# Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities

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### Abstract

**Question:** What is the relationship between species richness of vascular plants, bryophytes and macrolichens, and two important gradients in the alpine environment, altitude and local topography?

**Location:** Northernmost Fennoscandia, 250-1525 m a.s.l. corresponding to the range between timberline and mountain top. **Methods:** The vegetation was sampled in six mountain areas. For each 25 vertical metres, the local topographic gradient from wind-blown ridge to snowbed was sampled in quadrats of  $0.8 \text{ m} \times 0.8 \text{ m}$ . Patterns in species richness were explored using Poisson regression (Generalized Linear Models). Functional groups of species, i.e. evergreen and deciduous dwarfshrubs, forbs, graminoids, mosses, hepatics and lichens were investigated separately.

**Results:** Functional groups showed markedly different patterns with respect to both altitude and topography. Species richness of all vascular plants showed a unimodal relationship with altitude. The same was true for graminoids, forbs and lichens analysed separately, but forb richness peaked at much higher altitudes than total richness. The richness of dwarfshrubs decreased monotonically with altitude, whereas richness of mosses and liverworts showed an increasing trend. Significant interactions between altitude and local topography were present for several groups. The unimodal pattern for total plant species richness was interpreted in terms of local productivity, physical disturbance, trophic interactions, and in terms of species pool effects.

**Conclusions:** Patterns in local species richness result from the action of two opposing forces: declining species pool and decreasing intensity of competition with altitude.

**Keywords:** Diversity; Elevation; Macro-ecology; Snowbed; Species density.

**Nomenclature:** Nilsson (1986) and Hallingbäck (1995, 1996) for vascular plants, lichens and bryophytes, respectively.

# Introduction

A general decrease in species richness of all organism groups with altitude has long been well-established (e.g. von Haller (1742) for vascular plants). This diversity decrease is a pattern conceptually and ecologically related to the often cited biotic depauperation from the Equator towards the poles (Körner 2000; Lomolino 2001), although many differences between these two patterns exist (Körner 1995; Rahbek 1995). Species richness approaches zero in the most extreme environments in the Arctic as well as on alpine summits, but the shape of, and the factors behind, the relationship are still much debated.

Measures of species richness are by nature scale dependent, as are relationships between species richness and environmental variables (e.g. Whittaker et al. 2001). Here, we address the actual species number of a small area of unit size, i.e. species density or  $\alpha$ -diversity. This diversity measure reflects the balance between impoverishment due to local processes, e.g. competition, and enrichment from a regional species pool (Ricklefs 1989). The importance of competition on community structure appears to be especially pronounced in benign environments, whereas in more stressful ones, competition appears to be relaxed (Grime 1973a, b, 1979; Sammul et al. 2000; Callaway et al. 2002) and the relative importance of the size of the regional species pool increases (Huston 1999; Pärtel et al. 2000; Foster et al. 2004). One possible explanation for relaxed competition in stressful environments is that mammalian herbivores are food-limited and exert strong impacts on the vegetation in the limiting season (Oksanen 1980; Moen & Collins 1996; Oksanen & Oksanen 2000; Olofsson et al. 2002). The unifying prediction of this set of hypotheses is that local species richness displays a unimodal ('hump shaped') relationship with altitude, given that primary productivity and species pool size decrease monotonically with altitude. The scenario is that in

productive lowland areas, species pools are larger, but local species richness is severely limited by competitive exclusion. Up to intermediate altitudes, local species richness increases, as the positive impacts of relaxed competition outweigh the negative impacts of decreasing species pool size. At high altitudes, local communities are supposedly just samples of the regional species pool and, as the size of the species pool declines with increasing altitude, so does local species richness.

Several recent studies have questioned the linearity of the relationship between altitude and  $\gamma$ -diversity of vascular plants, and have often found a diversity peak at intermediate altitudes (e.g. Colwell & Hurtt 1994; Rahbek 1995; Odland & Birks 1999; Grytnes 2003). Little is known and has been summarized on bryophyte and macrolichen richness, but see Pintado et al. (2001), Austrheim (2002), Negi & Upreti (2000) and Gradstein & Pócs (1989). In a recent review, Lomolino (2001) presented a theoretical framework for explanation of observed patterns of species pool size ( $\gamma$ -diversity) in relation to altitude. These were a sampling artefact explanation and four alternative biogeographical hypotheses on the altitude-diversity pattern: gradients of area, gradients of climate, isolation of alpine communities and feedback among zonal communities. Of these hypotheses, at least two predicted y-diversity to peak at intermediate altitudes.

Above the forest limit, plant species are, on the scale of local communities, distributed along a steep environmental gradient from snowbeds to wind-exposed ridges with little or no snow-cover during winter (Vestergren 1902; Gjærevoll 1956; Billings & Mooney 1968). The end-points of this gradient both represent extreme environments. The ridge has lower winter temperatures, mechanical stress of above-ground parts by wind-blown ice crystals, less reliable water supply, no nutrient inflow with seeping soil water etc., but a longer growing season (Körner 1999, Ch. 5). The ecological conditions of the snowbed represent the opposite states of the mentioned variables. The mid-point of the gradient represents a less extreme environment. One should therefore expect to find few species at the endpoints and more species towards the centre. The difference in productivity between moderate snowbeds and moderately wind-blown microsites may be at least two-fold (Fisk et al. 1998) and probably much bigger between the centre and margin of an extreme snowbed. The existence of a local gradient in diversity perpendicular to an overall altitudinal gradient raises the questions of (1) the relative importance of the gradients to species richness, and (2) the consistency of patterns in species richness with altitude given a high variability at the local topographical scale.

In this paper we investigate how local species rich-

ness of all plants and of different taxonomic and functional groups, i.e. bryophytes (mosses and hepatics), macrolichens and vascular plants (evergreen and deciduous dwarf-shrubs, forbs, graminoids), is influenced by altitude in a northern area where plant growth is primarily limited by low temperatures. In doing so, we follow the research agenda proposed by Lomolino (2001), but focus on both species pool effects and local interactions. In addition, we investigate how the species density of these groups is related to the local topographical gradients and to the interactions between altitude, topography and mountain identity.

# **Material and Methods**

#### Study areas

Six mountain areas from suboceanic and subcontinental parts of northernmost Fennoscandia were chosen. The areas were numbered as follows (Fig. 1): (1) Ivggegáisat (Lyngsalpene), Troms Fylke (Norway), 275-1525 m a.s.l.; (2) Ráisduottar, Käsivarsi (Finland and adjacent areas in Norway), 500-1275 m a.s.l.; (3) Dárju, Enontekiö (Finland), 450-725 m; (4) Jávrisduottar, Enontekiö (Finland) and southern Finmark (Norway), 450-575 m a.s.l.; (5) Čakčaduottar-Gáissat, Finmark (Norway), 400-1000 m a.s.l.; and (6) Čáhppisduottar, Inari Lapland (Finland), 250-425 m a.s.l. The ranges given are the minimum and maximum elevation of



**Fig. 1.** Map of northernmost Fennoscandia with the investigated mountain areas numbered: 1. Ivggegáisat (Norway); 2. Ráisduottar (Finland/Norway); 3. Dárju, (Finland); 4. Jávrisduottar (Finland/Norway); 5. Čakčaduottar-Gáissat (Norway); 6. Čáhppisduottar (Finland).

samples. The toponym suffixes 'duottar' and 'gáisat' are North Sámi for 'treeless area' and 'sharp peaks', respectively. All six subareas are dominated by granitic bedrock (see Oksanen & Virtanen 1995 for details). The climate is varying along a gradient from oceanic with copious snowfall and mild winters (subarea 1) to continental with low precipitation, thin snow cover, cold winters and at least discontinuous permafrost (subarea 4). We follow the traditional classification of alpine elevational vegetation zones: low alpine (from the forest line to upper limit of coherent stands of *Vaccinium myrtillus*), middle alpine (up to the limit of coherent vegetation cover) and high alpine (Sjörs 1967).

#### Vegetation data

Within each subarea, a transect was placed going from the forest limit upwards to the highest mountain peaks. At elevational intervals of 25 m the local topographic gradient was sampled. A 15 m rope was placed from the top of a hillock or ridge towards an adjacent depression, in most cases reaching a snowbed with maximal snow cover. Eight plots of  $0.8 \times 0.8$  m were placed at regular intervals along the rope, plot 1 on the ridge and plot 8 in the snowbed. In case of a plot falling on bare rock, no recording was made. Only local gradients without calcicolous species or other signs of aberrant geology were included. Thus, all transects represent silica-rich bedrock. In total 125 transects comprising 874 sample plots were investigated (Fig. 2). In each plot presence of all vascular plant, bryophyte and macrolichen species were recorded. Whenever possible, specimens were identified to the species level. In practice, the taxa representing the lichen family Lecideaceae and the genera Ochrolechia, Stereocaulon and Umbilicaria, the moss genera Andreaea, Brachythecium, Pohlia (excluding P. nutans), Pogonatum and Sanionia, and the liverwort genera Anthelia, Barbilophozia, Gymnomitrion, Lophozia and Scapania were treated as collectives. Therefore the species richness for these taxa is somewhat underestimated. The data have previously been subjected to numerical classification by Oksanen & Virtanen (1995). Rare species omitted for those analyses have been retained in the present study.

Species were assigned to functional types differing in important attributes of resource capture and effect on the ecosystem (Chapin et al. 1996), viz. trees and shrubs (n = 6); evergreen dwarf-shrubs (n = 17); deciduous dwarf-shrubs (n = 7); forbs (n = 55); graminoids (n =25); liverworts (n = 9); mosses (*Bryopsida* + *Andreaeopsida*; n = 30) and macrolichens (n = 54). Lichens were almost exclusively arbuscular or foliolose, and mainly belonged to the genus *Cladonia*. The few thallous *Peltigera* species constituted too small a group to warrant further subdivision. The group of trees and shrubs was not considered any further. A list of taxa and their abundances can be found in App. 1.

#### Data analysis

The altitude of the forest limit is quite variable within the study area, depending on climate (lower in the more oceanic areas) and grazing history (Oksanen et al. 1995). Therefore, the approximate altitude of the forest limit was set to zero for each altitudinal transect. This altitude ranged between 275 and 525 m a.s.l. Since *Betula* forest extends farther up in depressions than on ridges, the altitude of the forest limit between these extremes was used. In some cases one or two topographical transects were included from below this limit (and given a negative value). Together with the variable vertical extension of the investigated mountains, this resulted in some variation in the number of samples from each (calibrated) altitude (Fig. 2).

The response of species richness to altitude and topography, and to the interaction between these variables, was modelled by means of generalized linear modelling (GLM; McCullagh & Nelder 1989) as implemented in S-plus (Hastie & Pregibon 1993) with a Poisson error distribution and logarithmic link function as is usual for variables with discrete values (McCullagh & Nelder 1989). The random effects of transects within subareas were estimated by fitting the subarea identity as a dummy variable first. Thereafter models were built by sequentially adding altitude, its interaction with subarea, topography and the three-way interaction. In the case of altitude and topography, the linear function was included by default, and the quadratic function only included if it explained significantly more of the variation than the linear function. In addition, models were built for topography alone after taking subarea into account. For plotting of relationships between species richness and explanatory variables individually, GLM models were built for that variable only (i.e. without random effects and interaction terms). Spatial autocorrelation cannot be ruled out (plots were nested in topographical transects, which were nested in altitudinal transects). Therefore, the reported p-values are approximate and we have chosen to only consider *p*-values smaller than 0.01 as significant.

Subarea 1 Subarea 2 Subarea 3 30 otal richness otal richness otal richness 200 400 600 1000 1200 0 200 400 600 800 1000 1200 200 400 600 800 1000 1200 0 800 0 Altitude Altitude Altitude Subarea 4 Subarea 5 Subarea 6 30 30 otal richness otal richness Total richness 20 20 200 400 600 1000 1200 200 400 600 800 1000 1200 200 400 600 1000 1200 800 0 800 Altitude Altitude Altitude

**Fig. 2.** Total species richness in relation to altitude (from 50 m below to 1200 m above the forest limit) plotted for each of the investigated mountain areas (subareas) separately. The figures give an indication of the number of samples originating from each mountain area and the distribution along (calibrated) altitude. Subarea numbers correspond to Fig. 1.

#### Results

The GLM showed a significant quadratic response in total species richness with altitude (Table 1, Fig. 3). The total richness peaked approximately 400 m vertically above the forest limit. This result was very similar to that for macrolichens, which constituted the most speciose functional group. The species richness of all vascular plants had a less marked, yet significant, quadratic response to altitude. However, between 0 and 700-800 m above the forest limit, mean vascular plant richness was reasonably constant, and the significant relationship was created by the much lower richness in the high-alpine plots. The less marked pattern for all vascular plants was fully compensated for by the different functional groups of vascular plants showing marked and differential trends in relation to altitude. The richness of dwarf-shrubs, both deciduous and evergreen, decreased with altitude, for the evergreen ones monotonically so, whereas deciduous dwarf-shrub richness peaked just 100-200 m above the forest limit. In contrast to these patterns, the richness of graminoids and forbs peaked far above the forest limit. For graminoid richness, the maximum values were, similarly to total and lichen richness, attained approximately 400 m above the forest limit. The richest quadrats in terms of forb number were found approximately 500 m above the forest limit, but mean richness of forbs peaked in the high-alpine

zone ca. 800 m vertically above the forest limit. This peak was attributable to the rather constant occurrence of alpine specialist forbs, e.g. *Oxyria digyna*, *Ranunculus glacialis*, *R. nivalis* and *Saxifraga cernua*.

Like richness of vascular plant groups, cryptogam group richness showed marked and differential trends with altitude (Table 1, Fig. 3). Lichen richness increased from the forest limit up to a maximum at ca. 400 vertical m above, and thereafter a gradual decrease. The species responsible for the peak were an array of *Cladonia* spp. (most notably *C. bellidiflora*, *C. gracilis* ssp. *elongata*, *C. macrophylla* and *C. uncialis*), *Cladina mitis*, *Cetraria* spp. (most notably *C. ericetorum* and *C. islandica*), *Lecidea* spp.,*Nephroma arcticum* and *Peltigera rufescens*. None of these species are alpine specialists.

The richness of both mosses and liverworts showed a significant increase with altitude, steepest for liverworts. For mosses, the richest quadrats were found at 600-700 m above the forest limit, but mean richness increased in the high-alpine quadrats. The peak in the middle alpine zone was mainly attributable to bryophytes: Andreaea spp., Conostomum tetragonum, Kiaeria starkei, Oligotrichum hercynicum, Pohlia spp. (except P. nutans), Racomitrium lanuginosum and R. microcarpon. These species constitute a mix of alpine specialists (Conostomum, Kiaeria and Pohlia) and generalists, some species in both groups are associated with disturbed soil or boulders in the soil surface.



**Fig. 3.** The relationship between species richness (total and in the functional groups of total vascular plants, deciduous dwarf-shrubs, evergreen dwarf-shrubs, forbs, graminoids, lichens, mosses, and liverworts) and altitude depicted as scatterplots with GLM functions superimposed. Altitude runs from 50 m below to 1200 m above the forest limit. Note that the scale of the ordinate is variable.

**Table 1.** Generalized linear models (F-values shown) of total species richness and richness of functional groups in relation to altitude (Alti) and local topography (Topo), both as linear and quadratic functions, as well as their interactions. Subarea was taken into consideration first. df = residual degrees of freedom. The residual degrees of freedom were slightly different in the models for mosses and liverworts because the quadratic function of altitude was not significant and hence not included in the model. n.s. = not significant; \* =  $p \le 0.001$ ; \*\*\* =  $p \le 0.0001$ .

	df	Total species richness	Vascular plant richness	Deciduous dwarf-shrubs	Evergreen dwarf-shrubs	Forb richness	Graminoid richness	Lichen richness	df	Moss richness	Liverwort richness
NULL (subarea)	868								868		
Alti	867	10.91 **	118.11 ***	202.84 ***	200.41	0.09 n.s.	12.85 **	0.01 n.s.	867	12.1 **	46.27 ***
Alti <sup>2</sup>	866	173.52 ***	80.96 ***	53.71 ***	16.02 ***	9.21 **	153.59 ***	93.32 ***	866	6.35 n.s.	3.99 n.s.
Subarea × Alti	856	10.56 ***	8.88 ***	9.29 ***	3.13	2.43	2.58 *	11.94 ***	862	19.60 ***	11.89 ***
Торо	855	16.16 ***	40.67 ***	0.10 n.s.	4.38 n.s.	13.61 **	34.20 ***	83.07 ***	861	0.52 n.s.	11.89 *
Topo <sup>2</sup>	854	0.30 n.s.	0.75 n.s.	2.81 n.s.	0.85 n.s.	0.16 n.s.	1.53 n.s.	0.03 n.s.	860	8.88 *	1.83 n.s.
Subarea $ imes$ Alti $ imes$ Topo	820	0.99 n.s.	1.34 n.s.	1.69 *	3.14	2.52 ***	2.63	1.65 n.s.	832	0.76 n.s.	4.71 ***

**Table 2.** Generalized linear models (F-values shown) of total species richness and richness of functional groups in relation to local topography (Topo). Subarea was taken into consideration first. In the cases of total richness, deciduous dwarf-shrubs, evergreen dwarf-shrubs and liverworts, the quadratic model was tested directly against the null model. n.s. = not significant;  $* = p \le 0.01$ ;  $** = p \le 0.001$ ;  $** = p \le 0.0001$ .

	df	Total species richness	Vascular plant richness	Deciduous dwarf- shrubs	Evergreen dwarf- shrubs	Forb richness	Graminoid richness	Lichen richness	Moss richness	Liverwort richness
NULL (subarea)	868									
Торо	867	3.59 n.s.	63.32 ***	2.70 n.s.	0.06 n.s.	74.89 ***	46.10 ***	46.42 ***	1.77 n.s.	19.25 ***
Topo <sup>2</sup>	866	0.75 n.s.	1.84 n.s.	3.85 n.s.	0.14 n.s.	1.22 n.s.	1.97 n.s.	0.00 n.s.	5.95 *	1.32 n.s.

Liverworts did not contribute much to the total species richness at any altitude. Only beyond 1000 m above the forest limit, the mean number of liverwort species per quadrat was > 1. However, the mean liverwort richness and their relative contribution to total richness appeared to increase with altitude. The species mainly responsible for the high-alpine richness peak were *Anastrophyllum minutum* and *Tetralophozia setiformis*.

Local topography from ridges to snowbeds added significant explanatory power to the model for total species richness, as well as for vascular plants, forbs, graminoids, lichens and liverworts (Table 1). However, when topography was fitted after subarea, excluding altitude, the model for total richness was not statistically significant (Table 2). This was due to opposite diversity trends among functional groups, with richness of lichens and liverworts decreasing away from wind-blown ridges and richness of forbs, graminoids and vascular plants as a whole increasing along the same gradient (Fig. 4). Moss richness showed a weak unimodal response to topography. This relationship was only significant when subarea was included in the model.

The interaction term between altitude and subarea was significant for total species richness and for all subgroups (Table 1). This was mainly attributable to a narrower unimodal response curve of richness to altitude in the subarea Čakčaduottar-Gáissat, and to a lesser extent the subarea Ráisduottar (Fig. 2). If Čakčaduottar-Gáissat was omitted from the data, most significant interaction terms disappeared and the remaining were only marginally significant. There was no obvious reason to expect species richness patterns to be markedly different in this mountain area, and we have chosen to analyse all subareas together in order to obtain as general results as possible.

The three-way interaction between subarea, altitude and topography was significant for deciduous and evergreen dwarf-shrubs, forbs, graminoids and liverworts. In order to partial out which factors contributed most to a significant three-way interaction, a forward selectionlike procedure of adding interaction terms to the simplest significant GLM model without the three-way interaction was used. First, the interaction term for topography  $\times$  subarea and for topography  $\times$  altitude were added in separate models and tested against a model adding both. The best of these three models was tested against the model altitude × topography × subarea. For deciduous dwarf-shrubs, this procedure showed that only the interaction between topography and altitude added significant explanatory power to the simple model (df = 850, F = 3.98, p = 0.0014). For evergreen dwarfshrubs, the model adding both topography  $\times$  subarea and topography  $\times$  altitude simultaneously was the best (df = 840, F = 3.77, p = 0.0047). For forbs, the full threeway interaction altitude  $\times$  topography  $\times$  subarea not only was the best model, but the only interaction model adding significantly to the simple model. For graminoids, adding the term topography × subarea improved the simple model significantly, whereas adding topography  $\times$  altitude did not. Nevertheless, the best model was the full three-way interaction model altitude  $\times$ topography × subarea. Finally for liverworts, all interaction models were significant, and the best model was the full three-way interaction model altitude  $\times$  topography  $\times$ subarea. The interaction model results are not easily interpreted. The simplest to interpret is the interaction between topography and altitude. For example, the increase in liverwort species richness with altitude mainly took place on ridges, and was attributable to species like Gymnomitrion spp. and Tetralophozia setiformis. However, the analysis of the three-way interaction shows that patterns of species richness along gradients in altitude and local topography, to some extent, are idiosyncratic to each mountain area.

Comparison of GLM models for altitude and topography separately (Table 1 and 2) showed that altitude was a better predictor of species richness than local topography for all species taken together as well as for nearly all species groups. However, forbs showed the opposite pattern, i.e. the major trends in forb species richness were a strong increase away from ridges at all altitudes and a relatively weak tendency for forb richness to increase from low alpine to middle alpine and to decrease again in the high alpine zone.



**Fig. 4.** The relationship between species richness (total and in the functional groups of total vascular plants, deciduous dwarf-shrubs, evergreen dwarf-shrubs, forbs, graminoids, lichens, mosses, and liverworts) and local topography depicted as scatterplots with GLM functions superimposed. The size of the points (bubbles) indicates the number of data points behind. Local topography runs from snow-covered depressions (1) to wind-blown ridges (8). Note that the scale of the ordinate is variable.

# Discussion

The present analyses of the relationship between altitude and plant species richness revealed both expected and unexpected patterns. Perhaps most importantly, we found total plant  $\alpha$ -diversity to peak at intermediate altitudes, but with considerable variation over functional groups. In addition, significant interactions between altitude and topography were found.

Behind the unimodal response in total number of species along the altitudinal gradient a number of patterns for separate plant functional groups was hidden, which included both monotonically decreasing (evergreen dwarfshrubs) and increasing groups (liverworts), as well as groups peaking at markedly different altitudes than total richness (e.g. deciduous dwarf-shrubs at lower altitude and forbs at higher altitude). Differences in diversity patterns for vascular plants and cryptogams have been reported previously (e.g. Oksanen 1983; Slack 1984; Herben 1987; Minchin 1989), but the between-group variation in richness patterns was stronger and more diverse than we would have anticipated from the existing literature.

The data did not allow us to directly evaluate the patterns of  $\alpha$ -diversity with altitude. However, the total Scandinavian species pool of low-alpine vascular plant species is much bigger than pools of middle- and high-

alpine species (ca. 400, 140 and 40 species respectively; counted from Nilsson 1986). This tentatively indicates that the regional species pool size decreases monotonically with altitude, even at the sub-regional level. The monotonically decreasing pattern has also been found for total species richness in the southern Scandes Mountains (Austrheim 2002). This observation, however, need not be true for all the functional groups discussed here.

The unimodal response of total species richness to altitude matched the predictions of Grime (1973a, b, 1979), emphasizing direct impacts of stress on the intensity of plant-plant competition, and to those of the natural grazing pattern hypothesis (Oksanen 1980; Oksanen & Ranta 1992; Moen & Collins 1996), emphasizing the indirect effects mediated via differences in natural herbivory pressure. Up to the altitude of about 400 m above the timberline, the positive impact of relaxing competition appeared to override the negative impact on decreasing species pool on  $\alpha$ -diversity. At higher altitudes, where competitive interactions appear to be relaxed,  $\alpha$ -diversity appeared to follow the decreasing altitudinal trend in the size of species pool.

Grime's (1979) intermediate stress hypothesis is, by and large, consistent with the heterogeneity of the groupspecific responses. Woody plants, with primarily boreal distribution and limited ability to cope with cold stress (Dahl 1957), are the first to decline. Deciduous dwarfshrubs extend upwards until the upper limit of the low alpine zone. Rhizomatous dwarf-shrubs, especially evergreens, dominate the low-alpine ecosystem, but are more sensitive to soil cryoturbation than are graminoids and forbs (Jonasson & Callaghan 1992). Strong dominance of Ericaceous dwarf-shrubs at low to intermediate altitudes appears to limit species richness of other growthforms. Conversely, decreased dwarf-shrub dominance at intermediate to high altitudes seems to give way to subordinate species. This was especially evident for graminoid richness, which increased upwards to a peak around the lower parts of the mid-alpine zone. Also lichen richness appeared to peak at approximately the same level. The richest sampling quadrats in terms of forbs were found at the same altitude, but mean forb richness peaked at the highest levels of the mid-alpine zone. This clearly indicates that forb species pool size was higher at a lower altitude than the peak in mean forb richness.

The peak in richness of macrolichens at ca. 400 m above the forest limit was not generated by arctic-alpine specialists, but rather by generalist species, which are common even in lowland forests. Since these lichens are small and heliophilic, it seems likely that the high abundance of more competitive plants accounts for their lower species richness in the low alpine zone, providing further corroboration for the viewpoint that competition limits local species richness. The scarcity of terricolous lichens and the abundance of forbs coinciding in high-alpine habitats could be interpreted as an outcome of competition between plants regaining importance towards high altitudes because the impact of herbivorous mammals weakens as phytomass production declines below a threshold critical to support this trophic level (Oksanen 1980; Moen & Collins 1996; Oksanen & Oksanen 2000).

Bryophytes, known for their ability to tackle the extreme cold of Antarctica and High Arctic islands (e.g. Longton 1988; Virtanen et al. 1997b; Heegaard 2002) reached their maximum species richness at the highest altitudes in the investigated area. One possible factor contributing to the patterns is the pioneer strategy of many bryophytes. The abundance of bare mineral soil increases with altitude and, whereas seed production of angiosperms is probably limited by low temperatures (Khodatchek 1997; Molau & Larsson 2000), this may be less pronounced for the spore production of cryptogams. However, the decline in another group of stress-tolerant plants – lichens – and the increase in the species richness of forbs at high altitudes are more difficult to reconcile with this interpretation.

Another potential explanation for the species richness maximum at mid-altitudes is the environmental heterogeneity hypothesis of Rosenzweig & Abramsky (1993), which proposes that diversity is positively related to heterogeneity, which in turn peaks with intermediate productivity. However, if environmental heterogeneity were the primary reason for the peak in local species richness, the peak should be at approximately similar altitudes for all functional plant groups, which was not found. Moreover, due to the small grain size of our data, heterogeneity should exist at a very small spatial scale to provide a plausible explanation for the observed patterns.

It is worth noting that the unimodal diversity-altitude curve would not have appeared without the inclusion of extreme habitats in the upper alpine zone and the inclusion of all species at the same trophic level despite taxonomic affiliation. These points may help explaining why empirical diversity-productivity patterns are not always unimodal, but often vary with the extent of investigation and among taxonomic groups (Mittelbach et al. 2001).

The patterns of species richness with local topography from ridges to depressions have not attracted much attention in the literature, although it is implicit in many phytosociological studies (e.g. Vestergren 1902; Ochsner 1954; Gjærevoll 1956; Bültmann & Daniels 2001). We found variable patterns for the functional groups considered. The richness of the comparatively species-poor, but ecologically significant, groups of deciduous and evergreen dwarf-shrubs seemed to be little affected by topography. Species richness of liverworts appeared to peak on ridges, but due to lack of taxonomic resolution for this group, the pattern should be interpreted with caution. The unimodal relationship of bryophytes to topography may indicate a direct impact of exposure and duration of snowfree periods. An alternative explanation is periodically intense lemming grazing, which, particularly in habitats with moderate snow cover, favours coexistence of potentially dominant bryophyte species (Moen et al. 1993; Virtanen et al. 1997a, 2002).

The importance of altitude in explaining trends in species richness was superior to local topography for all species groups except forbs. The overall result is perhaps explicable from the fact that the topographical and altitudinal gradients operate at different spatial scales, with the former nested within the latter. The aberrant pattern for forbs was probably due to the strong increase in forb species richness towards situations with a moderate snow cover in winter. The complicated interactions between altitude and topography indicate that asking for the relative importance of these two factors may have been too simplistic. Graminoids and forbs showed low but constant species numbers along the altitudinal gradient as long as only wind-swept ridges were considered, but a marked increasing trend with altitude as snowbed communities were approached. The opposite appeared to be the case with liverworts, which only exhibited an increase in species richness on the ridges. These results call for studies of the altitudinal patterns in species richness that include local heterogeneity, such as the topographical gradient in productivity and environmental stress

described here, edaphic factors (Wilson et al. 1990) or macro-aspect of mountain slopes (Mark et al. 2001).

Recently, there has been some focus on geometric constraints on species richness (e.g. Rahbek 1997; Jetz & Rahbek 2001; Grytnes & Vetaas 2002; but see Laurie & Silander 2002), i.e. towards the hard boundaries, such as edges of continents, mountain tops and valley bottoms, species richness tends to decrease even under a null model of random distribution limits of species. This should affect species density through a positive relationship between community and local species pool size. Still, species density should be relatively unaffected by geometric constraints. Similarly to the present study, Austrheim (2002) found species density to peak at intermediate elevations while total species richness decreased monotonically with elevation in the southern Scandes Mountains. Apart from the hard upper boundary created by mountain tops, we had a soft boundary, as many species' distributions are likely to continue downwards into the subalpine forest. However, on the coast of the Arctic Ocean, the Fennoscandian tundra may extend down to sea level, leading to a hard lower boundary.

In conclusion, both biotic factors, i.e. decreasing immigration of ubiquitous species with altitude, and abiotic factors contributed to explaining the patterns of species richness in relation to altitude. Patterns in local species richness seemed to derive primarily from the action of two opposing forces: declining species pool and decreasing intensity of competition with altitude.

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