime and more suitable conditions for denitrification (Nilsson et al. 2005), a process which can lead to δ^{15}N enrichment of the remaing N pool through gaseous losses. Taken together, increased rates of mineralization and nitrification due to the disturbance of soils, potential for higher nitrate leaching as a result of reduced understory biomass and better conditions for denitrification all likely contributed to the high δ^{15}N values in the younger restored sites.

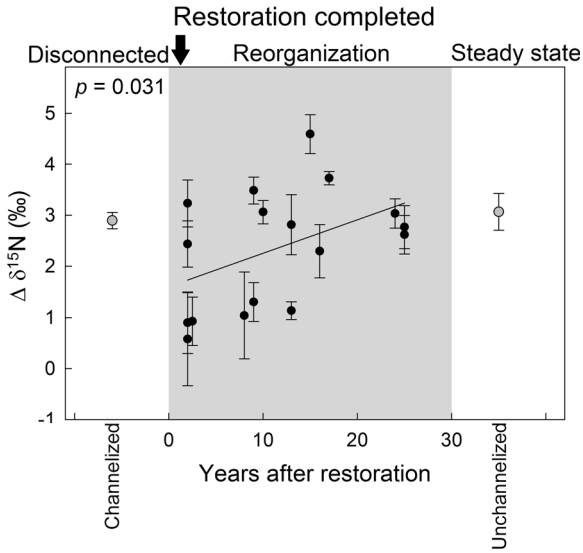

Fig. 3 Mean(± 1SE) $\Delta\delta^{15}$N values (i.e., soil δ^{15}N - foliar δ^{15}N) of *F. ulmaria* per site measured over time since restoration. Panels follow the convention of Molles et al. (1998) reorganization model as indicated at the top of the figure; means (± 1SE) of five disconnected, channelized sites are included on the left to represent disconnected conditions, the shaded region indicates the reorganization phase and includes the restoration chronosequence, and the means (± 1SE) of three unchannelized reaches represent a steady state condition found after reorganization. The *p*-value for the relationship between $\Delta\delta^{15}$N and years after restoration is included

Mechanisms for plant δ^{15}N decreases with time since restoration

Decreasing N availability with time after disturbance Changes in foliar δ^{15}N found in this study are similar to centuries old boreal forest fire chronosequences, that reported high δ^{15}N values soon after wildfires followed by gradually decreasing values over decades to centuries (Hyodo et al. 2013; Hu et al. 2014). Although the majority of the literature on N-cycling in boreal chronosequences is based on terrestrial forests affected by fire, this is the primary natural disturbance agent in boreal forests and may provide insight into how these systems would react to most disturbances.

The patterns in δ^{15}N of foliage are broadly consistent with the development of decreasing N availability during succession that has been seen in other boreal chronosequences (DeLuca et al. 2002; Hyodo et al. 2013; Hu et al. 2014). If this is the case, then %N of foliage in *F. ulmaria* and/or plant biomass should decrease with time. However, we found no significant change in %N in *F. ulmaria* or soil, nor did other studies of chronosequences in boreal systems (Hyodo et al. 2013; Hu et al. 2014). Instead, we found a negative quadratic relationship between the biomass of understory vegetation and time since restoration suggesting an initial pulse of N availability soon after restoration followed by decreasing N availability as indicated by a gradual decrease in understory vegetation 15 years after restoration. This notion of a pulse in N availability following stream restoration is further supported by a recent study in the same region that showed a positive relationship between the biomass of phytometers and δ^{15}N values of riparian soils collected 3–7 years after restoration (Dietrich et al. 2014).

N sources One possible explanation for the lack of change in foliar %N as well as a decreasing trend in foliar δ^{15}N may be linked to plants using other N sources over time, such as N derived from mycorrhizal fungi or N from the humus layer (LeDuc and Rothstein 2010; Mayor et al. 2012; Hu et al. 2014). In N-limited boreal forests, most plants rely on mycorrhizal fungi to acquire N, and as a consequence of N fractionation in mycorrhizal symbioses the N that is transferred to plants is typically depleted in ^{15}N (Hobbie and Högberg 2012). Previous studies have interpreted lower foliar δ^{15}N values and greater $\Delta\delta^{15}$N (i.e., the difference between

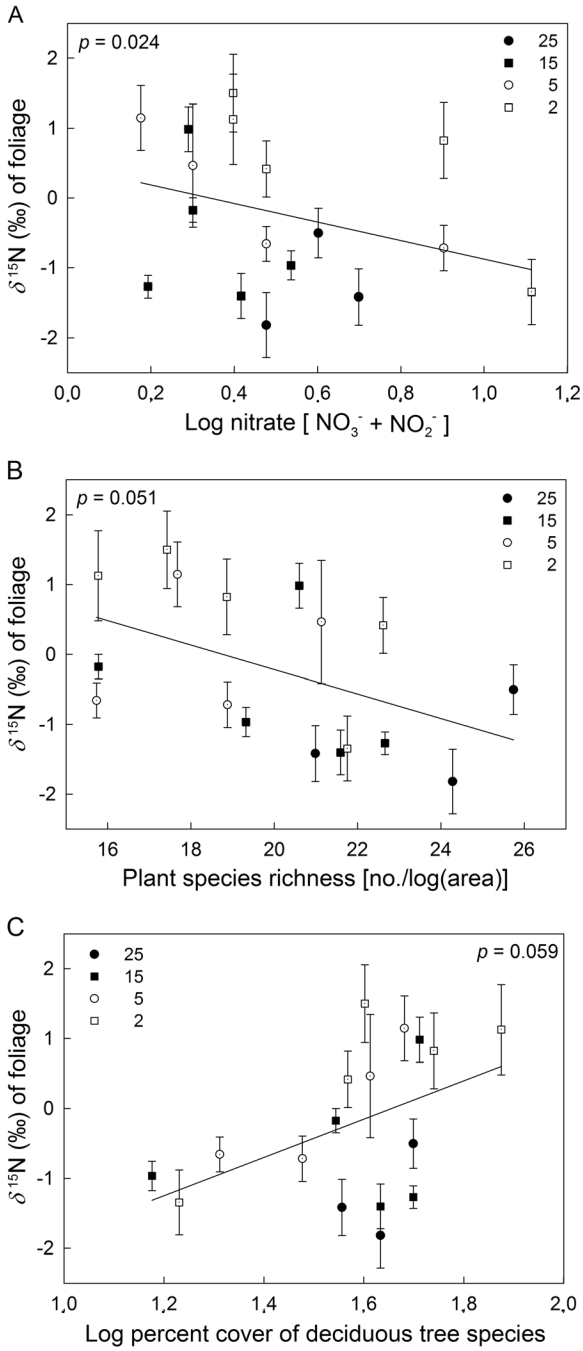

Fig. 4 Relationship between the mean (± 1SE) δ^{15}N of *F. ulmaria* foliage of 17 restored sites and (A) stream nitrate concentrations [NO_3^- + NO_2^-], (B) plant species richness, and (C) percent cover of deciduous tree species. For reference, the time category of each restored site is denoted with different symbols (e.g. "25" for the oldest, 25 year old sites). The p - value for each relationship is included in each panel

soil and foliage δ^{15}N), as evidence for greater reliance on mycorrhizal symbionts for N uptake under N-limited conditions (Högberg et al. 2011; Hobbie and Högberg 2012). The decreasing trend in δ^{15}N of *F. ulmaria* foliage combined with increasing $\Delta\delta^{15}$N (Fig. 3) in time after restoration may, therefore, reflect a greater dependency on mycorrhizal fungi for N uptake. This idea is consistent with previous studies that have shown a general decrease in mycorrhizal colonization after a disturbance, which is often attributed to an increase in nutrient availability (Allen 1991). Compton et al. (2007) previously attributed the decrease in δ^{15}N over 115 years in a white pine chronosequence as evidence for, at least in part, increased mycorrhizal colonization over time. An additional explanation for changes in $\Delta\delta^{15}$N could be that plants are taking up depleted organic N such as simple amino acids, which can occur when inorganic N availability is low such as in old-growth stands (LeDuc and Rothstein 2010). Finally, plants could also be accessing N from deeper soil layers soon after restoration because the upper humus soils have been removed during the restoration activities. Deeper soils are typically more enriched in δ^{15}N compared to the more depleted humus layer (Nadelhoffer and Fry 1994; Hobbie and Högberg 2012). Although we did not find a difference in humus depth, weight, or bulk density over time since restoration (EM Hasselquist, unpublished data), thus, it is unlikely that we found a higher percentage of open patches (percent cover of bare soil) in the youngest restored sites that supports the idea that plants at these sites may be accessing N at deeper soil depths. It is likely a combination of all of these factors that contributes to the depletion in δ^{15}N over time, and further experimental work is needed to determine which process is dominant.

Nitrate concentration of stream water was the only N-source besides transfer from mycorrhizae that had a significant relationship with foliar δ^{15}N. Although the nitrate concentration of our forested boreal streams was typically very low (median = 3.22 μg/l; Table 1), it was related to foliar δ^{15}N suggesting a strong (re)connection between these restored streams and their riparian zones. On the other hand, associative N-fixing bacteria or cyanobacteria, such as *A. incana* or bryophytes, were not important for describing foliar δ^{15}N values and may be relatively less important for N-cycling in riparian zones even though they have been found to be important contributors of N in upland boreal forests (Gundale et al. 2011). Further, we did not find evidence of overland flow of N from potentially fertilized upland areas as measured by δ^{15}N of upland soils (taken from the riparian–upland

forest ecotone at 80 cm elevation). Thus, it seems likely that the changes in $\delta^{15}N$ in the riparian zone is the result of processes within the riparian zone.

Plant species richness In addition to changes in N sources, decreasing foliar $\delta^{15}N$ over time could also, in part, be related to increasing plant species richness. Plant species richness was negatively related to foliar $\delta\ ^{15}N$ (Fig. 4b). This result combined with our previous finding of increased plant species richness with time since restoration at the same sites (Hasselquist et al. 2015) suggests greater plant N uptake and potentially less leaching of ^{15}N-depleted nitrate (Martinelli et al. 2006). Using $\delta^{15}N$ and $\Delta\delta^{15}N$ of foliage and soils from 150 European grasslands, Kleinebecker et al. (2014) found evidence of species complementarity through niche partitioning as the key mechanism responsible for enhanced resource-use efficiency and reduced N loss through leaching. Thus, diverse communities are expected to take up more of the available resources as species use different resources or vary spatially and/or temporally in their uptake patterns (Kleinebecker et al. 2014).

C-sources Although we did not find any relationships with time after restoration or $\delta^{15}N$ with humus C or humus C:N, we found a positive relationship between foliar $\delta^{15}N$ and percent cover of deciduous tree species. Similarly, Molles et al. (1998) reported a close relationship between soil respiration and the processing of organic matter pools and labile organic matter. Our finding suggests that N mineralization and denitrification may also be limited by the availability of C, and even more by high quality C like that found in deciduous tree litter (Duan et al. 2014). Microbes require C for N mineralization and denitrification, and in riparian systems these processes are often limited by low availability of C or of the quality of C (Hedin et al. 1998). In general, litter from deciduous trees is known to be a higher quality substrate for microbial processes compared to coniferous species such as pine (Duan et al. 2014). Given these findings and those reported by Molles et al. (1998) more research is needed to better understand the interactions and feedbacks between C and N cycling after stream restoration, especially in boreal ecosystems.

Practical implications Enhancing biodiversity has typically been the primary goal of restoration. As land managers are increasingly required to also include provision of ecosystem services in their restoration projects, such as N processing or filtration, their monitoring responsibilities may need to expand from the recovery of flora and fauna to the recovery of ecosystem processes (Matzek et al. 2016). Thus, finding methods to monitor these ecosystem processes as well as determine the time scale at which they should recover are becoming increasingly important. There is evidence that feedbacks exist between species composition and ecosystem processes and that different ecosystem processes will develop over different time scales. For example, after less than 15 years, restored riparian forests in California resembled remnant forests with respect to plant community composition (Holl and crone 2004) and biomass (Matzek et al. 2016), but soil properties and components of nutrient cycling were much slower to change with time (Matzek et al. 2016). Thus, it may be necessary to set sequential, multi-step goals for restoration projects (Palmer et al. 1997). However, in our study, we found that N cycling recovered on a similar time scale to that of the plant community (Hasselquist et al. 2015) suggesting that restoration goals in Fennoscandian boreal systems can be simplified to having just one expected time frame for recovery, albeit it may take 25 years

The restoration sites we studied fell into that found for the "Field of Dreams hypothesis" (Palmer et al. 1997), namely "if you build it, they will come" or in other words, restore the hydrological and geomorphological processes, and the plants and ecosystem processes will follow. There was no seeding or planting of riparian plant species at our restoration sites and it could be that seeding or planting (planting preferred, see Dietrich et al. 2015) could accelerate both the recovery of riparian species composition and N-processing. However, given that the arrival order of plants plays an important role for which type of vegetation will develop at restored sites (Sarneel et al. 2016; Young et al. 2016), the selection of species to be introduced has to be done with care.

Conclusions

This study highlights some of the key factors affecting the reorganization and recovery of N-cycling in the riparian zone of boreal streams after stream restoration. The isotope record suggests that stream restoration initiated a reorganization phase characterized by increased gaseous losses of N compared with reference sites. This was likely due to the disturbance of soils and vegetation that caused high rates of mineralization and nitrification

as well as reconnecting the riparain zone with the stream creating conditions more favorable for gaseous losses via denitrification. As the reorganization phase progressed, the $\delta^{15}N$ record indicates decreased rates of microbial N processing and ultimately decreased N availability as sites recovered from the disturbance of restoration. The notion of decreasing N availability with time since restoration is supported by our finding of a change in N source over time, and particularly the increased dependency on mycorrhizal fungi for plant N uptake as indicated by increasing $\Delta\delta^{15}N$ after restoration. Additionally, the decrease in $\delta^{15}N$ during the reorganization phase could also be due to increased plant species diversity and niche partitioning resulting in enhanced resource-use efficiency, and thus, less nitrate losses via leaching. Lastly, results from this study highlight the complexity of interactions influencing the N-cycle in restored boreal riparian zones, and stresses the need for additional studies to provide a more direct mechanistic understanding of the key factors influencing the recovery of the N-cycle after stream restoration.

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