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Importance of soil calcium for composition of understory vegetation in boreal forests of Finnish Lapland

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Abstract To focus conservation efforts into forest areas with high biodiversity, more information is needed about soil-vegetation dependencies in Finnish Lapland. We studied understory vegetation and soil variables along a transect across a felsic–mafic lithological sequence in central Finnish Lapland. At 119 northern boreal forest sites, coverages of understory vegetation, several mineral soil chemical elements, soil electrical conductivity, pH, and dielectric permittivity, as a measure of soil volumetric water content, were measured. We found that soil Ca concentration and Ca:Al ratio were the main variables determining vegetation composition and diversity. Ca-rich soils were characterised by high electrical conductivity, pH, and Mg concentration, and by low concentration of Al, S, Zn, and low C:N ratio. Soil Ca concentration is a diagnostic measure of plant diversity as concentration higher than 100 mg kg^{-1} resulted in a considerable increase in plant diversity. Sites with Ca concentration this high were rare, and probably important in maintaining high biodiversity. The median soil Ca:Al ratio was only 0.02, suggesting, according to general theory, a considerable risk for aluminium stress. We found *Geranium sylvaticum* and *Rubus saxatilis* to be good indicators for Ca-rich regimes and high plant diversity.

Keywords Calcium · Ca:Al ratio · Nonmetric multidimensional scaling · *Geranium sylvaticum* · *Rubus saxatilis* · Boreal forest

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Introduction

More information about soil-vegetation dependencies in Finnish Lapland is needed to identify forest areas with high diversity to focus conservation efforts and to develop forest classifications. Finnish boreal forests are generally dominated by a few tree species, each of them able to dominate a wide range of communities with differing understory composition. Various forest classifications, based partly on understory dissimilarities, are reported, some of them involving dominant tree species as a main classifier (Toivonen and Leivo 1993; Kuusipalo 1996; Tuominen et al. 2001). In similar climatic conditions, the main variables determining vegetation composition are soil moisture and nutrient content (Lahti and Väisänen 1987; Nieppola and Carleton 1991; Økland and Eilertsen 1993; Økland 1996). Some classifications focus on these variables, ignoring many others such as changes in tree and understory composition along with succession. Forest vegetation patterns and relationships between vegetation composition and fertility have been studied earlier especially in southern Finland (Kuusipalo 1985; Lahti and Väisänen 1987; Nieppola and Carleton 1991; Hokkanen 2006), whereas studies in which Finnish Lapland is included do not contain detailed soil variables (Oksanen 1983; Tonteri et al. 1990).

The majority of the soil parent material in Finnish Lapland is non-stratified glacial tills. Because of short glacial dispersal distances, tens to hundreds of meters in Finnish Lapland, chemical composition of the basal till is closely associated with the underlying bedrock (Lestinen 1980). A strong correlation between surface soil and basal till chemistry has been reported (Lahdenperä et al. 2001), and therefore bedrock may have a major impact on exchangeable elements of surface soils, and consequently on understory vegetation. The objective of the present research was to recognize the influences of different soil variables on the forest understory vegetation in central Finnish Lapland. We hypothesized that some soil variables have a high influence on diversity, distribution, and composition patterns of understory species, and consequently some species are reliable indicators of those variables.

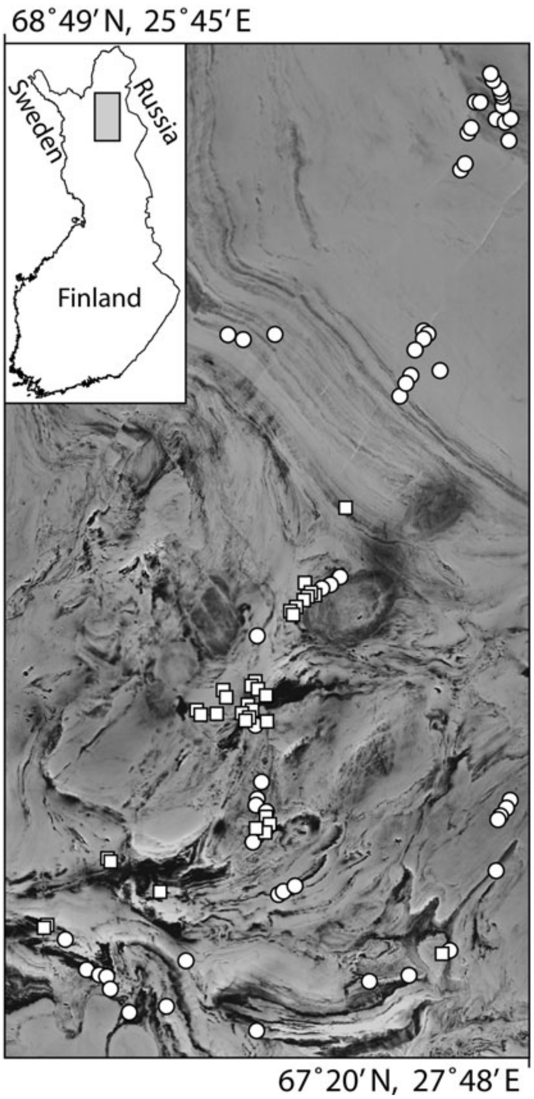

Fig. 1 Felsic (*circle*) and mafic (*square*) bedrock study sites on total intensity aeromagnetic map in central Finnish Lapland

Materials and methods

Study sites

The data included a total of 68 felsic and 51 mafic outcrops located in the northern boreal region of central Finnish Lapland between 67°20′N and 68°49′N, and 25°45′E and 27°48′E (Fig. 1). A number of variables, such as climate and topography, affect the relationship between vegetation and soil (Amundsen et al. 1994). Therefore, we selected study sites on the basis of similarity in climatic conditions and elevation, whereas bedrock was felsic in the Lapland granulite and mafic in the Greenstone belt. The climate is cool and humid with annual mean temperature ranging from −1 to 0°C. The permanent snow cover is present 200–210 days of the year and more than 45% of the annual 500–600 mm precipitation falls as snow (Finnish Meteorological Institute). The study sites, each one square meter, were randomly selected from a bedrock outcrops database by the Geological Survey of Finland. In order to acquire field data in a reasonable amount of time, only sites located less than 250 m from the road network were included. Since glacial till was predominant parent material, study sites were selected ≤30 m down-ice direction from the outcrops to catch the glacial dispersal. The roadside soils may be contaminated by lead and other metals (e.g. Garcia and Millán 1988), so a 20 m buffer between the road network and the sample sites was used in order to minimize the impacts of possible traffic pollution. None of the sites was in an entirely natural state and some of them had been clearcut quite recently. Species distribution in the area is also affected by the grazing of domesticated mountain reindeer, *Rangifer tarandus tarandus* (Suominen and Olofsson 2000). Cladina lichens are the main forage of reindeer during winter, so in grazed areas the coverages have decreased (Suominen and Olofsson 2000). The dominant tree species in the study sites were *Betula pubescens* Ehrh. (Downy birch), *Pinus sylvestris* L. (Scots pine), and *Picea abies* (L.) Karst (Norway spruce) (Table 1). Coverages of other tree species were minor. The most common understory species were *Calluna vulgaris*, *Cladina* spp., *Cladonia* spp., *Dicranum* spp., *Empetrum nigrum*, *Hylocomium splendens*, *Pleurozium schreberi*, *Rhododendron tomentosum*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea* (Table 1). The main felsic rock types were gneiss (35%), quartzite (21%), and granite (21%), whereas the main mafic rock types were vulcanite (63%) and amphibolite (14%).

Table 1 Mean coverages (%) of the most common canopy (*Betula pubescens*, *Picea abies*, *Pinus sylvestris*) and understory species in vegetation communities 1 ($n = 56$), 2 ($n = 23$), and 3 ($n = 40$)

Variable	Mean (%)		
	1	2	3
Betula pubescens	12	6	2
Picea abies	4	1	1
Pinus sylvestris	14	23	13
Calluna vulgaris	2	2	5
Cladina spp.	3	3	29
Cladonia spp.	1	1	3
Dicranum spp.	5	4	7
Empetrum nigrum	12	20	12
Hylocomium splendens	16	5	1
Pleurozium schreberi	38	58	20
Rhododendron tomentosum	1	3	1
Vaccinium myrtillus	14	10	7
Vaccinium uliginosum	9	4	4
Vaccinium vitis-idaea	14	16	6

Field measurements

At each site, soil dielectric permittivity (DP), as a measure of soil water content, and soil electrical conductivity (EC_b), as a measure of soil nutrient potential, were measured. The DP was determined using an electrical capacitance probe (Adek Ltd., Tallin, Estonia) having a measurement depth approximately 10 cm and measured soil volume approximated 500 cm^3. Because of the one-time sampling and rainy climate, variation in time from the previous rains reduced quality of the DP data. The EC_b was measured simultaneously with DP at each site using a four electrode Wenner configuration with 15 cm steel rods and 16 cm spacing (Geological Survey of Finland; Puranen et al. 1999). The actual measure was half-space resistivity, which was converted to EC_b (mS m^{-1}). The Wenner configuration measures EC_b to a depth of 0–30 cm, i.e. the root zone in northern Fennoscandia. In addition to total quantity of ions, soil texture, temperature, organic matter content, and water content are among the main variables affecting EC_b (Rhoades et al. 1976). In order to reduce measurement errors due to soil heterogeneity, two readings for both soil EC_b and DP were acquired.

At each site, coverage of all species was estimated in shrub, field, and bottom layers separately. Coverage from the field and bottom layer was estimated within one square meter plots. The shrub layer included shrubs and trees up to 1.3 m in height, and was measured as a volume in cubic meters within a circle of 2 m in radius, in order to receive more reliable values due to the large canopies and root systems. Volume measurement was considered to be ecologically more meaningful than coverage. All understory species absent within the one square meter plot but present within the circle were also recorded with minimum coverage. Along with vegetation analysis and soil electrical measurements, mineral soil was sampled to a depth of 20 cm for chemical analyses. The fieldwork was performed in August 2005.

Soil chemical analyses

Mineral soil Al, Ba, Be, Ca, Co, Cr, Cu, Fe, K, Li, Mg, Mn, Na, Ni, P, Pb, S, Sr, Ti, V, and Zn were extracted with 1 M ammonium acetate in pH 4.5

from samples sieved to grain size <2 mm, and analyzed (standard SFS-EN ISO 1885) using inductively coupled plasma atomic emission spectrometer (ICP-AES) as part of the iCAP 6500 Duo ICP emission spectrometer (Thermo Fisher Corp., Cambridge, UK). Total C and N were analyzed on a dry-weight percent basis (standard ISO 1387, CEN 15014) using Vario MAX CN analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and soil pH by potentiometric titration.

Statistical analyses

To analyze soil variables contributing to vegetation composition, a nonmetric multidimensional scaling (NMDS; Kruskal 1964) using Bray–Curtis dissimilarities with Wisconsin double standardization (Bray and Curtis 1957) was applied to vegetation data. The NMDS has been demonstrated to be superior to other ordination methods when applied to ecological data (Kenkel and Orlóci 1986; Minchin 1987). The NMDS places sites with similar species composition close together in the ordination space. It is an unconstrained method based only on vegetation dissimilarities, with no attempt to maximize correlations with the soil variables which are later related to vegetation ordination. The NMDS represents data in a few dimensions, so that distances in the ordination reflect the similarities between sample sites. Values of the coordinates are not essential, they only achieve the desired spacing. The soil variables are given as lines in the ordination graphics, the direction of each line indicating the direction of gradient and the length indicating the strength of the correlation between variable and ordination (Fig. 2). Significance of the correlations between vegetation and soil characteristics were tested with 5000 permutations. Out of a total of 103 plant species, 63 grew on ≤5 sites and covered >1% of the site only 15 times, and were therefore excluded from the ordination.

According to Feoli and Orlóci (1991) ordination and classification should be applied together to obtain more

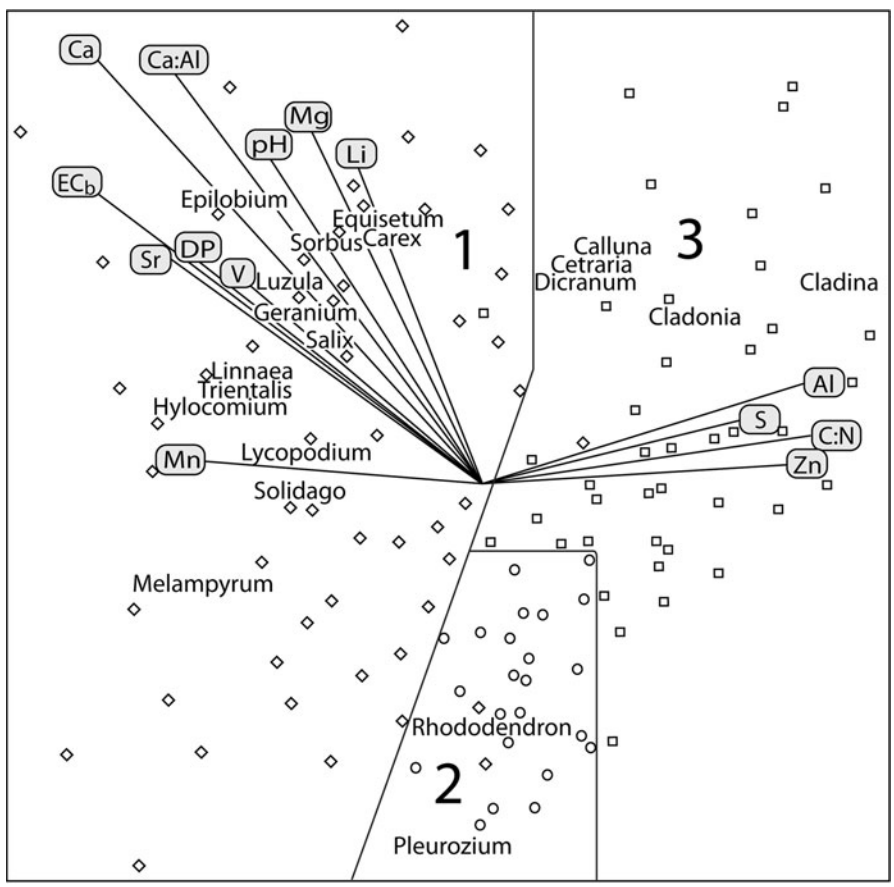

Fig. 2 Nonmetric multidimensional scaling of sites and species ($p \leq 0.001$) according Bray–Curtis dissimilarities. Soil variables ($p \leq 0.05$) are displayed by *lines*. *Diamonds* give vegetation community 1, *circles* community 2, and *squares* community 3 sites

reliable results. Hierarchical cluster analysis using Ward linkage (Orlóci 1967) based on Bray–Curtis dissimilarities with Wisconsin double standardization was applied to vegetation data to search for homogeneous communities among the study sites. Homogeneity of communities in the NMDS diagram was also required. Therefore no more than three vegetation communities were constructed (Table 1). Differences in soil variables between vegetation communities 1–3 were analyzed using the Kruskal–Wallis test.

Although every species has a definite ecological amplitude, the ones with relatively narrow ecological amplitude have the best indicator value. To research more specifically the potential indicator species demonstrated with the NMDS ($p \leq 0.05$), species that grew on <30 sites were analyzed for the soil variables using the Mann–Whitney test. The species richness S′ and the Shannon diversity H′ (Shannon and Weaver 1949) were selected to characterize the plant α-diversity of the sites. The species richness is simply the number of species present in the site. The estimator commonly used for the Shannon diversity is $H' = -\Sigma(n_i/\Sigma n_i)\ln(n_i/\Sigma n_i)$, where n_i is the coverage of individual species. Sites with high species richness and equal abundance between species generate high H′ values. To model the variation of H′ and S′ on soil Al, Ca, Ca:Al, C:N, EC_b, pH, and DP gradients, linear regression analysis was applied. A locally weighted regression using least squares with tricube weight function and a span of 0.5 was performed to generate curves for H′ and S′ to Ca gradient (Fig. 3). Curves were constructed to Ca gradient because the linear regression analysis showed the highest dependence between plant diversity and Ca concentration.

The correlation between Ca and other soil variables was analyzed using the Spearman correlation test. In addition, soil C:N ratio and Ca:Al molar ratio (Cronan and Grigal 1995) were calculated. The Ca alone was used instead of base cations of Ca, Mg, and K, since according to the linear regression analysis the ratio of base cations to Al (Sverdrup and Warfvinge 1993) was highly defined by Ca:Al ($\beta = 0.98$, $p < 0.001$), therefore indicating insignificance of Mg and K in the formula. Finally differences in soil variables between felsic and mafic bedrock sites were analyzed using the Mann–Whitney test. The cluster analysis, ordination, and curves were accomplished using R version 2.6 (R Development Core Team 2008) with Vegan version 1.1

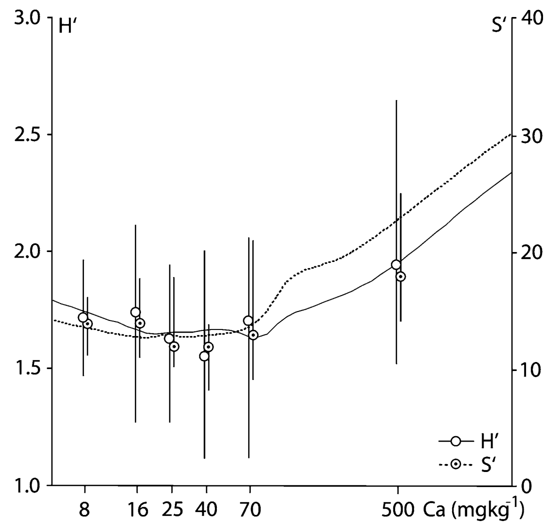

Fig. 3 Locally weighted regression curve of Shannon diversity H′ and species richness S′ on logarithmic Ca gradient. *Vertical lines* indicate 10th/90th percentile range divided by the median to sets of 20 sites. Both H′ ($\beta = 0.37$) and S′ ($\beta = 0.56$) depend on Ca ($p \leq 0.001$) according linear regression analysis

(Oksanen et al. 2008), and correlation tests using SPSS version 15.0 (SPSS Inc., Chicago, IL).

Results

Minimum and maximum values of studied soil variables and medians on vegetation communities 1–3 are given in Table 2. The soil on vegetation community 1 was characterized by high DP, Ca:Al, total C, Cr, and Ni as well as low C:N, Al, K, N, Pb, S, and Zn. Community 2 was characterized by high total C and low Ca:Al, C:N, total N, Cr, K, Ni, and Pb. In addition, soil DP was almost equal to community 1. Community 3 was characterized by high C:N, Al, K, N, Pb, S, and Zn as well as low DP, Ca:Al, and total C.

According to NMDS the following soil variables were significantly correlated with the vegetation ordination (Fig. 2): EC_b ($p < 0.001$), Ca ($p < 0.001$), Ca:Al ($p < 0.001$), Sr ($p = 0.005$), C:N ($p = 0.006$), Al ($p = 0.008$), DP ($p = 0.009$), pH ($p = 0.011$), Mg ($p = 0.014$), Zn ($p = 0.018$), Mn ($p = 0.032$), V ($p = 0.036$), S ($p = 0.046$), and Li ($p = 0.047$). *Carex globularis*, *Epilobium angustifolium*, *Equisetum sylvaticum*, *Geranium sylvaticum*, *Hylocomium splendens*, *Linnaea borealis*, *Luzula pilosa*, *Lycopodium*

Table 2 Soil electrical conductivity (EC_b; mS m^{-1}), dielectric permittivity, pH, Ca:Al and C:N ratios, total C and N (%), and other elemental concentrations (mg kg^{-1}) in vegetation communities 1 ($n = 56$), 2 ($n = 23$), and 3 ($n = 40$)

Variable	Median			Min.	Max.
	1	2	3		
EC_b	0.54	0.58	0.42	0.08	6.58
DP	14.1 a	14.4	11.7 b	3.8	48.6
pH	4.89	4.80	4.68	3.75	6.27
Ca:Al	0.047 a	0.016 b	0.015 b	0.0016	19.53
C:N	16.6 a	16.2 a	18.3 b	8.1	48.7
C (%)	1.50 a	1.28 a	2.47 b	0.42	11.60
N (%)	0.09 a	0.09 a	0.14 b	0.03	0.50
Al	819 a	871	1490 b	77	5050
Ba	7.43	6.58	7.94	0.73	123
Be	0.05	0.05	0.05	0.05	0.14
Ca	50.7	27.0	27.3	5.0	2250
Co	0.12	0.17	0.12	0.10	9.96
Cr	1.63 a	0.98 b	1.48	0.10	25.90
Cu	0.20	0.20	0.20	0.20	5.10
Fe	278	272	297	22	1470
K	18.0 a	17.2 a	22.5 b	10.0	73.7
Li	0.05	0.05	0.05	0.05	0.12
Mg	18.8	11.5	13.0	2.1	737
Mn	4.68	4.09	2.45	0.11	193
Na	6.65	6.84	7.97	4.23	30.50
Ni	0.17 a	0.10 b	0.13	0.10	9.61
P	11.0	10.4	11.0	3.1	76.7
Pb	0.50 a	0.50 a	1.15 b	0.50	28.30
S	27.5 a	41.9	54.5 b	5.2	288
Sr	0.35	0.32	0.42	0.10	10.90
Ti	1.52	1.63	1.34	0.15	10.10
V	0.50	0.50	0.50	0.50	2.20
Zn	0.67 a	0.71	0.99 b	0.22	6.13

Communities with significant difference ($p \leq 0.05$) according Kruskal–Wallis test are indicated by different letters. Also minimum and maximum values are given ($n = 119$)

annotinum, *Melampyrum sylvaticum*, *Salix phylicifolia*, *Solidago virgaurea*, *Sorbus aucuparia* L. (European Rowan), *Trientalis europaea*, soil DP, EC_b, Ca, Ca:Al, Li, Mg, Mn, pH, Sr, and V were associated with vegetation community 1 (Fig. 2). *Pleurozium schreberi* and *Rhododendron tomentosum* were associated with vegetation community 2, whereas *Calluna vulgaris*, *Cetraria islandica*, *Cladina* spp., *Cladonia* spp., *Dicranum* spp., Al, C:N, S, and Zn were associated with vegetation community 3. Only the species with $p \leq 0.001$ are shown in Fig. 2.

The presence/absence of several plant species indicated various soil variables. The presence of *Carex globularis*, *Epilobium angustifolium*, *Geranium sylvaticum*, *Linnaea borealis*, *Luzula pilosa*, *Rubus saxatilis*, and *Trientalis europaea* indicated low soil Al, C:N, Pb, S, Ti, and Zn, and high EC_b, pH, Ca, Ca:Al, Co, Mg, Mn, Ni, and Sr (Table 3). Only the species with more than five significant correlations to soil variables are presented. One of the indicator species, *Rubus saxatilis*, was not included in Fig. 2 because only the species with $p \leq 0.001$ were presented, whereas the p-value of *R. saxatilis* was 0.023.

Shannon diversity values in vegetation communities 1, 2, and 3 were 1.74, 1.55, and 1.75, respectively, whereas species richness values were 15.4, 11.6, and 12.3. Shannon diversity was significantly related to extractable soil Ca ($\beta = 0.37$), Ca:Al ($\beta = 0.35$), EC_b ($\beta = 0.35$), and pH ($\beta = 0.30$), all at $p \leq 0.001$, and to DP ($\beta = 0.27$, $p = 0.004$). Species richness was also significantly related to extractable soil Ca ($\beta = 0.56$), Ca:Al ($\beta = 0.55$), EC_b ($\beta = 0.55$), pH ($\beta = 0.38$), and DP ($\beta = 0.38$), all at $p \leq 0.001$. Neither extractable soil Al nor C:N were correlated to either Shannon diversity or species richness. The locally weighted regression curves of Shannon diversity and species richness on soil Ca gradient are given in Fig. 3.

The soil variables correlated to Ca ($p \leq 0.001$) were Al ($r_s = -0.35$), Ca:Al ($r_s = 0.89$), K ($r_s = 0.28$), Mg ($r_s = 0.82$), Na ($r_s = 0.33$), Ni ($r_s = 0.50$), S ($r_s = -0.45$), Sr ($r_s = 0.82$), and EC_b ($r_s = 0.34$). On mafic bedrock sites soil Co ($p < 0.001$), Cu ($p = 0.001$), Mn ($p = 0.008$), pH ($p = 0.011$), and Cr ($p = 0.013$) were high, whereas in felsic sites Pb ($p < 0.001$) and Zn ($p = 0.006$) were high. Vegetation community 1 contained 20 felsic and 36 mafic sites, community 2 contained 12 felsic and 11 mafic sites, and finally community 3 contained 36 felsic and 4 mafic sites.

Discussion

The results demonstrate that the forest vegetation communities in Finnish Lapland are closely related to soil chemical properties. The strongest gradients in the NMDS among measured soil variables were extractable Ca, Ca:Al ratio, and EC_b. Soil Al

Table 3 Significant differences in soil variables (medians indicated) by presence and absence of *Carex globularis*, *Epilobium angustifolium*, *Geranium sylvaticum*, *Linnaea borealis*, *Luzula pilosa*, *Rubus saxatilis*, and *Trientalis europae* according Mann–Whitney test

	EC_b	pH	Ca:Al	C:N	Al	Ca	Co	Mg	Mn	Ni	Pb	S	Sr	Ti	Zn
C. globularis ($n = 17$)			0.08		599	68.3		25.0			0.50	24.4			0.60
Absent ($n = 102$)			0.02		1075	30.7		13.0			0.70	44.9			0.81
E. angustifolium ($n = 19$)			0.09	16.4	671	58.7		25.0			0.50	24.3			0.49
Absent ($n = 100$)			0.02	17.0	1075	30.3		13.0			0.70	44.9			0.82
G. sylcaticum ($n = 6$)	1.23		1.07	12.8	265	733.5		70.0		1.10		16.1	2.83	0.57	
Absent ($n = 113$)	0.51		0.02	16.9	1060	30.2		13.0		0.10		42.3	0.33	1.52	
L. borealis ($n = 28$)			0.10	15.1	570	57.2	0.30	26.5	11.65		0.50	20.1			
Absent ($n = 91$)			0.02	17.7	1200	27.0	0.10	12.0	2.58		0.70	45.5			
L. pilosa ($n = 20$)			0.08		706	62.9		21.5		0.20	0.50				
Absent ($n = 99$)			0.02		1090	28.4		13.0		0.10	0.60				
R. saxatilis ($n = 8$)	0.88	5.52	1.42	13.0	338	733.5	0.40	110.0	22.95	0.85		15.8	2.26	0.46	
Absent ($n = 111$)	0.51	4.71	0.02	16.9	1090	28.4	0.10	13.0	3.35	0.10		43.4	0.33	1.52	
T. europaea ($n = 9$)	0.61	5.14	0.62	13.6		326.0	0.20	56.0		0.40			1.19		
Absent ($n = 110$)	0.50	4.73	0.02	16.9		30.3	0.10	13.0		0.10			0.34		

Variables include soil electrical conductivity (EC_b; mS m^{-1}), pH, Ca:Al and C:N ratios, and elemental concentrations (mg kg^{-1})

concentration and Ca:Al ratio also varied between the three defined vegetation communities. The major measured variables defining indicator plant species distribution were soil Ca:Al ratio, Ca, Al, and Mg, whereas the major variable defining plant diversity was Ca concentration. Furthermore, correlations between plant diversity and soil Ca:Al ratio or EC_b were strong, yet correlations with Al did not occur. Therefore, the main soil variables determining understory composition and diversity were Ca:Al ratio and Ca concentration, one of the most important variables controlling plant species composition and diversity (Kinzel 1983). Ca-rich soils were characterised by high Mg concentration, pH, and EC_b, whereas Ca-poor soils were characterised by high C:N ratio and concentrations of Al, S, and Zn. Correlations with other elements occured occasionally. Lately the importance of the soil Ca:Al ratio, as an indicator of acidity and phytotoxicity, has received growing attention. Soil Ca:Al ratio less than one has been reported to indicate a risk of having adverse impacts on tree growth (Cronan and Grigal 1995), whereas the median ratio in our study sites was only 0.02. By the standard criteria, this suggests considerable risk of aluminium stress, although the critical values of Ca:Al ratio has been debated (Högberg and Jensén 1994; De Wit et al. 2001). Forest vegetation in the study area has probably adapted to acid conditions, and complexation with soil organic matter reduces Al toxicity (Walker et al. 1990; Berggren and Mulder 1995), so 1:1 ratio for the Ca:Al critical value is probably not applicable.

Concentration of soil Ca was higher than average in sites with *C. globularis*, *E. angustifolium*, *L. borealis*, *L. pilosa*, or *T. europaea*, and considerably high only at sites with *G. sylvaticum* and *R. saxatilis*. Calcifuge behavior of plants is usually caused by low solubility of cationic elements in calcareous soils (Tyler 1992, 1994, 1996). Different organic acid exudation patterns define the ability to solubilize chemical elements and therefore the ability to grow in particular soils (Treeby et al. 1989, Ström et al. 1994; Tyler and Ström 1995). Instead of the possible negative effects of very high Ca concentration, moderately high concentration with coexistence of other elements is favorable even to many so-called calcifuge species, e.g. *L. pilosa* is generally considered as calcifuge (Tyler 1994, 1996). All the above species indicated fertile soils, with the most notable positive correlations being with soil Ca, Ca:Al ratio, and Mg, and negative with Al. On the other hand, correlations with soil pH and EC_b were surprisingly weak, and there was no significant correlation between soil pH and Ca. Despite a low median, mean Pb concentration at sites with *L. borealis* was above average. However, Ca:Pb molar ratio, rather than the absolute concentration, determines Pb toxicity (Simon 1978; Eltrop et al. 1991), resulting from decreased Pb uptake (Garland and Wilkins 1981; Brown and Brinkmann 1992). Since mean Ca:Pb ratio was also above average at sites with *L. borealis*, detected Pb concentrations probably had no influence on vegetation. Altogether, the best indicators of Ca-rich soils, and also the most rarely occurring indicator species, were *G. sylvaticum* and *R. saxatilis*.

The three vegetation communities were characterized by different combinations of soil Ca concentration and water content. Plant species associated with community 1 sites were mainly hydrophilous (Hämet-Ahti et al. 1998; Reinikainen et al. 2001) and favoured Ca-rich soils with coexistence of high Mg concentration, pH, and EC_b. Canopy composition affects soil pH, C:N ratio, micro-organism composition, shading, moisture, temperature, and other microclimatological factors (Augusto et al. 2002; Barbier et al. 2008), and therefore understory species composition. Litterfall of deciduous trees is substantially more nutrient rich than in conifers (Augusto et al. 2002), and vegetation community 1 sites had high *Betula pubescens* coverage. Vegetation community 2 sites were intermediate on the soil Ca gradient, *Pinus sylvestris* canopy coverage was high, and hydrophilous species associated were *P. schreberi* and *R. tomentosum* (Hämet-Ahti et al. 1998; Reinikainen et al. 2001). Finally, *C. vulgaris*, *C. islandica*, *Cladina* spp., *Cladonia* spp., and *Dicranum* spp., hydrophobous species indicating infertile soils (Hämet-Ahti et al. 1998; Reinikainen et al. 2001), were associated with the Ca-poor community 3 sites with high concentrations of soil Al, Pb, S, and Zn. These dwarf shrub and *Cladina* dominated sites had a higher soil C:N ratio than those with herb rich vegetation, similarly to Elgersma and Dhillion's (2002) results, probably due to a higher litter lignin content which can hinder litter decomposition (Berendse et al. 1987; McClaugherty and Berg 1987; Berg et al. 1996). Total N, correlating with ammonium mineralization (Sjögersten and Wookey 2005), was high on dwarf shrub dominated Ca-poor vegetation community 3 (median 0.14%, 0.09% on other communities). Apart from this, there were no correlations with N or P (median 10–11 mg kg^{-1} in all communities), suggesting a low influence of detected variations to understory composition, although N is often found to be related to diversity in boreal forests vegetation communities (Diekmann and Falkengren-Grerup 1998).

Plant diversity was high at sites with high soil Ca concentration, Ca:Al ratio, and EC_b. Diversity is a scale-dependent pattern (Wiens 1989; Levin 1992), and the scale we used was very small, only two meters in radius, which explains the small Shannon diversity and species richness values. As Fig. 3 indicates, sites with considerably high diversity or high soil Ca concentration were few. Therefore communities did not differ notably in Shannon diversity, although species richness was about 30% higher in Ca-rich community 1 compared to others. At low Ca concentration diversity had no clear trend, indicating that only Ca > 100 mg kg^{-1} results in a considerable increase in diversity. The dependence on Ca was only slightly stronger than on Ca:Al ratio or EC_b, but there was significant correlations between Ca and Ca:Al or EC_b, similar to previous results by McBride et al. (1990). Diversity also increased with soil pH, as reported by many authors (Pärtel et al. 2004; Lenière and Houle 2006). Positive correlations between soil pH and Ca concentration, and therefore similar correlations with plant diversity are common (Koptsik et al. 2003; Rodríguez-Loinaz et al. 2008). However, we did not find a direct correlation with pH and Ca concentration, although Ca-rich soils were generally characterised by high pH.

Till chemistry was related to the source bedrock to some extent, the most notable variable being pH. However the important variables to understory composition such as soil EC_b, Al, Ca, and Mg were not associated with the bedrock. Similar to results by Akselsson et al. (2006), bedrock type alone was an insufficient variable to predict soil chemistry, and hence vegetation composition. Total Al concentrations of tills are high and total Ca concentrations are low on the Lapland granulite, and conversely on the Greenstone belt (Koljonen 1992; Reimann et al. 1998). With partial dissolution these differences are weaker (Koljonen 1992; Reimann et al. 1998), so comparison between till and bedrock using total elemental concentrations would probably offer better correlations. The Ca-poor community 3 sites were almost completely located on felsic bedrock, yet also a substantial part of the Ca-rich community 1 sites were located on felsic bedrock. Fisher and Binkley

(2000) reported a strong relationship between topographical position, soil chemistry, and vegetation composition in boreal forest soils due the downslope migration of water and elements. Processes related to downslope migration, glacial and postglacial dispersal, vegetation, and soil microbial composition may explain why many of the Ca-rich sites located on felsic bedrock. Human activity, particularly logging and other forestry related activities, also caused variation in both understory vegetation and soil properties.

Conclusions

The most important measured soil variables related to forest vegetation composition and diversity in the study area were Ca concentration and Ca:Al ratio. The Ca-rich soils in the study area were characterised by high Mg, pH, and EC_b, and by low Al, C:N, S, and Zn. Hokkanen (2006) studied vegetation and soil of herb-rich forests in Southern Finland and found that the most important soil variable affecting vegetation composition was soil water content, followed by Ca and N for bryophytes and Mg for vascular plants. Our results agree on the importance of soil Ca and Mg, but we found the relationship between vegetation composition and soil water content to be surprisingly low. However, the quality of the DP data was reduced in consequence of variation in time from the previous rains. Detected variation in total N appeared to have a low influence on understory composition, although soil-extractable N, a better estimate of plant-available nitrogen, was not measured. Soil Ca concentration higher than 100 mg kg^{-1} resulted in a considerable increase in plant diversity, yet sites with concentration this high were rare, and probably important in maintaining high biodiversity. The median soil Ca:Al ratio was only 0.02, indicating, according to general theory, considerable risk for aluminium stress. A significant long-term decrease of soil EC_b, correlating with Ca concentration, has been observed after mechanical site preparation in the study area (Sutinen et al. 2006). To maintain long-term forest productivity and to prevent eutrophication of waters due to leaching of nutrients, it is important to find methods for suitable mechanical site preparation. The strong influence of soil Ca concentration on vegetation composition should also be taken into account in forest classifications. *Geranium sylvaticum* and *Rubus saxatilis* were found to be especially good indicators of Ca-rich soil. Mapping these indicator species is a potential method for identifying areas of high biodiversity.

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