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Influence of Two N-Fixing Legumes on Plant Community Properties and Soil Nutrient Levels in an Alpine Ecosystem

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Abstract

Low nitrogen (N) supply is a limiting factor for plant growth in most terrestrial ecosystems. N-fixing legumes therefore have the potential to facilitate surrounding vegetation by increasing soil N levels. This effect should be especially pronounced in low-productivity habitats where ambient soil N levels are low, such as in alpine areas. We examined whether plant species composition, community diversity measures, and soil N levels differed with and without the presence of two alpine legumes, *Oxytropis lapponica* (Wahlenb.) Gay and *Astragalus alpinus* L., in a *Dryas octopetala* heath at Finse, Norway. Species composition and richness differed between plots with and without *Oxytropis* in one of two study sites, as other plant species were positively associated with the legume. None of the measured community properties differed between plots with and without the presence of *Astragalus*. The contrasting influence of the two legume species corresponds to our findings of higher soil N levels below *Oxytropis*, but not *Astragalus*. Differences in microhabitat N levels may explain why only *Oxytropis* acts as a facilitator. By affecting local species composition *Oxytropis* increases spatial heterogeneity, which may increase total species richness of the ecosystem.

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Introduction

Positive interactions among species, or facilitation, are fundamental processes in plant communities (Callaway 1995). Facilitation not only affects the growth and survival of individual plants, but may also cascade into community-wide effects. Nitrogen (N)-fixing legumes have a great potential as facilitators, as low soil N levels limit plant growth in many terrestrial ecosystems. N fixation gives legumes a competitive advantage where soil N levels are low (e.g. Vitousek and Field, 1999), but may also increase soil N levels through leaf leaking of soluble compounds, root exudates, decomposition of N rich litter (Høgh-Jensen, 2006, and references therein), and reduced competition for N (Temperton et al., 2007), thereby positively affecting other species of the plant community.

Legumes have been found to increase soil N levels in a variety of ecosystems (e.g. Tiedemann and Klemmedson, 1973; Fornara and Tilman, 2008; Halvorson and Smith, 2009). This positive effect of legumes on soil N levels may result in increased growth (e.g. Jefferies et al., 1981; Pugnaire et al., 1996; Rodríguez-Echeverría and Pérez-Fernándes, 2003) and fertility (Morris and Wood, 1989; Pugnaire et al., 1996) of neighboring plants, which may in turn influence plant community structure and composition. For instance, the presence of legumes may affect the course of succession (Halvorson et al., 1991; Bellingham et al., 2001; del Moral and Rozzell, 2005), and legumes can facilitate alien plant species, thereby indirectly changing the native community composition (Maron and Connors, 1996; Maron and Jefferies, 1999; Carino and Daehler, 2002). A few studies have also examined how legumes influence the distribution of plants in non-successional native plant communities, with results ranging from positive (Perroni-Ventura et al., 2006) to neutral (Thomas and Bowman, 1998; Rossi and Villagra, 2003) to negative (Rodríguez-Echeverría and Pérez-Fernándes, 2003) effects on plant species richness, diversity, and evenness.

The positive effects of legumes on soil N levels may be especially pronounced in low-productivity habitats where ambient soil N levels are low (Belsky et al., 1993; Pugnaire and Luque, 2001), implying that legumes may act as facilitators in alpine areas where low biomass production and low decomposition rates limit the supply of nutrients, including N (e.g. Bliss, 1971). Alpine legumes fix significant amounts of N (Granhall and Lid-Torsvik, 1975; Johnson and Rumbaugh, 1986; Bowman et al., 1996; Jacot et al., 2000), thereby increasing soil N levels (Kenny and Cuany, 1990; Thomas and Bowman, 1998; but see Wolf et al., 2004) and potentially affecting alpine plant communities. However, we know of only two studies, Thomas and Bowman (1998) and Jacot et al. (2005), that examined the effects of legumes on alpine plant community diversity and composition. Thus, our knowledge of the influence of alpine legumes on community properties is limited.

In this study we examined whether plant species composition, community diversity measures, and soil N levels (total N, NH_4^+-N, NO_3^--N) differed with and without the presence of two alpine legumes, *Oxytropis lapponica* (Wahlenb.) Gay and *Astragalus alpinus* L., in a *Dryas octopetala* heath at Finse, Norway. Moreover, we examined whether the richness and cover of different functional groups differed with and without a legume present, and whether the two legume species had similar effects on community properties and soil N levels.

Materials and Methods

STUDY AREA AND STUDY SPECIES

Field work was conducted during the summers of 2008 and 2009 at Finse (60°36′59″N, 07°31′23″E) in the alpine region of

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southwest Norway. Finse has a slightly oceanic climate (Moen, 1998) with a mean monthly temperature and rainfall during the growing season (May–September) of 4.4 °C and 89 mm, respectively (Norwegian Meteorological Institute, 2010). The study area is located on the southwest slope of Mount Sanddalsnuten (peak at 1554 m a.s.l.), where the phyllitic bedrock supports a species-rich *Dryas octopetala* heath. The study was conducted in three sites (10 × 10 m) situated along the slope of Mount Sanddalsnuten: a low-elevation site (1460 m a.s.l.), a mid-elevation site (1510 m a.s.l.), and a high-elevation site (1554 m a.s.l.). The locations of the sites were chosen according to where the two study species occurred: *Astragalus alpinus* was present in the low- and high-elevation sites, while *Oxytropis lapponica* was present in the mid- and high-elevation sites. In the high-elevation site the two species grow intermingled. The low- and mid-elevation sites were fenced to prevent disturbance by sheep occasionally visiting these sites. Sheep very rarely occur in the high-elevation site.

The vegetation in the mid- and high-elevation sites is typical of *Dryas* heath communities. In addition to the dominant *Dryas octopetala*, the most common vascular plant species are *Astragalus alpinus*, *Bartsia alpina*, *Bistorta vivipara*, *Carex rupestris*, *C. vaginata*, *Festuca vivipara*, *Oxytropis lapponica*, *Potentilla crantzii*, *Salix herbacea*, *S. reticulata*, *Saussurea alpina*, *Silene acaulis*, and *Thalictrum alpinum*. Both sites are found on exposed ridges, with the high-elevation site being situated at the peak of Mount Sanddalsnuten. The substrate in these sites is mainly mineral soil, and patches of gravel and bare rock are frequent. The low-elevation site differs from the other two by being less exposed and more productive. In addition to the typical *Dryas* heath species, the vegetation consists of species characteristic of more protected habitats, such as *Carex capillaris*, *Festuca ovina*, *Parnassia palustris*, *Selaginella selaginoides*, *Tofieldia pusilla*, and *Vaccinium uliginosum*. The vegetation cover is continuous, and the mineral soil is covered by a several-centimeter-thick organic layer.

Astragalus alpinus and *Oxytropis lapponica* are both perennial, herbaceous legumes. *Astragalus* grows in many types of alpine plant communities, while *Oxytropis* is restricted to calcareous, but barren, ridges and slopes as well as *Dryas* heaths (Lunde, 1962). The mean vegetation height in the study area is approximately 2 cm (Klanderud and Totland, 2005a; Nybakken et al., 2011), and the legumes rarely grow taller than this (personal observation). Both *Astragalus* spp. and *Oxytropis* spp. fix N in arctic and alpine areas (Granhall and Lid-Torsvik, 1975; Karagatzides et al., 1985; Johnson and Rumbaugh, 1986; Schulman et al., 1988; Makarov et al., 2011) and should therefore have the potential to increase soil N levels in the study area. Nodules of both species were pink inside (personal observation) indicating active N fixation (Sprent, 1989).

Nomenclature follows Lid and Lid (2005).

STUDY DESIGN AND CHEMICAL ANALYSES

To examine whether nutrient levels differed in soil from below and outside legumes, we collected 40 pairs of soil samples in August 2008. Each pair consisted of one sample taken from the soil below a fully grown legume and one soil sample taken 30–100 cm away from that legume and at least 30 cm away from any other legume. In the low-elevation site we collected 10 soil sample pairs from below and outside *Astragalus*; in the mid-elevation site 10 pairs from below and outside *Oxytropis*; and in the high-elevation site 10 pairs from below and outside each of the legume species. Soil was collected within a quadrat of 15 × 15 cm to a depth of 15 cm. All nodules were removed and counted, and the soil was thoroughly mixed and kept frozen until analyses were performed.

In the laboratory the soil samples were thawed, dried at 40 °C overnight, and sieved (2 mm). Inorganic N was extracted from 10 g subsamples with 40 mL 1 M KCl, and the extracts were filtered (Whatman no. 42) and frozen. From the extracts exchangeable soil NH_4^+-N (mg/kg) content was determined colorimetrically using the phenol-hypochlorite method (Zolórzano, 1969), while soil NO_3^--N (mg/kg) content was determined by flow injection analysis. Total N and total carbon (C) content (%) were determined from subsamples of 0.5 g finely ground soil using the Dumas method (Bremmer and Mulvaney, 1982) and dry combustion (Nelson and Sommers, 1982), respectively. Plant available phosphorus (P) was extracted from 2 g subsamples with 40 mL Al solution (0.1 M NH_4^+-lactate + 0.4 M acetic acid, adjusted to pH 3.75). The extracts were filtered (Whatman no. 589/3, Blue ribbon), and soil P content was determined using the P-Al method (Egnér et al., 1960). Soil pH was measured from a suspension of 10 mL dry soil in 25 mL deionized water that had been shaken and left overnight (InoLab pH 720 pH meter, WTW, Weilheim, Germany). Analyses of NH_4^+-N, P, and pH were performed by the authors, while the remaining soil analyses were performed by the Soil and Water Chemistry Laboratory at the Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, Ås, Norway.

Freezing and drying of soils before analyses of inorganic N may affect NH_4^+-N and NO_3^--N levels (Mulvaney, 1996), and thus the results for absolute amounts of these N forms should be treated with caution. However, the main focus of this study is the relative difference in soil N levels below and outside legumes, not the exact values of NH_4^+-N and NO_3^--N.

To examine whether species richness, diversity, evenness, and composition differed with and without the presence of legumes, we conducted vegetation analyses in 120 pairs of 15 × 15 cm plots with and without legumes in July 2009. Each plot pair consisted of one plot with a fully grown legume in the center, and one plot 30–100 cm away from the legume plot and at least 30 cm away from any other legume. We selected 30 plot pairs with and without *Astragalus* in the low-elevation site, 30 plot pairs with and without *Oxytropis* in the mid-elevation site, and 30 plot pairs with and without each of the legume species in the high-elevation site.

We identified all vascular plant species in each plot and visually estimated their percentage cover. We then used the Excel add-in module Diversity to calculate total species richness, species diversity (Shannon-Weaver diversity index), and species evenness (Shannon's evenness index) in each plot. In all calculations we removed the legumes from the data set, as they would automatically bias the results for the legume plots (see del Moral and Rozzell, 2005).

STATISTICAL ANALYSES

We used multivariate ordination to examine whether species composition differed between plots with and without legumes. First, we used detrended correspondence analysis (DCA) with default settings to examine the gradient lengths of the species cover data. The longest gradients were between 2.7 and 3.8 SD units, which means that both canonical correspondence analysis (CCA) and redundancy analysis (RDA) may be appropriate for further analyses (Lepš and Šmilauer, 2003). Consequently, we performed both CCA and RDA, but the two methods yielded contrasting results. Repeating the DCA with presence-absence data gave gradient lengths of between 1.7 and 2.5 SD units, suggesting that RDA is the appropriate method (Lepš and Šmilauer, 2003). RDA with presence-absence data was therefore used to test for differences in species composition. Separate analyses were conducted for each site. We used legume presence as an environmental variable and pair as a covariable in Monte Carlo permutation tests with 999 permutations, where the covariable defined the blocks within which to permute. Otherwise the analyses were performed with default settings: untransformed species data, centering by species, species scores divided by standard deviation, and scaling focusing on inter-species correlations (ter Braak and Šmilauer, 1998).

We used analysis of variance (ANOVA) to test whether total species richness, diversity, and evenness differed between plots with and without legumes and whether there was a legume-by-site interaction. All tests were two-way ANOVAs with site and legume presence as fixed main factors and pair as a random factor nested under site. To save degrees of freedom, the pair factor was omitted from models where it was non-significant. To examine whether different functional groups responded differently to legume presence, the ANOVA was repeated with species richness and total cover (%) of graminoids and herbs as response variables. Woody species and pteridophytes were not frequent enough to be included in the analyses. If the legume-by-site interaction was significant, paired *t*-tests were used to compare the different response variables with and without legumes within each site. Data on evenness was arcsine-transformed and total cover of graminoids and herbs was square root-transformed to fulfill the ANOVA assumptions of normality and equal variances.

Similar ANOVA models were used to test whether total N content (%), $NH_4{}^+$-N levels (mg/kg), $NO_3{}^-$-N levels (mg/kg), total C content (%), P levels (mg/kg), and pH differed in soil from below and outside legumes and whether there was a legume-by-site interaction. Data on $NH_4{}^+$-N and $NO_3{}^-$-N content for *Astragalus* were ln-transformed. Moreover, we used Mann-Whitney U tests to examine whether the number of nodules differed between sites.

The two legume species were analyzed separately in all tests, as preliminary analyses indicated that they differed in their effects on response variables. ANOVAs, *t*-tests, and Mann-Whitney U tests were performed in Minitab 15.1 (Minitab Inc.) and ordinations in CANOCO 4.5 (Microcomputer Power).

Results

OXYTROPIS

The RDA showed that species composition differed in plots with and without *Oxytropis* in the high-elevation site ($F = 2.19$, $P = 0.01$, % variance in species data explained by the first axis $= 7.0$) (Fig. 1, part B), but not in the mid-elevation site ($F = 0.85$, $P = 0.63$, % variance in species data explained by the first axis $= 2.9$) (Fig. 1, part A).

The ANOVA showed that there was a significant legume-by-site interaction for total species richness (Fig. 2, part A; Table 1). In the high-elevation site, species richness was significantly higher in plots with *Oxytropis* ($t = 3.56$, $P = 0.001$), while in the mid-elevation site there was no significant difference in species richness between plots with and without *Oxytropis* ($t = 0.62$, $P = 0.54$). There was no difference in species diversity (Fig. 2, part B) in plots with and without *Oxytropis* or between sites. Evenness (Fig. 2, part C) was significantly lower in the legume plots, but did not differ between sites. Graminoid species richness (Fig. 3, part A) was significantly higher with *Oxytropis* and higher in the mid-elevation site than the high-elevation site (Table 2), but there was no significant legume-by-site interaction. Moreover, there was no difference in herb species richness between plots with and without *Oxytropis* or between sites. The total cover of both graminoids and herbs (Fig. 3, part B) was significantly higher in plots with *Oxytropis*, and the difference was always greater for graminoids than for herbs (54.6% vs. 38.9% in the mid-elevation site and 158.4% vs. 110.0% in the high-elevation site). Graminoid cover was higher in the mid- than the high-elevation site, while herb cover was similar in the two sites.

Moreover, the ANOVAs showed that total N, $NH_4{}^+$-N, $NO_3{}^-$-N, and total C content were significantly higher in soil below

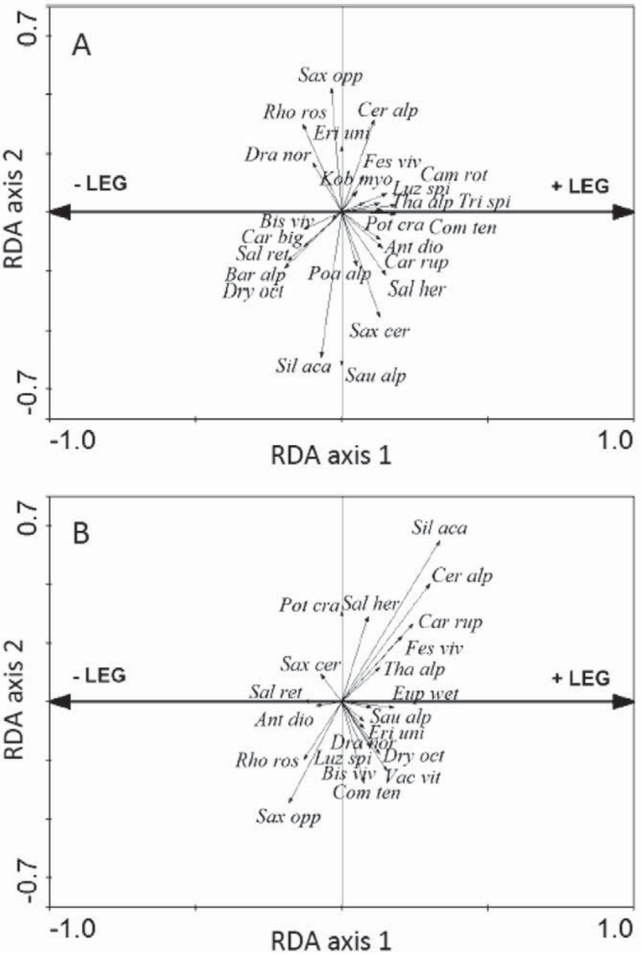

FIGURE 1. Redundancy analysis (RDA) biplot of the relationship between species presence and the presence of the legume *Oxytropis lapponica* in the (A) mid- and (B) high-elevation study sites at Mount Sanddalsnuten, Finse, Norway, summer 2009. +LEG = legume presence; –LEG = legume absence.

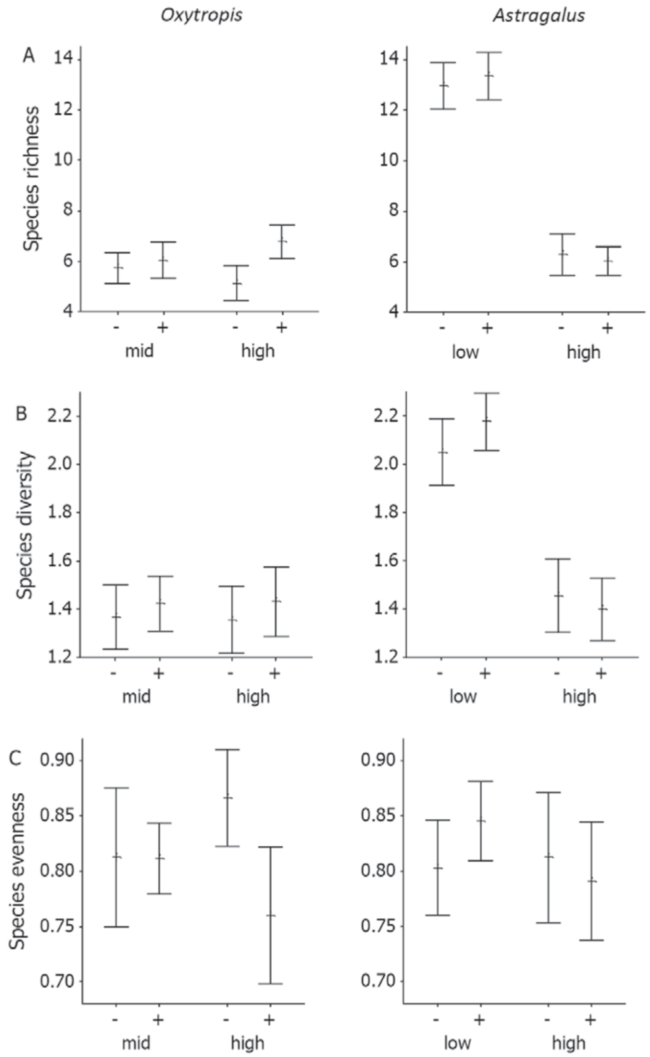

FIGURE 2. (A) Species richness, (B) diversity, and (C) evenness in 15 × 15 cm plots with (+) and without (–) the legumes *Oxytropis lapponica* (left) and *Astragalus alpinus* (right) in the low-, mid-, and high-elevation study sites at Mount Sanddalsnuten, Finse, Norway, summer 2009. All figures show mean values with 95% CI. $N = 30$ except for *Astragalus* in the low-elevation site, where $N = 29$.

TABLE 1

$F_{\text{degrees of freedom}}$ and P-values for two-way ANOVAs of species richness, diversity (Shannon-Weaver diversity index), and evenness (Shannon's evenness index) in 15 × 15 cm plots with and without the legumes *Oxytropis lapponica* and *Astragalus alpinus* in three study sites at Mount Sanddalsnuten, Finse, Norway, summer 2009. Bold letters indicate P-values significant at the 0.05 level. Pair was omitted (—) from the analyses when initial tests showed that the pair factor was not significant.

Source of variation	Richness		Diversity		Evenness	
	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P
Oxytropis						
Oxytropis	$8.52_{1,116}$	**0.004**	$1.04_{1,116}$	0.309	$6.93_{1,116}$	**0.010**
Site	$0.04_{1,116}$	0.841	$<0.01_{1,116}$	0.985	$0.25_{1,116}$	0.618
Oxytropis × Site	$4.05_{1,116}$	**0.046**	$0.02_{1,116}$	0.880	$3.34_{1,116}$	0.070
Pair (Site)	—	—	—	—	—	—
Astragalus						
Astragalus	$0.02_{1,115}$	0.899	$0.29_{1,115}$	0.592	$0.25_{1,115}$	0.621
Site	$307.20_{1,115}$	**<0.001**	$108.62_{1,115}$	**<0.001**	$0.37_{1,115}$	0.542
Astragalus × Site	$0.63_{1,115}$	0.427	$1.92_{1,115}$	0.169	$2.08_{1,115}$	0.152
Pair (Site)	—	—	—	—	—	—

TABLE 2

$F_{\text{degrees of freedom}}$ **and** P**-values for two-way ANOVAs of species richness and total cover (%) of graminoids and herbs in 15 × 15 cm plots with and without the legumes *Oxytropis lapponica* and *Astragalus alpinus* in three study sites at Mount Sanddalsnuten, Finse, Norway, summer 2009. Bold letters indicate** P**-values significant at the 0.05 level. Pair was omitted (—) from the analyses when initial tests showed that the pair factor was not significant.**

Source of variation	Graminoids				Herbs			
	Species richness		Total cover (%)		Species richness		Total cover (%)	
	$F_{\text{d.f}}$	P	$F_{\text{d.f.}}$	P	$F_{\text{d.f}}$	P	$F_{\text{d.f.}}$	P
<u>*Oxytropis*</u>								
Oxytropis	$14.73_{1,58}$	**<0.001**	$20.57_{1,58}$	**<0.001**	$2.92_{1,116}$	0.090	$13.96_{1,116}$	**<0.001**
Site	$4.07_{1,58}$	**0.048**	$12.73_{1,58}$	**0.001**	$1.16_{1,116}$	0.284	$3.28_{1,116}$	0.073
Oxytropis × Site	$0.92_{1,58}$	0.341	$0.98_{1,58}$	0.326	$1.16_{1,116}$	0.284	$1.08_{1,116}$	0.300
Pair (Site)	$2.04_{58,58}$	**0.004**	$2.28_{58,58}$	**0.001**	—	—	—	—
<u>*Astragalus*</u>								
Astragalus	$<0.01_{1,115}$	0.976	$0.53_{1,115}$	0.468	$0.72_{1,57}$	0.401	$0.10_{1,115}$	0.758
Site	$233.96_{1,115}$	**<0.001**	$56.41_{1,115}$	**<0.001**	$74.25_{1,58}$	**<0.001**	$68.41_{1,115}$	**<0.001**
Astragalus × Site	$0.18_{1,115}$	0.673	$0.18_{1,115}$	0.674	$1.49_{1,57}$	0.228	$0.10_{1,115}$	0.758
Pair (Site)	—	—	—	—	$1.71_{58,57}$	**0.022**	—	—

Oxytropis plants, but did not differ between sites (Table 3; Fig. 4, parts A–D). P levels (Fig. 4, part E) and pH (Fig. 4, part F) did not differ in soil from below and outside *Oxytropis*, but were significantly higher in the mid-elevation site compared to the high-elevation site. The mean number of nodules of *Oxytropis* plants in the mid- and high-elevation sites was 10.1 ± 2.7 and 18.0 ± 4.8 per 15 × 15 × 15 cm soil, respectively, but the difference between sites was not significant ($P = 0.29$).

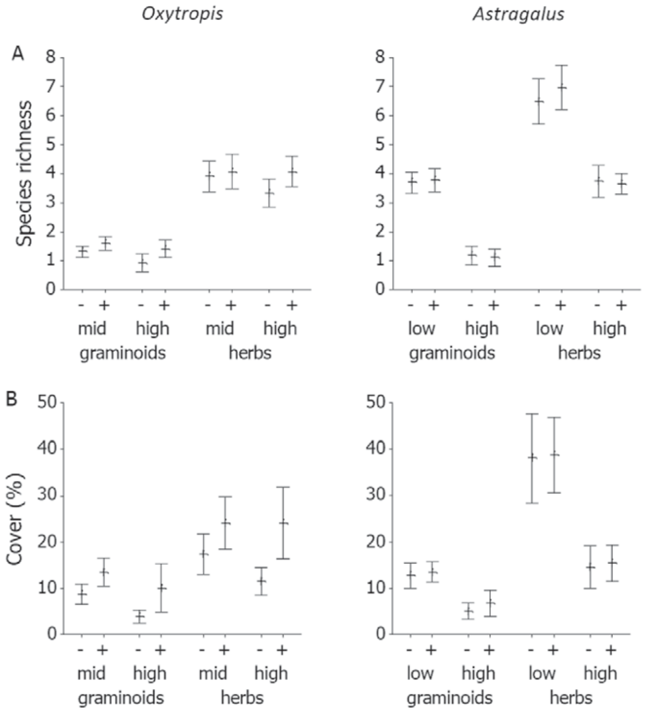

FIGURE 3. (A) Species richness and (B) total cover (%) of graminoids and herbs in 15 × 15 cm plots with (+) and without (–) the legumes *Oxytropis lapponica* (left) and *Astragalus alpinus* (right) in the low-, mid-, and high-elevation study sites at Mount Sanddalsnuten, Finse, Norway, summer 2009. All figures show mean values with 95% Cl. $N = 30$ except for *Astragalus* in the low-elevation site, where $N = 29$.

ASTRAGALUS

The RDA showed that there was no significant difference in species composition in plots with and without *Astragalus* in the low- ($F = 0.76$, $P = 0.81$, % variance in species data explained by the first axis = 2.7) or high-elevation site ($F = 1.28$, $P = 0.22$, % variance in species data explained by the first axis = 4.2) (not shown).

The ANOVAs showed that there was no difference in total species richness (Fig. 2, part A), diversity (Fig. 2, part B), evenness (Fig. 2, part C), or graminoid or herb species richness (Fig. 3, part A) or cover (Fig. 3, part B) between plots with and without *Astragalus* (Tables 1 and 2). Moreover, there was no difference in any soil variable below and outside *Astragalus* plants (Table 3; Fig. 5, parts A–F). All response variables, except species evenness, differed significantly between sites (Table 1, Fig. 2, parts A–C; Table 2, Fig. 3, parts A–B; Table 3, Fig. 5, parts A–F). The mean number of nodules of *Astragalus* plants in the low- and high-elevation sites was 18.3 ± 7.8 and 10.7 ± 2.7 per 15 × 15 × 15 cm soil, respectively, but the difference between sites was not significant ($P = 0.88$).

Discussion

Species composition differed with and without the presence of *Oxytropis* in the high-elevation study site at Finse, while there was no difference with and without *Astragalus* in any site. This difference in species composition seems to be due to a positive association between *Oxytropis* and other plant species in the high-elevation site, which is reflected in the higher species richness in the high-elevation *Oxytropis* plots. In addition, total species evenness was lower and richness and cover of graminoids, as well as the cover of herbs, was higher in the presence of *Oxytropis* in both sites. Overall, our findings suggest that the presence of this alpine legume may affect several properties of the plant community.

TABLE 3

$F_{\text{degrees of freedom}}$ and *P*-values for two-way ANOVAs of total N content (%), NH_4^+-N (mg/kg), NO_3^--N (mg/kg), total C content (%), P (mg/kg), and pH in soil samples from below and outside the legumes *Oxytropis lapponica* and *Astragalus alpinus* in three study sites at Mount Sanddalsnuten, Finse, Norway, summer 2008. Bold letters indicate *P*-values significant at the 0.05 level. Pair was omitted (—) from the analyses when initial tests showed that the pair factor was not significant.

Source of variation	Total N (%)		NH_4-N (mg/kg)		NO_3-N (mg/kg)	
	$F_{\text{d.f.}}$	*P*	$F_{\text{d.f.}}$	*P*	$F_{\text{d.f.}}$	*P*
Oxytropis						
Oxytropis	$6.56_{1,36}$	**0.015**	$6.25_{1,36}$	**0.017**	$6.27_{1,36}$	**0.017**
Site	$1.17_{1,36}$	0.286	$0.03_{1,36}$	0.862	$0.43_{1,36}$	0.517
Oxytropis × Site	$3.14_{1,36}$	0.085	$1.13_{1,36}$	0.294	$0.07_{1,36}$	0.795
Pair (Site)	—	—	—	—	—	—
Astragalus						
Astragalus	$0.10_{1,18}$	0.755	$0.61_{1,36}$	0.440	$0.53_{1,36}$	0.473
Site	$23.20_{1,18}$	**<0.001**	$4.33_{1,36}$	**0.045**	$14.26_{1,36}$	**0.001**
Astragalus × Site	$0.11_{1,18}$	0.753	$0.25_{1,36}$	0.620	$0.04_{1,36}$	0.838
Pair (Site)	$2.62_{18,18}$	**0.024**	—	—	—	—

Source of variation	Total C (%)		P (mg/kg)		pH	
	$F_{\text{d.f.}}$	*P*	$F_{\text{d.f.}}$	*P*	$F_{\text{d.f.}}$	*P*
Oxytropis						
Oxytropis	$6.19_{1,36}$	**0.018**	$0.39_{1,36}$	0.535	$3.21_{1,36}$	0.081
Site	$1.71_{1,36}$	0.199	$12.84_{1,36}$	**0.001**	$9.90_{1,36}$	**0.003**
Oxytropis × Site	$3.27_{1,36}$	0.079	$0.62_{1,36}$	0.435	$0.04_{1,36}$	0.851
Pair (Site)	—	—	—	—	—	—
Astragalus						
Astragalus	$0.15_{1,36}$	0.702	$1.29_{1,36}$	0.263	$0.89_{1,36}$	0.351
Site	$33.20_{1,36}$	**<0.001**	$18.75_{1,36}$	**<0.001**	$11.27_{1,36}$	**0.002**
Astragalus × Site	$0.11_{1,36}$	0.741	$0.70_{1,36}$	0.409	$0.97_{1,36}$	0.331
Pair (Site)	—	—	—	—	—	—

The difference in species composition between plots with and without *Oxytropis* in the high-elevation site corresponds to our findings of higher N levels in soil below this species. Fertilization experiments in arctic and alpine habitats have shown that nutrient addition may lead to profound changes in plant communities (e.g. Chapin et al., 1995; van Wijk et al., 2003; Klanderud and Totland, 2005a), suggesting that increased N levels below legumes may also affect plant species composition and diversity. Many of the species that were positively associated with *Oxytropis* in the high-elevation site, such as *Cerastium alpinum* (Cer alp), *Draba norvegica* (Dra nor), *Euphrasia wetsteinii* (Eup wet), *Festuca vivipara* (Fes viv), *Saussurea alpina* (Sau alp), *Silene acaulis* (Sil aca), and *Thalictrum alpinum* (Tha alp) (Fig. 1, part B), increased in abundance with nutrient addition in the study area (Klanderud, 2008), indicating that the presence of *Oxytropis* in the high-elevation site does have a ''fertilizing effect'' on the surrounding vegetation.

Above-ground facilitation by the legume could be another possible explanation for the differences in community properties with and without *Oxytropis* in the high-elevation study site. However, this seems unlikely due to the modest size of the *Oxytropis* plants, which have a limited ability to shelter other plants from e.g. strong winds or low temperatures. Furthermore, above-ground removal of non-legume neighbors had a positive effect on plant growth in the study area (Klanderud, 2005; Klanderud and Totland, 2005b), suggesting competition from neighbors rather than facilitation. Thus, higher soil N levels below the legumes is the most likely explanation for the observed patterns in community composition and diversity.

While species richness often decreases with nutrient addition in arctic and alpine habitats (e.g. Chapin et al., 1995; Shaver et al., 2001; Wang et al., 2010; but see Fox, 1992), species richness was higher in the presence of *Oxytropis* plots in the high-elevation study site at Finse. According to the ''hump-backed'' model of productivity and diversity (e.g. Grime, 1979), species richness should increase with soil nutrient levels up to a certain level as more species are able to survive, and then decrease as some species become dominant and competitively exclude others. In our study, the higher soil fertility below *Oxytropis* was probably just high enough for more species to establish without any being competitively excluded. Our results contradict those of Thomas and Bowman (1998), who found no difference in species richness between patches with and without the legume *Trifolium dasyphyllum* in the Rocky Mountains. However, while this lack of increase in richness was attributed to lower soil P levels in the legume patches, we found no difference in soil P in plots with and without legumes at Finse. Thus, lower P levels could not have offset the positive effect of higher soil N levels on species richness in the high-elevation *Oxytropis* plots in our study.

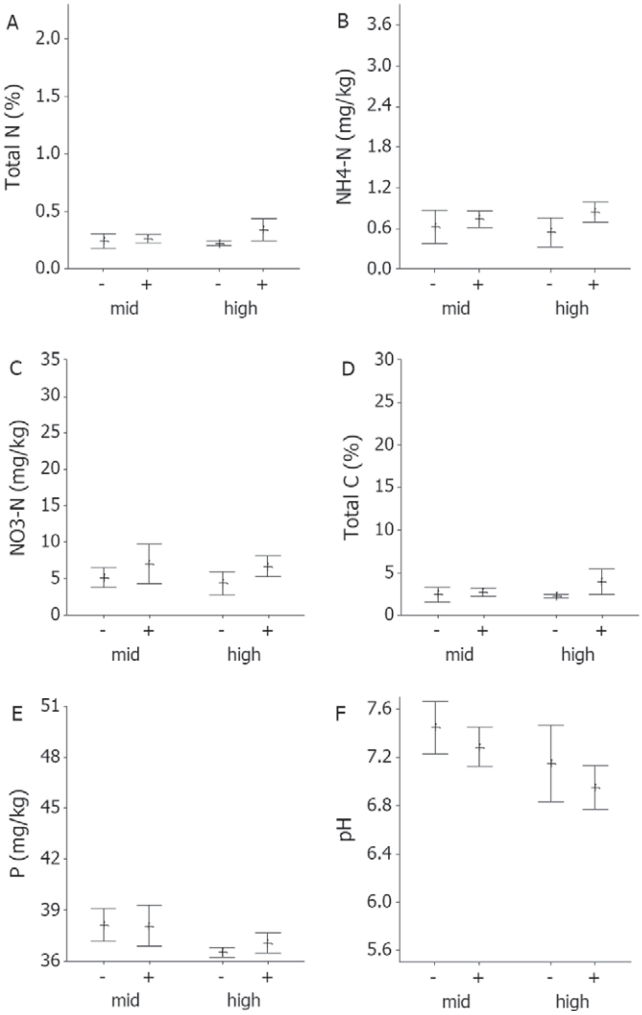

FIGURE 4. **(A) Total N content (%), (B) NH_4^+-N (mg/kg), (C) NO_3^--N (mg/kg), (D) total C content (%), (E) P (mg/kg), and (F) pH in soil samples from below (+) and outside (–) the legume *Oxytropis lapponica* in the mid- and high-elevation study sites at Mount Sanddalsnuten, Finse, Norway, summer 2008. All figures show mean values with 95% CI. $N = 10$.**

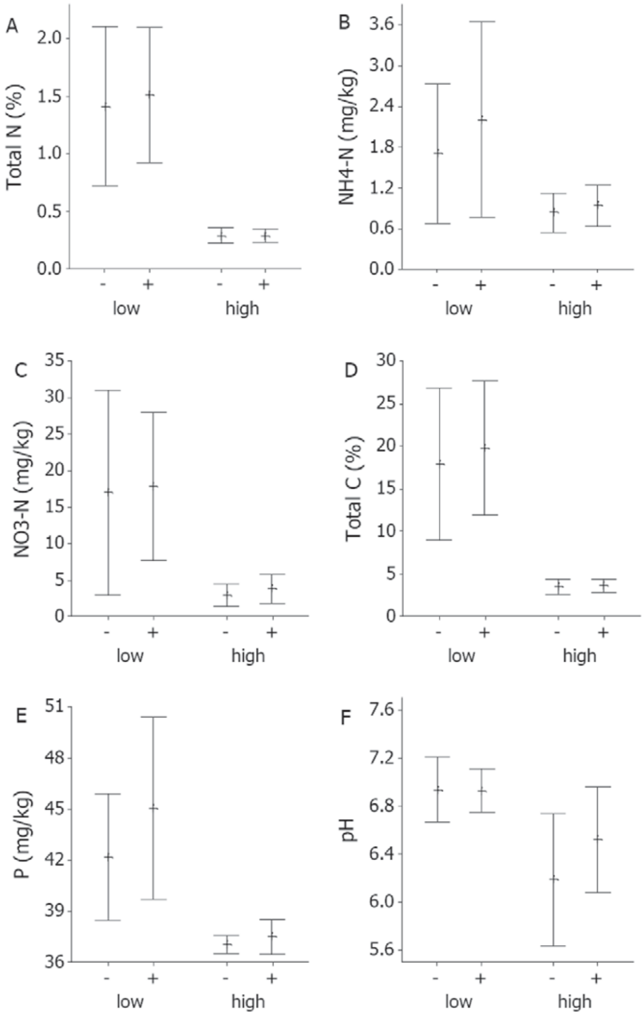

FIGURE 5. **(A) Total N content (%), (B) NH_4^+-N (mg/kg), (C) NO_3^--N (mg/kg), (D) total C content (%), (E) P (mg/kg), and (F) pH in soil samples from below (+) and outside (–) the legume *Astragalus alpinus* in the low- and high-elevation study sites at Mount Sanddalsnuten, Finse, Norway, summer 2008. All figures show mean values with 95% CI. $N = 10$.**

The lower species evenness in plots with *Oxytropis* may be due the presence of one or more dominant species associated with the legumes. We found a higher total cover of both graminoids and herbs where *Oxytropis* was present. However, graminoids were the only functional group with higher species richness in the *Oxytropis* plots, and the difference in total cover between plots with and without *Oxytropis* was larger for graminoids than for herbs. Thus, the lower evenness in the legume plots is most likely due to the presence of dominant graminoids. Our findings of increased richness and cover of graminoids are in accordance with most nutrient addition experiments, which often result in a strong increase in graminoid abundance and biomass in arctic and alpine plant communities (e.g. Theodose and Bowman, 1997; van Wijk et al., 2003; Jägerbrand et al., 2009). Klanderud and Totland (2005a) showed that increased graminoid abundance following nutrient addition may reduce species richness of other functional groups in the study area. Contrasting these results, the higher graminoid cover in the *Oxytropis* plots in our study was apparently not high enough to negatively affect the richness of other functional groups, resulting in higher total species richness where *Oxytropis* was present.

The higher soil N levels below *Oxytropis*, which appear to influence plant community composition and diversity measures in the high-elevation study site, are most likely due to biological N fixation by the legumes. This is in line with previous studies showing that legumes may have a positive effect on soil N levels in alpine habitats (Kenny and Cuany, 1990; Thomas and Bowman, 1998). A weakness of our study is that we did not measure N fixation, and it could be that *Oxytropis* simply establishes in microhabitats with initially high soil N levels. However, Maron and Connors (1996), who studied the N-fixing legume *Lupinus arboreus* on the California coastal prairie, concluded that high levels of soil N below lupines did not result from a preference for N rich microhabitats. They found that soil N levels below young legumes were identical to surrounding areas, whereas N levels below adult legumes were higher, indicating that *L. arboreus* improves soil N conditions. Therefore, it seems probable that the higher soil N levels below *Oxytropis* are due to N fixation rather than specific habitat preferences. *Oxytropis* is a perennial and probably long-lived species. Thus, although the yearly N fixation of alpine legumes is relatively low (e.g. Bowman et al., 1996), N may accumulate in the soil below the legumes over time, thereby increasing soil N levels sufficiently to affect plant community properties.

While *Oxytropis* appeared to influence soil N levels and thereby community properties at Finse, *Astragalus* did not. The two legume species had approximately the same number of nodules, and previous studies show that the N fixation rate of *Astragalus* is equal to or greater than that of *Oxytropis* spp. (Karagatzides et al., 1985; Schulman et al., 1988). Hence, the contrasting influence of the two species is probably not due to differences in N-fixing capacity. Alternatively, the lack of influence of *Astragalus* on soil N levels may be due to the more productive microhabitats of this species. Soil N levels in the low-elevation site were higher than in any other site, and comparing soil N levels in the plots without legumes in the high-elevation site indicates that the microhabitats of *Astragalus* have higher background soil N levels than those of *Oxytropis* (Fig. 4, parts A–C, vs. Fig. 5, parts A–C). Schulman et al. (1988) found the same pattern of higher soil nutrient levels in the habitat of *Astragalus* compared to two species of *Oxytropis* in the Canadian Arctic. In microhabitats with relatively high soil nutrient levels, biologically fixed N may contribute too little to the total soil N content to produce significantly higher soil N levels below the legumes, explaining why *Astragalus* does not appear to increase N levels in the study area.

Thomas and Bowman (1998) concluded that legumes ''represent an important biotic factor contributing to spatial heterogeneity in species composition ... of alpine tundra.'' *Oxytropis*, which we found to alter species composition in one of two study sites, probably plays a similar role in the *Dryas* heath community at Finse. As the legume influences community properties on a local scale, namely in close vicinity of the legume plants (Jacot et al., 2005) and apparently only in some habitats, *Oxytropis* contributes to increased spatial heterogeneity, which may in turn influence total species richness of the ecosystem.

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