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Simulated N and S deposition affected soil chemistry and understory plant communities in a boreal forest in western Canada

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Abstract

Aims

We conducted a simulated nitrogen (N) and sulfur (S) deposition experiment from 2006 to 2012 to answer the following questions: (i) does chronic N and S deposition decrease cation concentrations in the soil and foliage of understory plant species, and (ii) does chronic N and S deposition decrease plant diversity and alter species composition of the understory plant community in a boreal forest in western Canada where intensifying industrial activities are increasing N and S deposition?

Methods

Our field site was a mixedwood boreal forest stand located ~100 km southeast of Fort McMurray, Alberta, Canada. The experiment involved a 2 × 2 factorial design, with two levels each of N (0 and 30 kg N ha^{-1} yr^{-1}; applied as NH_4NO_3) and S addition (0 and 30 kg S ha^{-1} yr^{-1}; applied as Na_2SO_4). Four blocks were established in July 2006, each with four plots of 20 × 20 m randomly assigned to the treatments. Soil and understory vegetation were sampled and cover (%) of individual species of herb (height ≤ 0.5 m) and shrub (height 0.5–1 m) layers was determined in August 2012.

Important Findings

Seven years after the treatments began, N addition increased dissolved organic carbon and N in the mineral soil ($P < 0.05$), whereas S addition decreased exchangeable cations ($P < 0.05$) in the forest floor. In the shrub layer, species evenness, and overall diversity were decreased by N addition ($P < 0.05$) due to increases in abundance of nitrophilous species and S addition ($P < 0.01$) due to decreased cation concentrations in soils. Total shrub cover decreased with S addition ($P < 0.10$). Nitrogen and S addition affected neither species richness nor evenness in the herb layer. However, permutational multivariate analysis of variance and non-metric multidimensional scaling analyses (based on plant cover) indicated that the effect of N and S addition on understory plant species composition in the both shrub and herb layers was species-specific. Addition of N decreased foliar phosphorus and potassium concentrations in some species, suggesting potential risk of N-meditated nutrient imbalance in those species. Our results indicate that long-term elevated levels of N and S deposition can negatively impact plant nutrition and decrease the diversity of the understory plant community in boreal forests in northern Alberta, Canada. However, considering that the current N and S deposition rates in northern Alberta are much lower than the rates used in this study, N and S deposition should not negatively affect plant diversity in the near future.

Keywords: species diversity, nutrient imbalance, cation leaching, understory foliar chemistry, acid deposition, soil acidification

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INTRODUCTION

Biodiversity has declined globally as a result of anthropogenic environmental perturbations, including changes in land-use practices and the climate (Reidsma *et al.* 2006; Thuiller 2007). Emission of acidic precursors, such as NO_x and SO_2, and their subsequent deposition that cause nitrogen (N) enrichment and acidification (Fenn *et al.* 2011), is a serious threat to plant

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diversity in a variety of ecosystems (Gilliam 2006 2014b; Lovett *et al.* 2009). The Athabasca oil sands region (AOSR) is the largest oil sands mining area in the world (Alberta Government 2013). Oil sands mining/extraction and upgrading activities release considerable NO_x and SO_2 to the atmosphere. Emissions of NO_x increased steadily from 20 Mg day^{-1} in 1970 to 300 Mg day^{-1} in the mid-2000s and SO_2 emission has been ~300 Mg day^{-1} since the late 1990s (Hazewinkel *et al.* 2008), with further increases in emissions of NO_x and SO_2 expected from expansion of oil sands mining activities and increases in the human population (Aherne and Shaw 2010; Golder Associates 2003).

Chronic N deposition can shift plant species composition, typically related to increasing abundance of nitrophilous species and decreasing abundance of species adapted to the low N supply conditions (Gilliam 2014b; Gilliam *et al.* 2016b; Hruška *et al.* 2012). Also, resistance of plants to pathogens and insects may decrease associated with N-enhanced pathogenic fungal infestation (Gilliam 2006). Coincidentally, excess N and S deposition can decrease the availability of nutrient cations in the soil, arising from increased leaching loss of nitrate (NO_3^-) and sulfate (SO_4^{2-}) to maintain charge balance in the soil solution (Likens and Bormann 1995). Acid stress, including base cation deficiency and aluminum (Al) toxicity, can affect understory plant species differently and thus alter plant community composition, for example, through reducing the abundance of Al-sensitive species (Lu *et al.* 2010, 2014). Loss of cations can be a stress for plant species requiring high base cation supply, such as *Acer saccharum* (sugar maple) and *Cornus florida* (flowering dogwood). Furthermore, stress from cation nutrient deficiency is often associated with insect outbreaks (Horsley *et al.* 2002). Hence, the impact of N enrichment and acidification on understory plant communities is an area requiring more research for regions exposed to elevated levels of atmospheric N and S deposition.

Previous work on excess N-mediated changes in understory communities has been conducted mostly in temperate forest ecosystems, with studies on boreal forests far more limited. Previous research in the AOSR suggests that N availability and soil acidification have increased since the beginning of oil sands mining (Jung *et al.* 2013; Laxton *et al.* 2010). Chronic N deposition alleviated N limitation of forest ecosystems as indicated by the increase of N availability in soils in the AOSR (Jung *et al.* 2013). Increased foliar N concentrations in *Pinus banksiana* (jack pine) and lichen species (*Hypogymnia physodes* and *Evernia mesomorpha*) with increased annual NO_2 emission rates suggested that increased N deposition enhanced N availability in ecosystems in the AOSR (Laxton *et al.* 2010). Such increases in N availability could change the overall plant community diversity by increasing the abundance of nitrophilous species.

There is no direct evidence of S deposition effect on plant diversity; however, indirect effects of excess S on plant growth and species diversity include cation leaching, soil acidification, and Al toxicity (Lovett *et al.* 2009). Large areas in the AOSR have been reported to have S deposition in excess of critical loads (Whitfield *et al.* 2010b), although deposition rates are low compared with many other sites, including eastern North America (Vet *et al.* 2005; World Meteorological Organization 2004), the western and central parts of Europe (Vanguelova *et al.* 2007), and eastern Asia (Fujii *et al.* 2008). Soils in the AOSR have low SO_4^{2-} adsorption capacity and low weathering rates (Jung *et al.* 2011; Whitfield *et al.* 2010a), thus having a greater risk of base cation leaching which would contribute to soil acidification and eventual Al toxicity. A possible direct effect of increased S deposition is to increase soil S availability and eliminate the otherwise deficient S supply (Jung and Chang 2012) as low S availabilities are typically secondary nutrient limitations in boreal forest ecosystems (Liang and Chang 2004). Although numerous studies have examined effects of N deposition on plant diversity in temperate forest ecosystems in Europe and the United States (Bobbink *et al.* 1998; Gilliam 2006; Gundale *et al.* 2014; Hurd *et al.* 1998; Rainey *et al.* 1999), no study has investigated the effects of S deposition alone or N and S deposition combined on plant community diversity in boreal forest ecosystems.

We conducted a field experiment to simulate elevated N and S deposition rates in a less polluted area that is remote from the current center of oil sands mining and upgrading activities in AOSR, with a focus on biogeochemical and plant responses in forest ecosystems (Aber *et al.* 1998; Moore and Houle 2009). In particular, we tested the following hypotheses: (i) chronic N and S deposition would increase cation leaching and soil acidification (or Al toxicity), (ii) chronic N and S deposition would decrease cation concentrations in the soil and foliage of understory plant species, and (iii) chronic N and S deposition would decrease plant diversity and alter species composition of the understory plant community; for example, the abundance of nitrophilic species would be increased due to changes in soil chemistry in the boreal forest in northern Alberta, Canada.

MATERIALS AND METHODS

Site description and experimental design

Research plots were established in a boreal mixedwood forest stand (56.1°N, 110.9°W) located ~100 km southeast of Fort McMurray in the AOSR in northern Alberta, Canada (Jung and Chang 2012). Most of the surface mining activities and upgrading facilities in the AOSR were located north of Fort McMurray. Accordingly, our site has received minimal effects from acid deposition originating from the oil sands mining and upgrading activities. Although rates of N and S deposition at the study site were not measured directly, Proemse *et al.* (2012, 2013) measured N and S deposition in the AOSR and remote forest sites between May 2008 and 2009. The mean bulk deposition rate was 1.5 kg N ha^{-1} yr^{-1} at two sites 94 and 113 km away from the center of oil sands mining and upgrading activities, with 1.0 and 0.5 kg N ha^{-1} yr^{-1} for NH_4^+ and NO_3^-, respectively. Bulk deposition of S at the two sites was similar at ~1.2 kg S ha^{-1} yr^{-1}. Such N and S deposition rates

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are similar to Fenn (2015), who measured N and S deposition rates in AOSR between 2008 and 2011 using ion exchange resins. Distance from the oil sand mining and upgrading activities of our study site (~100 km) was similar to the two sites reported in Proemse *et al.* (2012, 2013) and Fenn (2015), and we expect that N and S deposition rates at our site were similar to theirs.

In the AOSR, the mean annual temperature was 1.0°C, with the mean relative humidity of 66% and mean annual precipitation of 418 mm from 1981 to 2010 (Environment Canada 2014). Dominant canopy tree species were ~60-year-old *Populus tremuloides* (trembling aspen) and *Picea glauca* (white spruce) between 25 and 55 years old, based on increment cores collected in 2011. Aspen and white spruce constituted 71% and 22% of the canopy trees, respectively, based on density, and dominant trees (based on tree height) were aspen. Other canopy trees found in the plots were *Abies balsamea* (balsam fir), *Populus balsamifera* (balsam poplar), *Picea mariana* (black spruce) and *Betula Papyrifera* (paper birch). The site had a medium nutrient regime and a mesic moisture regime based on ecological site classification (Beckingham and Archibald 1996). Soils were classified as Gray Luvisols based on the Canadian system of soil classification (Soil Classification Working Group 1998) or Cryralf in Soil Taxonomy (Soil Survey Staff 1994).

The experiment used a 2 × 2 factorial design with blocking. The N and S treatments each comprised two levels: 0 and 30 kg N ha^{-1} yr^{-1} (applied as NH_4NO_3), and 0 and 30 kg S ha^{-1} yr^{-1} (applied as Na_2SO_4), respectively, resulting in four treatment combinations: control (no N or S, CK), N addition (+N), S addition (+S), and N and S addition (+NS). Experimental treatments were initiated in July 2006 and continued through 2012. Granular form of NH_4NO_3 and Na_2SO_4 were broadcast applied using a manual spreader. In the first 3 years of the study, N and S were applied once a year in early summer. We changed the N and S application to three equal applications in early June, late July, and mid-August from 2009 to better simulate natural deposition during the growing season. Four blocks were established based on topographic position to ensure relatively uniform soil/site conditions and similar composition of canopy trees within each block. Each block was ~40 × 100 m in size. Four plots of 20 × 20 m in size with a 5–10 m buffer zone between plots were established in each block and the treatments were randomly assigned to the plots. Soil texture of surface mineral soil (0–15 cm) was sandy loam in two blocks and silt loam in the other two blocks. The deeper soil (15–45 cm) had greater clay content than the surface mineral soil but the texture in the deeper soil was more variable between blocks than in the surface soil.

Soil sampling and analysis

Soil samples were collected from the forest floor (LFH horizon or the O horizon in the US system) and the surface mineral soil (A horizon, 0–15 cm) in each plot in August, 2012. For each soil layer, samples were collected from three points in each plot, at the same locations used for plant sampling, and combined to form a composite sample; ~500 g of the forest floor and 2 kg of the mineral soil samples were collected from each plot. Fresh samples were sieved to pass a 2-mm screen, with coarse fragments, roots, and debris removed. Soil moisture content was determined by drying at 105°C for 24 h in a forced-air oven. To analyze available NH_4-N and NO_3-N and dissolved organic carbon (DOC) and N (DON) concentrations, fresh soil samples equivalent to 2 (forest floor) or 5 g (mineral soil) of oven-dried soil were weighed and extracted with 50 ml of 1 mol l^{-1} KCl. After filtration, concentrations of C and N in the filtrate were measured with a TOC-V_{CSN} (Shimadzu, Kyoto, Japan) and available NH_4-N and NO_3-N were determined using colorimetric methods with indophenol blue and vanadium, sulfanilamide and N-(1-naphthyl) ethylenediamine, respectively (Keeney and Nelson 1982). Extractable C was used to estimate DOC and the difference between extractable N and NH_4-N and NO_3-N was used to estimate DON. For other analysis, the remainder soil samples were air-dried. Soil pH and electrical conductivity were measured using 10 g of air-dried soil in 40 ml of deionized water for forest floor samples or 20 ml of deionized water for surface mineral soil samples. Each soil sample was further ground with a ball mill and used for total C and N analysis on a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Instruments, Milano, Italy). Exchangeable cations, including Ca^{2+}, Mg^{2+}, K^+, Na^+ and Al^{3+}, were determined after extraction with 1 mol l^{-1} NH_4Cl at a ratio of 2 g (forest floor) or 5 g (mineral soil) of soil to 100 ml extractant. After filtration, the filtrates were analyzed using an ICP-MS (Elan 6000 quadrupole, Perkin-Elmer, Inc., CT).

Plant sampling and analysis

Although the herbaceous layer of forest ecosystems is typically defined as vascular species ≤1 m in height (Gilliam 2007, 2014a), we subdivided the lower stratum into herb (≤0.5 m) and shrub (0.5–1 m) layers because of the distinctive presence of low-growing woody species at our site (Jung and Chang 2012). Three 1 × 1 m subplots were randomly established in each plot to assess the strata. Cover (%) of vegetation was estimated visually for each layer and each species in August, 2012, with species composition based on these estimates. This method is commonly used in studies of forest herb communities (see Gilliam 2007 for a review of sampling methodologies), and has recently been demonstrated to correlate closely with leaf area measurements made via destructive sampling and direct determination of specific leaf area (i.e., with a leaf area meter; Mueller-Dombois and Ellenberg 1974; Walter *et al.* 2015). Species richness was determined as the number of species in each plot. The Shannon index (H′) and the Pielou's evenness index (J) were calculated as a measure of species abundance and richness and as a measure for evenness of spread, respectively. The Shannon index was used to estimate understory species diversity in this study. Foliar samples of the following six species that were common across the plots were collected for nutrient analysis: *Rosa acicularis*,

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Viburnum edule, *Linnaea borealis*, *Cornus canadensis*, *Aralia nudicaulis* and *Petasites palmatus*. Foliar samples were oven-dried at 65°C until constant weight and ground with a ball mill. Total N was determined with a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Instruments). Each sample was digested using concentrated HNO_3 at 125°C for 4 h and 30% H_2O_2 was added to assist with the digestion. Total P, K, Ca and Mg concentrations in the digested solutions were determined with an ICP-MS (Elan 6000 quadrupole, Perkin-Elmer, Inc.).

Statistical analyses

Two-way analysis of variance (ANOVA) was performed for the 2 × 2 factorial design with blocking to determine the effects of N and S addition on soil chemistry, species richness, species diversity, species evenness, cover of plants and foliar chemistry. The Tukey's HSD test was used to test the treatment effects. Prior to the ANOVA, the normality of distribution and homogeneity of variance were checked with Kolmogorov–Smirnov and Levene's tests, respectively. The ANOVA was performed using version 9.02 of the SAS software (SAS Institute Inc, NC). If there were no interactions between N and S addition, we presented results of the main treatment (N or S addition) effects, i.e., N0 vs. N30 for the N addition treatment and S0 vs. S30 for the S addition treatment.

Two-dimensional non-metric multidimensional scaling (NMS) and permutational multivariate ANOVA (perMANOVA) were conducted to analyze the impact of N and S addition on species composition using PC-ORD (version 5.10; MjM Software, OR). The NMS ordination is a non-parametric, iterative technique that uses ranked distances to arrange value, along a number of axis determined by reducing "stress" (McCune and Grace 2002). Axis values were generated with the Bray–Curtis distance, which is appropriate to express differences in community structure (Anderson 2001), using 100 random starting configuration. We restricted the species to those that occurred in at least one quadrat in at least 3 of the 16 plots. The perMANOVA is a multivariate analysis of variance which uses permutation procedures of reshuffling treatment labels to generate a null distribution. The outputs are probabilities based on comparing the null distribution to the original F statistic obtained from the real ordering of the data relative to the treatment. Sørenson's distance was used for this test, with 4999 permutations (Anderson 2001; McCune and Mefford 2011). An α value of 0.05 was chosen to indicate statistical significance unless otherwise stated.

RESULTS

Soil chemistry

There had been little changes in soil chemistry after 7 years of N and S addition in both the forest floor and the mineral soil (Table 1). Exchangeable base cations in the forest floor were the greatest in the CK among treatments and the lowest values were found in the S addition treatment for Ca^{2+} and K^+ (Table 1). Exchangeable Ca^{2+} was greater in CK than in other treatments ($P < 0.05$) and its concentration in the +S was only 64% of that in the CK treatment. Nitrogen addition increased Al^{3+} concentration and decreased the $(Ca^{2+} + K^+ + Mg^{2+})/Al^{3+}$ ratio in the forest floor. Other soil properties in the forest floor were not significantly affected by either N or S addition. The DOC (29%) and DON (50%) were increased by N addition ($P < 0.05$) in the surface mineral soil, with no difference in inorganic N found among treatments.

Foliar chemistry of understory species

Nitrogen addition affected foliar chemistry, whereas S addition did not (Fig. 1). For individual species, the +N treatment increased foliar N concentrations in *P. palmatus* ($P < 0.05$) and *L. borealis* ($P < 0.01$); however, their cover was reduced by N addition (Fig. 3). For these species, foliar N concentrations increased by 15–16% in +N than in CK and by 10–13% in +NS than in +S. Nitrogen addition decreased foliar phosphorus (P) in *R. acicularis* ($P < 0.01$), *V. edule* ($P < 0.05$), *C. canadensis* ($P < 0.05$) and *A. nudicaulis* ($P < 0.05$). Nitrogen addition also reduced foliar potassium (K) in *V. edule* ($P < 0.05$) and *A. nudicaulis* ($P < 0.05$). Nitrogen addition, however, did not affect foliar P and K in *P. palmatus* and *L. borealis*.

Understory community

There were no differences in species richness, evenness, diversity, % cover and composition in either the shrub or herb layer in 2005, prior to application of the N and S (Fig. 2; Table 3). According to NMS ordination, data of each treatment overlapped each other in both shrub (Fig. 4A) and herb (Fig. 4C) layers, indicating that understory species composition was not different among treatments before the N and S addition treatments commenced. Species richness in the shrub layer was similar between 2012 and 2005, whereas in the herb layer species richness increased regardless of the treatment. Species evenness and overall diversity increased over time in all treatments, including the control, in both layers (Fig. 2).

Species richness in the shrub layer was decreased by 7 years of S addition ($P < 0.05$) although not affected by N addition (Fig. 2; Table 3). Species evenness and overall diversity in the shrub layer were decreased by both N ($P < 0.05$) and S addition ($P < 0.01$), leading to the lowest diversity and evenness in +NS, which was ~64% that in the CK (Fig. 2). Based on perMANOVA, the total shrub cover was decreased ($P < 0.05$; Fig. 3A) by S addition and species composition in the shrub layer was influenced by N ($P < 0.05$) and S addition ($P < 0.05$). In particular, the % cover of *V. edule* was decreased by both N ($P < 0.05$) and S ($P < 0.05$) addition (Table 2), resulting in % cover of *V. edule* in +NS being only 13% that in CK. Nitrogen and S addition decreased the % cover of *C. canadensis* ($P < 0.05$) and *Vaccinium myrtilloides* ($P < 0.05$), respectively. The NMS ordination explained 95% of variation in the data, with a stress of 7.0 for the shrub layer and clustering of treatments; samples of +NS were more tightly clustered than samples of other treatments (Fig. 4B).

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Table 1: soil properties in the forest floor and the surface mineral soil in a mixedwood boreal forest in the Athabasca oil sands region in northern Alberta, Canada

										Exchangeable cations				
			Total C	Total N		NH_4-N	NO_3-N	DOC	DON	Ca^{2+}	Mg^{2+}	K^+	Al^{3+}	$(Ca^{2+} + K^+ + Mg^{2+})/Al^{3+}$
Treatment	pH	EC (dS m^{-1})	(g kg^{-1})		C:N	(mg kg^{-1})				(cmol kg^{-1})				
Forest floor														
CK	5.7 (0.4)	1.3 (0.3)	348 (43)	19 (2.4)	19 (0.3)	346 (104)	70 (7.9)	3326 (705)	755 (65)	47 (7.9)	9.0 (1.1)	3.1 (0.4)	0.03 (0.01)	2300.5 (396.0)
+N	5.5 (0.1)	0.8 (0.2)	354 (27)	18 (1.2)	19 (0.5)	389 (105)	65 (15.5)	3720 (896)	690 (162)	37 (2.7)	7.5 (1.1)	2.8 (0.2)	0.05 (0.02)	1458.5 (512.8)
+S	5.7 (0.1)	1.4 (0.5)	326 (53)	16 (2.1)	20 (0.7)	433 (140)	48 (12.3)	3582 (1203)	904 (187)	30 (1.4)	6.0 (0.4)	2.4 (0.3)	0.02 (0.00)	2291.5 (192.8)
+NS	5.6 (0.2)	1.0 (0.1)	338 (37)	17 (1.6)	20 (0.6)	320 (100)	75 (7.1)	3533 (852)	796 (85)	33 (5.1)	6.7 (1.5)	2.2 (0.2)	0.03 (0.01)	1783.3 (601.7)
Two-way ANOVA (*P* value)														
N	0.68	0.18	0.83	0.93	0.56	0.61	0.16	0.65	0.66	0.53	0.70	0.51	0.05	0.02
S	0.84	0.68	0.66	0.31	0.10	0.89	0.61	0.84	0.54	0.05	0.11	0.04	0.08	0.52
N × S	0.84	0.76	0.94	0.72	0.44	0.26	0.15	0.81	0.46	0.21	0.33	0.87	0.68	0.50
Surface mineral soil														
CK	4.4 (0.1)	0.07 (0.02)	6.8 (0.3)	0.2 (0.1)	44 (12)	6.3 (0.7)	4.0 (0.5)	99 (4)	14 (3)	2.6 (0.1)	0.67 (0.08)	0.34 (0.07)	0.19 (0.04)	25.4 (9.8)
+N	4.3 (0.2)	0.04 (0.00)	6.8 (0.9)	0.3 (0.1)	40 (13)	6.4 (2.3)	2.8 (1.3)	126 (5)	19 (7)	2.0 (0.1)	0.53 (0.06)	0.22 (0.03)	0.39 (0.10)	9.8 (3.6)
+S	4.4 (0.1)	0.06 (0.01)	7.0 (0.8)	0.6 (0.1)	13 (3.8)	5.6 (0.8)	3.3 (1.2)	86 (14)	13 (5)	2.1 (0.3)	0.55 (0.06)	0.33 (0.08)	0.43 (0.14)	11.9 (5.1)
+NS	4.5 (0.1)	0.10 (0.01)	7.7 (0.9)	0.5 (0.2)	20 (6.7)	6.9 (0.6)	3.4 (0.7)	130 (23)	23 (6)	2.1 (0.4)	0.52 (0.06)	0.28 (0.11)	0.41 (0.13)	18.1 (12.8)
Two-way ANOVA (*P* value)														
N	0.86	0.98	0.64	0.74	0.86	0.39	0.09	0.02	0.02	0.20	0.22	0.28	0.45	0.60
S	0.64	0.06	0.51	0.01	0.02	0.15	1.00	0.69	0.60	0.38	0.36	0.74	0.28	0.77
N × S	0.28	0.07	0.66	0.44	0.55	0.23	0.85	0.51	0.51	0.22	0.42	0.67	0.36	0.24

Values are mean (standard error) ($n = 4$).

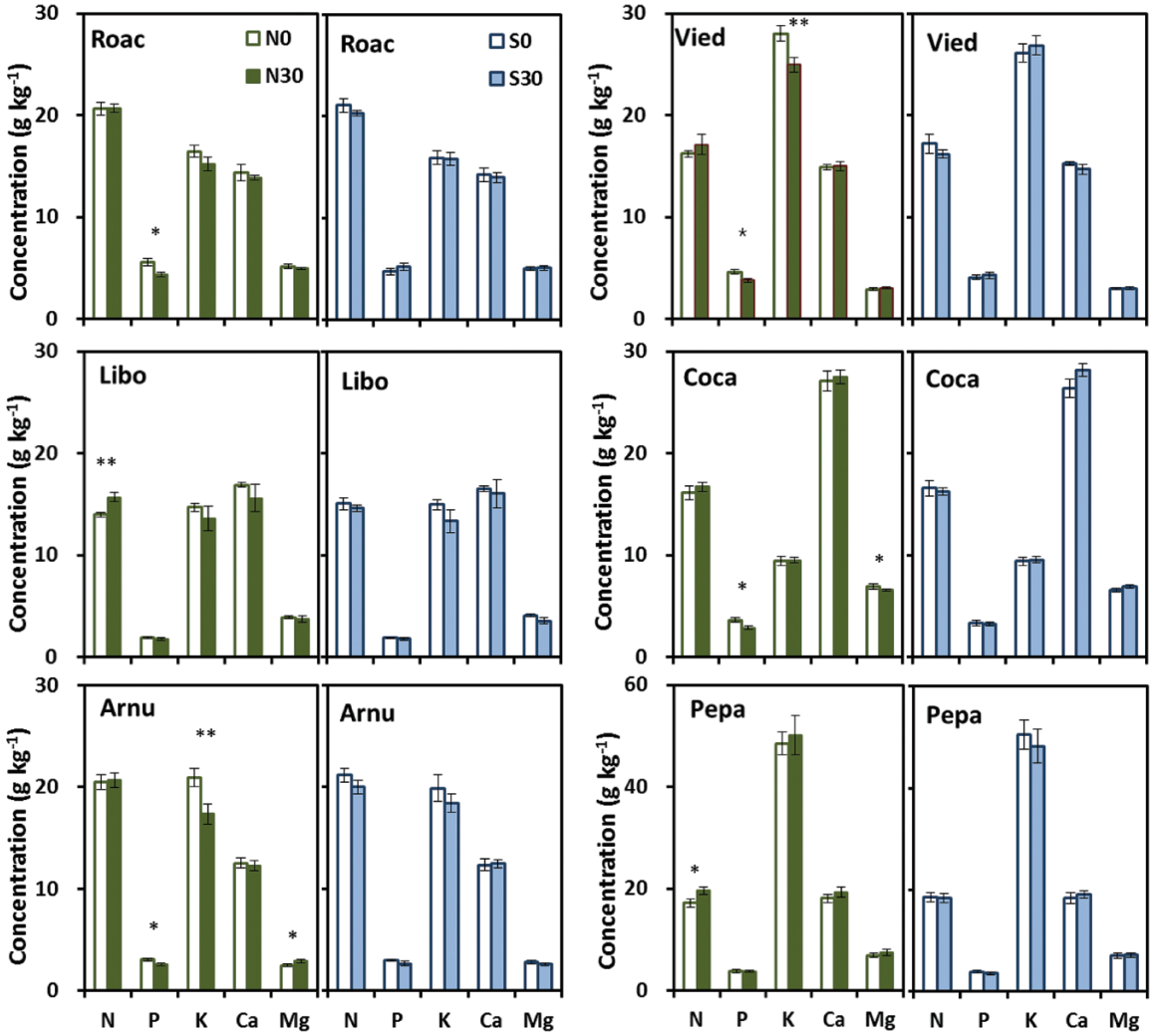

Figure 1: changes in foliar chemistry of understory species in response to N and S addition in a mixedwood boreal forest in northern Alberta, Canada: Roac (*Rosa acicularis*), Vied (*Viburnum edule*), Libo (*Linnaea borealis*), Coca (*Cornus canadensis*), Arnu (*Aralia nudicaulis*) and Pepa (*Petasites palmatus*). Vertical bars are standard error of the mean ($n = 4$). Asterisks indicate significant differences between treatments for each nutrient and species (*$P < 0.05$; **$P < 0.01$).

Species richness, evenness, and diversity in the herb layer were not affected by the treatments (Fig. 2; Table 3). No difference in total cover of the herb layer was found between treatments, whereas effects of N and S addition on % cover varied among species (Fig. 3B). Nitrogen addition increased the % cover of *A. nudicaulis* ($P < 0.01$), *Maianthemum canadense* ($P < 0.05$) and *Equisetum arvense* ($P < 0.05$), while decreasing the % cover of *L. borealis* ($P < 0.01$), *Lathyrus venosus* ($P < 0.05$) and *P. palmatus* ($P < 0.01$); significant interactions between N and S addition were found for *L. borealis* ($P < 0.05$) and *P. palmatus* ($P < 0.05$; Table2; Fig. 3). Sulfur addition increased the % cover of *P. palmatus* ($P < 0.05$), while reducing the % cover of *Trientalis borealis* ($P < 0.05$) and *Pyrola secunda* ($P < 0.05$; Table 2; Fig. 3). The 2-dimensional NMS ordination explained 91% of variation in the data for the herb layer, with a stress of 9.9. The NMS ordination showed variation of the species composition of the plant community in the herb layer between and within treatments (Fig. 4D). Sample points for +N and +NS were clearly separated from CK (Fig. 4D), indicating that the plant community composition was changed by N and S deposition. The perMANOVA also indicated that N addition affected species composition in the herb layer based on the % cover of each species ($P < 0.01$).

DISCUSSION

Effects of N and S deposition on soil chemistry

Seven years of simulated N and S deposition did not cause soil acidification in either the forest floor or the mineral soil, rejecting our first hypothesis. Soil pH was not significantly different among the treatments and, although the $(Ca^{2+} + K^{+} + Mg^{2+})/Al^{3+}$ ratio was decreased by the +N treatment, soil pH was still high, even higher than the response threshold (Table 1). These results indicate that either the amount of

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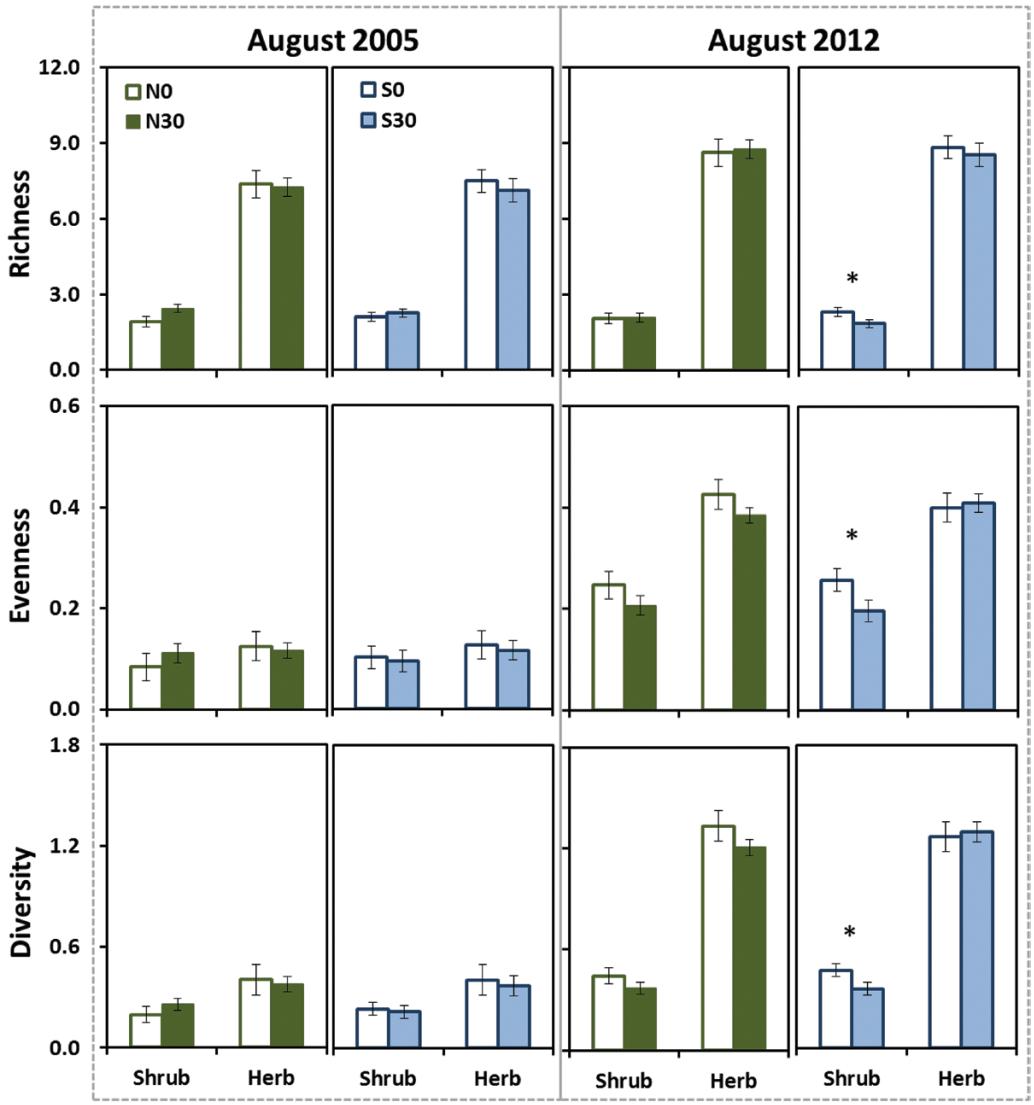

Figure 2: changes in species richness, Shannon diversity index and evenness in the shrub and herb layers in response to N and S addition in a mixedwood boreal forest in northern Alberta, Canada. Vertical bars are standard error of the mean ($n = 4$). Asterisks indicate significant differences between treatments within each vegetation layer ($*P < 0.05$).

applied N and S or the 7-year study period was insufficient to affect soil properties. Several earlier studies conducted at the same research plots (Cheng *et al.* 2011; Hu *et al.* 2013; Jung and Chang 2012) found no differences in soil properties among the treatments, consistent with the current study. Several studies that applied higher rates of N or for longer periods reported soil acidification. For example, 5.5 years of simulated N deposition (as NH_4NO_3) at 66 and 198 kg N ha^{-1} yr^{-1} decreased soil pH to 4.07 and 3.81, respectively, from 4.51 in the control soil in a *Fagus sylvatica* forest (Bergkvist and Folkeson 1992), and 6 years of N addition at 100 and 150 kg ha^{-1} yr^{-1} decreased soil pH in the upper 30 cm mineral soil in a tropical forest in China (Lu *et al.* 2014).

Despite the addition of N as NH_4NO_3 for 7 years, neither NH_4^+ nor NO_3^- concentrations in the soil were affected, likely related to the uptake of available N in these N-limited soils by plants (Jung *et al.* 2011; Whitfield *et al.* 2010a) and N immobilization by microbes (Hari and Kulmala 2008; Tietema 1998). Increased tree growth by elevated N deposition (Jung *et al.* 2011; Whitfield *et al.* 2010a) and increased N concentrations in most understory species (Fig. 1) may result in similar NH_4^+ and NO_3^- concentrations in soils between the N addition and the control plots. Leaching loss in soils in the AOSR can be greater than that in other forest ecosystems (Jung *et al.* 2011; Whitfield *et al.* 2010a). Increased DOC and DON concentrations in surface mineral soils is attributable to leaching of DOC and DON from the forest floor, as the increased amount of litter fall could induce leaching of DOC and DON from the forest floor.

It is well established that S deposition can increase base cation leaching, soil acidity, and Al toxicity (Likens and Bormann 1995). In this study, S deposition decreased Ca^{2+} and K^+

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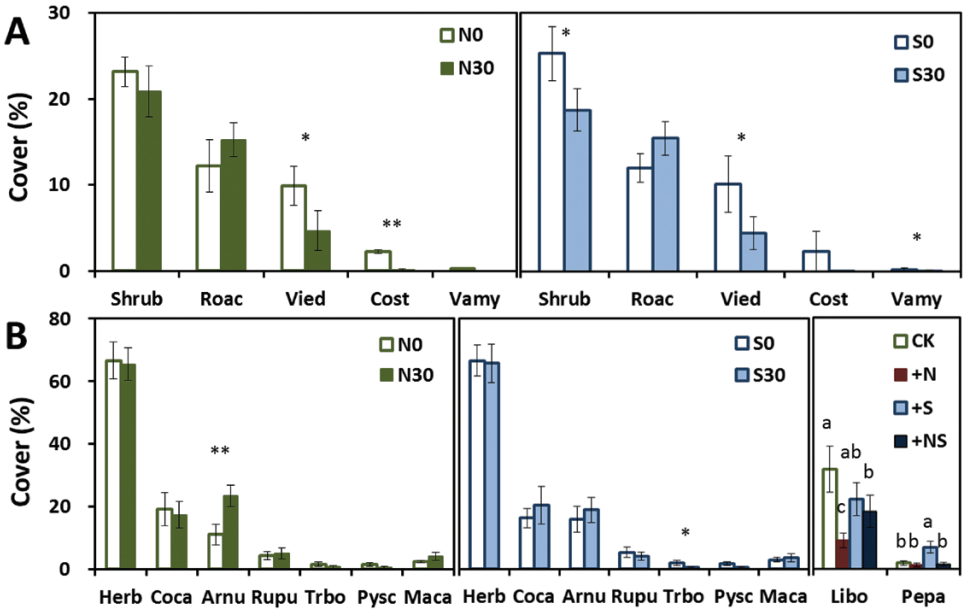

Figure 3: changes in the % cover of understory plants in (**A**) the shrub layer and (**B**) the herb layer in response to N and S addition in a mixed-wood boreal forest in northern Alberta, Canada: Roac (*Rosa acicularis*), Vied (*Viburnum edule*), Cost (*Cornus stolonifera*), Vamy (*Vaccinium myrtilloides*), Libo (*Linnaea borealis*), Coca (*Cornus canadensis*), Arnu (*Aralia nudicaulis*), Rupu (*Rubus pubescens*), Trbo (*Trientalis borealis*), Pyse (*Pyrola secunda*), Maca (*Maianthemum canadense*) and Pepa (*Petasites palmatus*). Vertical bars are standard error of the mean ($n = 4$). Different lowercase letters and asterisks indicate significant differences between treatments for each species/vegetation layer (*$P < 0.05$; **$P < 0.01$).

concentrations in the forest floor (Table 1). Soils in the AOSR have low adsorption capacity of SO_4^{2-} (Jung *et al.* 2011); thus, we expected that 7 years of S additions would significantly affect cation concentrations and soil pH. Experimental additions of S in this study, however, did not change soil pH, although cation concentrations decreased. This suggests that more time will be required to cause soil acidification with the current rate of S deposition at the studied site.

Effects of N and S deposition on foliar chemistry

Foliar chemistry exhibited species-specific responses to N and S deposition in this study. Nitrogen addition decreased nutrient content relative to N in understory species, supporting our second hypothesis. Addition of N increased foliar N concentration while decreasing foliar P and K concentrations in several species (Fig. 1). Long-term studies have demonstrated that chronic N deposition or repeated N fertilization in forest ecosystems may increase the risk of nutrient imbalance or deficiency of other nutrients in the ecosystem (Aber *et al.* 1989; Gilliam *et al.* 2016a; Skeffington and Wilson 1998). Nitrogen-enhanced plant growth increases the demand for other nutrients, such as P and K (Erisman and de Vries 2000), exacerbating growth limitation by these nutrients in forest ecosystems, decreasing foliar nutrient concentrations. In contrast to the effect of N addition, S addition did not alter the ratio of $(Ca^{2+} + K^{+} + Mg^{2+})/Al^{3+}$ in soils or foliar chemistry, even for *V. edule*, contrary to expectations of our second hypothesis, and inconsistent with the general expectation that S deposition induces adverse effects on plant growth due to deficiency of cationic nutrients or Al toxicity. Accordingly, future research should examine more closely the effect of S deposition on understory species.

Effects of N and S deposition on the understory communities

Additions of N and S in this study changed the % cover of the shrub layer, but not that of the herb layer (Fig. 3) and altered understory community composition (Fig. 4), supporting our third hypothesis. Nitrogen addition did not change the total % cover of the shrub layer in the study, but decreased the % cover of *V. edule* and *Cornus stolonifera* due to the increased competition for N between understory species and canopy trees by N addition (Jung and Chang 2012) reflects the N limitation in boreal forest ecosystems (Jung and Chang 2012). A number of studies, consistent with this study, reported that increased N availability in ecosystems with N deposition decreased the biomass, cover and diversity of understory plants in forests in USA and Sweden (Gilliam 2006; Gundale *et al.* 2014; Hurd *et al.* 1998; Rainey *et al.* 1999) and decreased understory plant species diversity (Gilliam *et al.* 2016b; Strengbom *et al.* 2001), even though tree growth increased (Aber *et al.* 1998; Jung and Chang 2012). Improved tree growth by N addition at the same research site (Jung and Chang 2012) may decrease the growth of understory species by increased competition for N between understory species and canopy trees and increased canopy cover intercepts more light, although the effect of reduced light availability on understory plant growth is an indirect effect. The response of understory species diversity to experimental N addition varies with duration of the treatment, rate of N addition and soil N status. For example, no

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Table 2: the % cover of individual species in the shrub and herb layers in the control plots and responses to N and S addition in a mixedwood boreal forest in the Athabasca oil sands region in northern Alberta, Canada

Layer	Plant species name (common name)	Cover (%)[a]	N^b	S^b
Shrub	*Rosa acicularis* (prickly rose)	11.8 (1.2)		
	Viburnum edule (low bush cranberry)	12.6 (1.5)	–	–
	Cornus stolonifera (dogwood)	4.6 (1.6)		
	Vaccinium myrtilloides (Canadian blue berry)	0.4 (0.2)	–	
	Rhododendron groenlandicum (Labrador tea)	<0.1 (0.0)		
	Symphoricarpos occidentalis (snowberry)	<0.1 (0.0)		
Herb	*Linnaea borealis* (twinflower)	31.8 (3.6)	–	
	Cornus canadensis (bunchberry)	17.3 (1.6)		
	Aralia nudicaulis (wild sarsaparilla)	8.6 (1.6)	+	
	Rubus pubescens (dewberry)	4.8 (0.4)		
	Trientalis borealis (Northern starflower)	2.7 (0.5)		–
	Epilobium angustifolium (fireweed)	2.6 (0.8)		
	Pyrola secunda (one-sided wintergreen)	2.5 (0.6)		–
	Maianthemum canadense (Canadian May-lily)	2.1 (0.3)	+	
	Mertensia paniculata (tall lungwort)	2.1 (0.4)		
	Petasites palmatus (palmate coltsfoot)	1.9 (0.4)	–	+
	Lathyrus venosus (purple peavine)	1.8 (0.3)	–	
	Arctostaphylos uva-ursi (bearberry)	1.7 (0.8)		
	Galium boreale (North bedstraw)	1.1 (0.2)		
	Fragaria virginiana (smooth wild strawberry)	0.9 (0.3)		
	Aster ciliolatus (Lindley's aster)	0.7 (0.2)		
	Circaea alpine (Alpine enchanter's nightshade)	0.3 (0.1)		
	Equisetum arvense (field horsetail)	<0.1 (0.0)	+	
	Achillea millefolium (yarrow)	<0.1 (0.0)		
	Erigeron philadelphicus (Philadelphia fleabane)	<0.1 (0.0)		
	Aster puniceus (purple-stemmed aster)	<0.1 (0.0)		
	Disporum trachycarpum (fairybells)	<0.1 (0.0)		
	Lycopodium obscurum (ground pine)	<0.1 (0.0)		

[a]Values are mean (standard error) ($n = 4$).
[b]The signs of + and – indicate increase and decrease of cover, respectively.

significant response of the herb layer to 5 years of N addition to an entire watershed was found in a central Appalachian hardwood forest (Gilliam 2006), but species diversity in the herb layer significantly declined after 14 years (Gilliam 2014c; Thomas *et al.* 1999), and further declined after 25 years of N addition (Gilliam *et al.* 2016b). Seven years of N addition (50 and 150 kg N ha^{-1} yr^{-1}) to the forest floor of *Pinus resinosa* stands in the Harvard Forest in western Massachusetts decreased the density and biomass of species in the herb layer by 80 and ~90%, respectively (Rainey *et al.* 1999). Changes in understory species diversity by experimental N addition were more pronounced at a site with a lower ambient input of atmospheric N (Gilliam 2006; Hurd *et al.* 1998). These studies are conducted in temperate forest ecosystems and there have been few studies conducted in boreal forests that can be used to compare with our results. Results of this study suggest that long-term elevated levels of N deposition would change understory species diversity and composition in temperate and boreal forest ecosystems. However, results from this and earlier studies are site-specific; therefore, more research is needed in boreal forests to further understand the response of understory species diversity to N deposition.

The % cover of the herb layer was not significantly changed by N addition, again likely arising from the insufficient duration and/or amount of N addition relative to studies reviewed earlier in this paper. In addition, however, some of this lack of apparent response may have arisen from the mixed effects of N addition on the cover of different species. For example, although the % cover of *L. borealis* and *P. palmatus* decreased, the % cover of *A. nudicaulis* and *M. canadense* increased (Table 2). Species evenness and diversity decreased significantly with the addition of N in the shrub layer but not in the herb layer. *Linnaea borealis* is adapted to nutrient-poor sites and *Petasites* congeners (e.g. *Petasites albus* and *Petasites fragrans*) are adapted to medium N availability (Hill *et al.* 1999). Increased N deposition may decrease the % cover of *L. borealis* and *P. palmatus* via direct toxicity of NH_4^+ on plant roots or competition from nitrophilic species. Decreased % cover of

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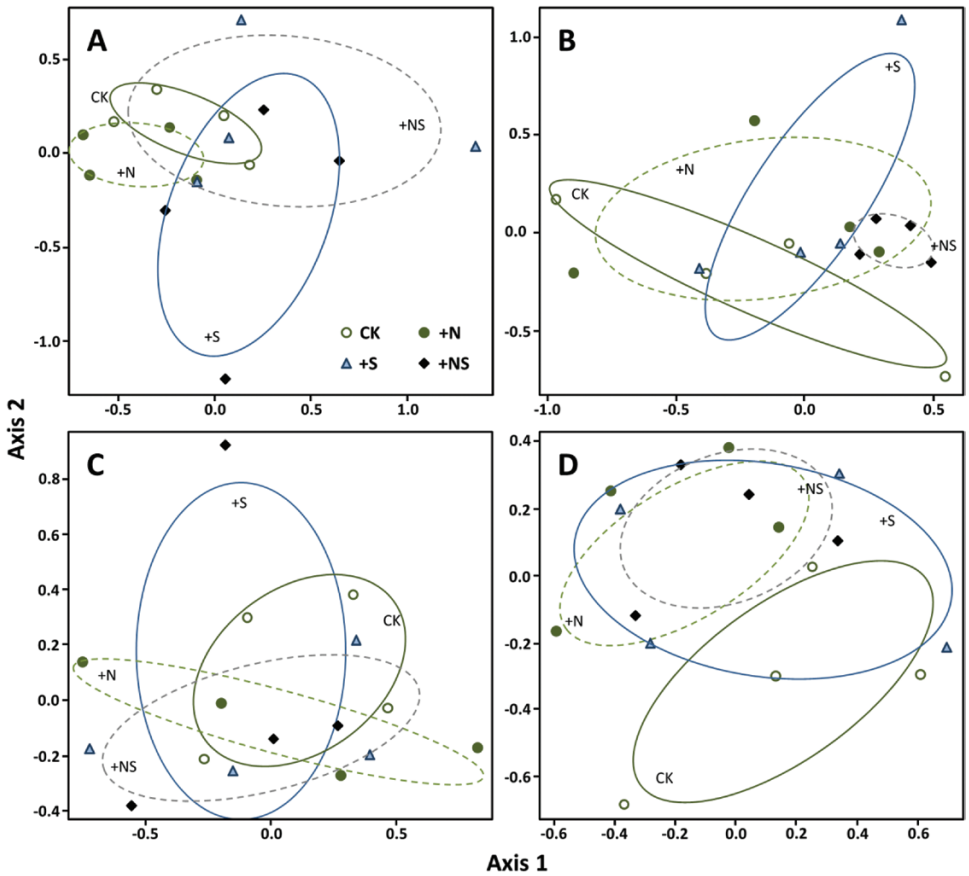

Figure 4: the NMS ordination for cover of understory plant species in the shrub layer (**A**) in 2005 and (**B**) in 2012 and the herb layer (**C**) in 2005 and (**D**) in 2012 in a mixedwood boreal forest in the Athabasca oil sands region in northern Alberta, Canada. The ordination was based on four samples per treatment and 6 species for the shrub layer and 23 species for the herb layer.

P. palmatus might not be affected by light availability because *P. palmatus* is a very shade tolerant species (Brian 2014). These results suggest that (i) N deposition likely decreased the % cover of the shrub layer via increased competition for N availability with canopy trees, rather than alleviating N limitation and (ii) the shrub layer was more vulnerable to N deposition than the herb layer. Considering the elevated level of chronic N deposition occurring in the AOSR (Fenn 2015; Hazewinkel *et al.* 2008), N-mediated decreases in cover, species evenness, and species diversity of the shrub layer would be a major concern for the integrity of forest ecosystems in the region.

The S-meditated decreases in % cover, evenness, and species diversity in the shrub layer support our third hypothesis, and likely arose from decreased cation concentrations, such as Ca^{2+} and K^{+}, in the forest floor. Sulfur deposition rarely affects plant growth or species composition directly, but does so through increasing cation leaching and soil acidification (Lovett *et al.* 2009). Chronic S deposition has been reported to accelerate leaching loss of base cations as they accompany SO_4^{2-} leaching (Bouwman *et al.* 2002). Because the SO_4^{2-} adsorption capacity in soils in the AOSR is relatively low compared to soils in other regions, soils in AOSR are sensitive to leaching loss of SO_4^{2-} ions and base cations (Jung *et al.* 2011; Whitfield *et al.* 2010a). Therefore, reduced soil nutrient cation concentrations caused by elevated levels of S deposition could increase the relative abundance of acid-tolerant species (Brunet *et al.* 1998; van Dobben and de Vries 2010), while the abundance of other species may decrease. Decreased cover of *V. edule* by S and N addition likely resulted from N-mediated increases in N availability and decreases in light availability and S-mediated decreases in base cation concentrations, suggesting that *V. edule* may serve as an indicator species for studying the impact of atmospheric N and S deposition in the AOSR.

Addition of N and S did not affect the % cover and indices of diversity in the herb layer (Figs. 2 and 3). The NMS ordination analysis, however, showed that samples were grouped by N and S addition, indicating that N and S addition segregated the understory plant communities (Fig. 4). Chronic N deposition has been shown to decrease the abundance of species adapted to environments with a low N supply and increase the abundance of nitrophilous species in the field layer (height < 1.5 m) in southern Swedish oak forests (Brunet *et al.* 1998), in the herb layer of western Ukraine spruce forests (Hruška *et al.* 2012) and in the herb layer of Appalachian hardwood forests in the USA (Gilliam *et al.* 2016b). Our results showed that *L. borealis*, *P. palmatus* and *L. venosus* were vulnerable to

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Table 3: probability representing the effect of N and S addition on the richness, evenness, diversity and % cover by ANOVA and on understory composition by permutational MANOVA

Layer	Factor	Richness	Evenness	Diversity	Cover	Composition
Before N and S application (2005)						
Shrub	N	0.23	0.17	0.18	0.22	0.29
	S	0.50	0.57	0.57	0.47	0.09
	N × S	0.54	0.55	0.05	0.23	0.12
Herb	N	0.08	0.72	0.72	0.50	0.17
	S	0.45	0.49	0.49	0.98	0.77
	N × S	0.80	0.58	0.57	0.80	0.21
Seven years after N and S application (2012)						
Shrub	N	0.85	0.05	0.05	0.85	0.01
	S	0.04	0.01	0.01	0.04	0.02
	N × S	0.56	0.57	0.59	0.28	0.38
Herb	N	0.83	0.17	0.17	0.82	0.01
	S	0.61	0.75	0.75	0.60	0.17
	N × S	0.94	0.78	0.79	0.94	0.53

N deposition, whereas *A. nudicaulis* and *M. canadense* were nitrophilous species. Increased foliar N concentration but decreased cover of vulnerable species suggests that they were not adapted to the increased N availability. On the other hand, the increased cover of nitrophilous species indicate that they benefited from the increased N availability, even though N addition decreased foliar P and K concentrations in *A. nudicaulis* (Fig. 1).

CONCLUSION

Elevated levels of N and S deposition changed the understory plant community in the AOSR. Based on diversity and evenness indices analyzed through NMS ordination and perMANOVA, 7 years of N and S addition resulted in decreased plant diversity in the shrub layer in the AOSR. Furthermore, potential risk of nutrient imbalance, such as P and K deficiency, could be caused by long-term chronic N deposition. *V. edule* was a sensitive species that responded to both N and S addition and could serve as an indicator species to determine the impact of N and S deposition on understory plant communities in the AOSR. Considering that the current rates of N and S deposition in northern Alberta are much lower than rates used in this study, it will likely take a long time for forest ecosystems to develop a negative response to N and S deposition. However, N and S deposition rates are much higher near oil sands mining areas, such that forest ecosystems would be more vulnerable to N and S deposition in those areas. Therefore, close monitoring is required to determine the impact of N and S deposition in vulnerable locations.

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