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Original article

Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway

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ABSTRACT

Species richness patterns of ground-dwelling vascular plants, bryophytes, and lichens were compared along an altitudinal gradient (310–1135 m a.s.l.), in western Norway. Total species richness peaked at intermediate altitudes, vascular plant species richness peaked immediately above the forest limit (at 600–700 m a.s.l.), bryophyte species richness had no statistically significant trend, whereas lichen richness increased from the lowest point and up to the forest limit, with no trend above. It is proposed that the pattern in vascular plant species richness is enhanced by an ecotone effect. Bryophyte species richness responds to local scale factors whereas the lichen species richness may be responding to the shading from the forest trees.

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1. Introduction

The change in vegetation along a mountainside is conspicuous. It is therefore natural that changes in species composition and species richness along altitudinal gradients have been studied by ecologists for a long time (Lomolino, 2001). Despite the many studies of species richness patterns along altitudinal gradients no consistent altitudinal species-richness pattern has emerged so far. Some of the studies involving vascular plants have found maximum species richness at intermediate altitudes (e.g. Whittaker, 1960; Whittaker and Niering, 1975; Lieberman et al., 1996; Kessler, 2000; Grytnes and Vetaas, 2002; Grytnes, 2003), whereas other studies of the same taxonomic group report monotonically decreasing trends (e.g. Hamilton, 1975; Shmida and Wilson, 1985; Gentry,

1988; Kitayama, 1992; Vazquez and Givnish, 1998; Odland and Birks, 1999; Grytnes, 2003; Fosaa, 2004). Similar non-consistent results have also been reported from other taxa (Rahbek, 1995).

Comparison of different taxonomic groups along the same altitudinal transect may give valuable information in our effort to understand altitudinal species richness patterns (Lomolino, 2001). Diversity studies have only rarely been carried out on bryophytes (Lee and La Roi, 1979), lichens (Holién, 1997), or both (Wolf, 1993; Mucina et al., 2000). As far as we are aware, no studies have compared the species richness of these cryptogams with vascular plant richness along altitudinal gradients. Earlier studies of richness patterns along gradients other than altitude, have demonstrated that vascular plants, bryophytes, and lichens, often show different patterns (Pausas, 1994; Dirkse and Martakis, 1998; Molau and Alatalo, 1998; Pharo et al., 1999).

The most conspicuous and perhaps the most discussed phenomenon along altitudinal gradients is the forest limit

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or treeline (Körner and Paulsen, 2004). Because this feature is so evident, it is often believed that this represents a critical altitude where species composition and diversity change abruptly, reflected in, for example, the division of vegetation zones or flora elements in boreal (below forest line) and alpine (above forest line) (Dahl, 1998; Moen, 1999). Such abrupt changes or ecotones may cause inflation of species richness due to mass effects or source sink effects (Shmida and Wilson, 1985; Pulliam, 1988). Mass effect is the establishment of species in sites where a self-maintaining population cannot exist (Shmida and Wilson, 1985), and in areas like the forest-alpine transition some species from the forest may establish short-lived populations (sinks) in the alpine area and vice-versa resulting in inflated species richness around the ecotone.

The aims of our paper are twofold. First, describe and compare the altitudinal richness patterns of vascular plants, bryophytes, and lichens along one altitudinal transect, and second, examine the influence of the tree-line ecotone on these patterns.

2. Study area and methods

The study area (60°13'N and 6°15'E) is situated in the Jondalen municipality close to the Hardangerfjord in Hordaland province, western Norway. The area has an oceanic climate with a precipitation of 2200 mm/year (342 m above sea level (a.s.l.), Førland, 1993), and with relatively warm winters and cold summers. The selected altitudinal gradient is a north-facing hillside and starts at lake Torsnesvatnet at 310 m a.s.l. and ends on the summit of a local mountain, 1135 m a.s.l. To avoid possible biases due to different aspects we started the transect at 300 m. The hillside is steep (the 825 vertical metres of the transect is along approximately 1200 horizontal metres) but towards the local summit where the transect ended the slope becomes more gentle. The bedrock of the hillside is composed of acidic and hard granite (Holtedahl and Dons, 1960).

The lower part of the gradient is a birch (*Betula pubescens*) forest interspersed with *Sorbus aucuparia*, and with *Athyrium filix-femina*, *Linnaea borealis*, *Melampyrum pratense*, and *Vaccinium myrtillus* as the most common species in the field layer. Here, lichens are almost absent, whereas the bryophytes *Mnium hornum*, *Plagiomnium undulatum*, and *Plagiochila asplenoides* are quite common. At altitudes ranging from about 350 to about 550 m, pine (*Pinus sylvestris*), interspersed with *B. pubescens*, is the dominant forest tree, with *V. myrtillus*, *V. uliginosum*, *V. vitis-idaea*, and *Calluna vulgaris* as the most common species in the field layer. *Cladonia* species are well represented but cover only small areas. Common bryophytes include *Dicranum majus*, *Ptilium crista-castrensis*, *Aulacomnium palustre*, and *Bazzania trilobata*. Above the forest limit, which is at approximately 600 m (set to 615 m in this study because we had our last sample with trees at 610), the vegetation is a mosaic with mires, containing *Eriophorum vaginatum*, *Rubus chamaemorus*, *Narthecium ossifragum*, and various *Sphagnum* species in small depressions, and ericaceous shrubs like *Empetrum nigrum*, *Loiseleuria procumbens*, and *Vaccinium* species

dominating in drier areas. Lichens become more abundant, and include, for example, *Cetraria delisei*, *C. islandica*, *Cladonia arbuscula*, *C. coccifera*, *C. gracilis*, and *C. mitis*. Bryophytes common at higher altitudes include *Racomitrium lanuginosum*, *Ptilidium ciliare*, *Barbilophozia lycopodioides*, *Kiaeria starkei*, and *Conostomum tetragonum*. Common throughout the altitudinal gradient are *Hylocomium splendens*, *Pleurozium schreberi*, *Sphagnum* spp., *Polytrichum commune*, and *Rhytidiadelphus loreus*.

There were 42 quadrats, each 25 m², placed along the transect at intervals of approximately 20 vertical metres. Wet or very dry places were avoided when placing the plots. The placement of the plots was constrained by topography (steepness and availability).

In each plot all ground-dwelling vascular plants, bryophytes and lichens were recorded, omitting all epiphytic and epilithic species. We omitted epiphytic and epilithic species because including these species would probably cause a major bias when comparing vascular plant pattern with bryophyte and lichen patterns as epiphytic or epilithic vascular plant species are almost absent in the area. We found it therefore most meaningful to compare the three groups of organisms by considering only specimens growing on soil. All identifications were done in the field, except for some *Cladonia* and bryophyte specimens that were brought to the laboratory for microscopical and chemical examination. A total of 63 lichen specimens was examined by thin-layer chromatography (TLC) according to the method of Culberson and Kristinsson (1970), with later modifications. Nomenclature of vascular plants follows Lid and Lid (1994), for bryophytes Frisvoll et al. (1995), and lichens Santesson et al. (2004). *Cladonia ecmocyna* Leight. and *C. maxima* (Asahina) Ahti are here treated as the same species.

Generalised linear models (GLM, McCullagh and Nelder, 1989) were used to relate species richness of the three taxonomic groups and all groups combined to altitude. As the response variables are counts, we assume a Poisson distribution and a logarithmic link. An inspection of the diagnostic plots confirmed that this performed better than a normal distribution and identity link. Using a parametric GLM restricts the estimated pattern very much, and any abrupt changes around ecotones will in most cases not be detected by GLM. We therefore used a cubic smooth spline, within the framework of generalised additive models (GAM) (Hastie and Tibshirani, 1990), to evaluate whether any trends in the data that could not be captured by parametric regression were present. To describe the relationship between species richness and altitude we constructed five different models, two with GLM (a linear and unimodal relationship), and three with GAM (using three to five degrees of freedom, respectively). An F-test was performed to choose the best of the five models. Even though the vascular plant species richness pattern is described earlier (Grytnes, 2003), the main findings for this group are described here as well to ease comparison with lichen and bryophyte richness patterns.

In order to quantify the major changes in species composition, a correspondence analysis of the species data were performed, using Canoco for Windows 4.0 (ter Braak and Šmilauer, 1998). Species that could not be identified to species level and were found in several samples were made passive in the ordinations. Three separate ordinations were

made for the taxonomic groups separately to evaluate if the three groups responded differently to altitude, and especially if there is a change in response to the forest limit. For this we considered only the first axes of the CA ordination, which is assumed to summarise the major trend in species composition. The sample scores of this axis were used as a response variable in a regression where altitude was used as a predictor variable. Since we are explicitly looking for abrupt changes in the relationship we used smoothing spline to describe the trend in species composition with altitude. We made nine different models using from one to nine degrees of freedom and chose the model with the lowest Mallows Cp (Hastie and Tibshirani, 1990). If the forest line is a critical altitude for the species composition there will be a steeper slope of the line describing the relationship between altitude and the first CA-axis around the forest line.

3. Results

Total species richness showed a unimodal relationship with altitude. The smooth spline did not significantly improve the fit. Maximum species number occurred at about 750 m above sea level (Fig. 1a).

The altitudinal patterns of species richness clearly differed between taxonomic groups (Fig. 1). This was also indicated by the low correlations between species richness of vascular plants, bryophytes, and lichens. The highest correlation coefficient was found between bryophyte and lichen species richness ($r = 0.076$), the vascular plant species richness and bryophyte species richness correlation was slightly less $r = 0.074$, and the vascular plant and lichen richness correlation was 0.033. Vascular plant species richness showed a humped relationship with altitude. The second-order polynomial statistically explained about 50% of the null deviance (Table 1). A statistically significant improvement was achieved with smooth spline with five degrees of freedom and this model described a sharp hump between 600 and 800 m (Fig. 1b). The number of bryophytes showed no statistically significant relationship with altitude (Fig. 1c). The polynomial model for lichen species richness indicates a humped relationship with a maximum slightly below the maximum altitude investigated. The smooth spline indicate a rather steep increase in species richness with altitude up to approximately 600 m (the forest limit) and a more moderately increasing species richness above this altitude (Fig. 1d).

The first axis of the CA ordination is clearly related to altitude for all three taxonomical groups (Fig. 2). The best smoothing spline model found with our approach used three

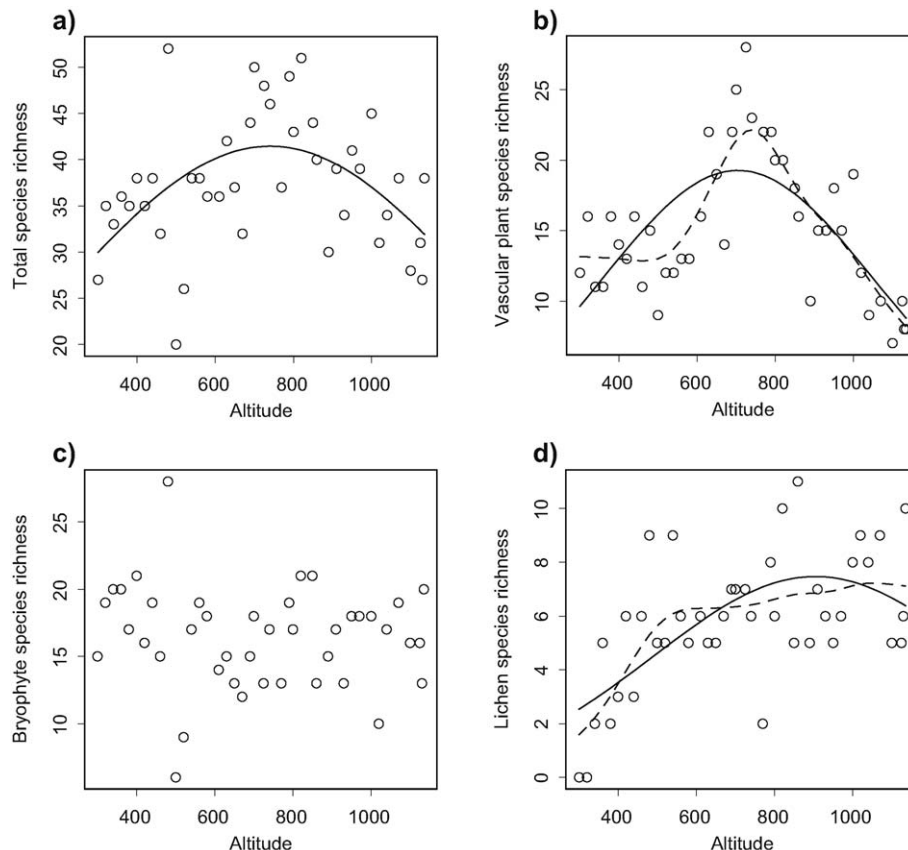


Fig. 1 – Scatterplots of the relationship between species richness and altitude. The unbroken line is the polynomial regression line, whereas the broken line is the fitted line using a cubic smooth spline (cf. Table 1). a) shows the unimodal relationship between total species richness and altitude, b) shows the mid-altitude hump in vascular plant species richness, c) shows the constant bryophyte species richness with altitude, and d) shows the steep increase in lichen species richness up to 600 m and that above this altitude only a weak trend with altitude is present.

Table 1 – Summary of the regression models between species richness as response variable and altitude as predictor variable. The statistically best model is in bold. The results are graphically displayed in Fig. 1. The models are either GLM with first- or second-order polynomial (p1 or p2, respectively), or GAM (with cubic smooth spline) using three to five, or six degrees of freedom (s3, s4, s5, s6). The F and P-value refers to the test described in the test column. Res. dev = residual deviance

	Res. dev	Test	F	P
<i>Total species richness</i>				
Null	56.93			
p1	56.67	Null vs. p1	0.18	0.67
p2	42.87	Null vs. p2	6.63	0.0033
s3	39.88	p2 vs. s3	2.9	0.097
s4	38.33	p2 vs. s4	2.28	0.116
s5	36.75	p2 vs. s5	2.03	0.127
<i>Vascular plant species richness</i>				
Null	67.5			
p1	66.85	Null vs. p1	0.38	0.54
p2	33.75	Null vs. p2	19.73	0.000012
s3	24.57	p2 vs. s3	14.17	0.00054
s4	20.96	s3 vs. s4	6.49	0.015
s5	18.58	s4 vs. s5	4.65	0.038
s6	16.82	s5 vs. s6	3.69	0.063
<i>Bryophyte species richness</i>				
Null	37.88			
p1	37.52	Null vs. p1	0.41	0.53
p2	36.43	Null vs. p2	0.81	0.45
s3	35.30	Null vs. s3	0.96	0.42
s4	34.58	Null vs. s4	0.92	0.46
s5	33.86	Null vs. s5	0.89	0.5
<i>Lichen species richness</i>				
Null	55.70			
p1	42.91	Null vs. p1	14.5	0.00047
p2	36.60	p1 vs. p2	7.77	0.0081
s3	32.53	p2 vs. s3	5.43	0.025
s4	29.35	s3 vs. s4	4.02	0.049
s5	27.35	s4 vs. s5	2.87	0.099

degrees of freedom for bryophytes and lichens and five degrees of freedom for vascular plants. The explanatory power is high for the models ($R^2 = 0.90$ for vascular plants, 0.88 for bryophytes, and 0.67 for lichens). The similarity of species composition gradients are also demonstrated by the high Pearson correlation coefficients between the first CA axis sample score for the groups ($r = 0.95$ between vascular plants and bryophytes, 0.75 between vascular plants and lichens, and 0.72 between bryophytes and lichens). It is clear that the change in species composition of vascular plants and bryophytes is less abrupt around the tree line than anywhere else along the gradient contrary to the expectation that there are abrupt changes in species composition around the tree line (Fig. 2a, b). For lichens the slope is steep from the lowlands and until after the tree line, and in the alpine zone species composition changes very little with altitude (Fig. 2c).

4. Discussion

The statistical analyses clearly demonstrate that the species richness of the three taxonomical groups respond very differently to altitude. This corresponds to observations from previous studies that species richness of different functional and taxonomic groups shows different patterns along environ-

mental gradients (Pausas, 1994; Pharo et al., 1999). However, the relationship between the first axis of the CA for the three taxonomical groups and altitude shows that the species composition of all three groups respond similarly and very strongly to altitude. So although species richness does not respond similarly to this gradient it is a strong environmental gradient for all three taxonomic groups.

The change in species richness of vascular plants and lichens appears to occur approximately at the forest limit (about 600 m a.s.l.), although it is only vascular plant species richness that seems to respond as expected to an ecotone at the forest limit. According to the smoothing spline line, there is an evident hump in vascular plant species richness which starts immediately above the forest limit (Fig. 1b). In a previous paper using the same data as used here for vascular plants plus data for vascular plant species richness along with six other hill sides, the source-sink effect are discussed as the most likely cause explaining the majority of these seven altitudinal patterns (Grytnes, 2003). The hump observed in this study above the forest line may be interpreted as the forest species having more sink populations (populations that cannot be sustained for long periods of time without input from source populations) above the forest limit than alpine species have sink populations below the forest line. The decrease in vascular plant species richness above 750 m may be explained by the more extreme and harsh conditions found towards the top of the mountain. A source-sink effect will dampen the change in species composition at an ecotone and may be at least partly responsible for the surprising lack of any sign of an abrupt change in species composition around the forest limit ecotone. However, if the lack of change in CA sample scores for vascular plants around the forest line ecotone (Fig. 2a) reflects a real feature of beta-diversity around the forest line we doubt that the source-sink effect is sufficient to explain the pattern of species composition change around the forest line. An alternative to the source-sink explanation can be based on the notion that the climatic forest limit in this area is 100–200 m above the present boundary due to sheep grazing in the area which has made it difficult for a forest to establish on the steep hillside. Climatically, the forest species should therefore have no problems surviving above the observed forest limit also as source-populations. The combination of sheep grazing and disturbance due to soil movement on the steep hillside where the trees are absent means that many alpine species may be able to establish and grow in the zone where forest climatically could establish. This may actually cause a decrease in the species composition change as observed in Fig. 2a. Against this is that the lack of change in species composition seems to continue well below the forest line. It should also be noted that in two other Norwegian studies changes in richness and composition of vascular plant showed no consistent abrupt changes (Hofgaard, 1997; Odland and Birks, 1999).

The lack of any pattern in bryophyte richness with altitude is rather surprising. The species composition gradient in bryophytes is as strongly correlated to altitude as it is for vascular plants and lichens. Yet there is no evidence of any abrupt change for bryophyte species composition (Fig. 2b). Bryophytes are known to have the ability to respond to environ-

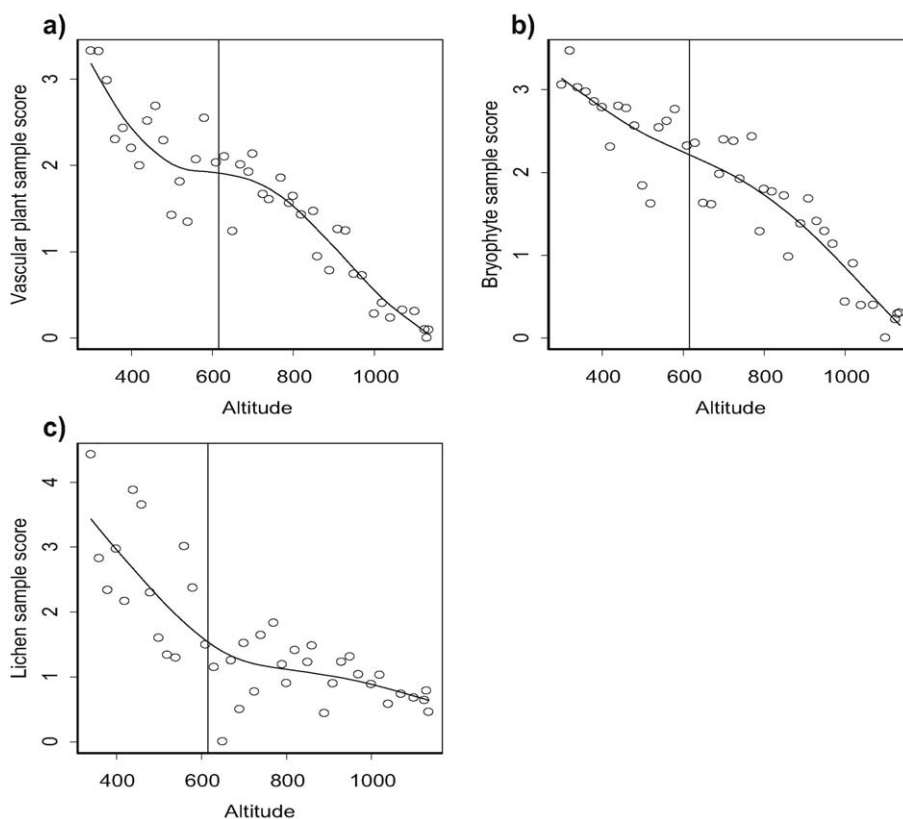


Fig. 2 – Scatterplots of the relationship between sample score from CA and altitude. The line is the fitted line using a cubic smooth spline (see text for details on the models). The vertical line indicates the forest line at 615 m a.s.l.

omental variation at fine spatial scales (Alpert, 1985, 1991; Frego and Carleton, 1995). Hence, the bryophyte species richness may be more dependent on the fine scale heterogeneity within each plot than the coarse scale between plot variations. Fine scale differences in moisture conditions probably have a major effect on the bryophyte community but do not affect vascular plant communities to the same extent. The large variance in species richness of bryophytes at similar altitudes may just reflect the random variation in types and number of microhabitats for bryophytes (Fig. 1c). The number of suitable microhabitats within a plot is probably independent of altitude (at least when excluding epiphytic and epilithic species) and therefore no relationship between species richness and altitude emerged in this study.

The lichen species richness in the area is generally low as a total of 31 lichen species was found in our plots (compared to 97 species of bryophytes and 61 species of vascular plants). The decrease in lichen richness below the forest limit may be explained by the low light availability at the ground level within the forest. As precipitation is generally high in this area throughout the year, ground-dwelling lichens in this area are probably not limited by moisture, but rather light may be limiting lichen growth (Palmquist, 2000), as the forest becomes denser from forest limit and downwards. During field work we observed that the cover of bryophytes increased below the forest limit. Higher bryophyte cover may have a further negative impact on lichens through competition for light and space. No evidence for an abrupt change around the forest line ecotone was found for lichen

species richness either. Below the forest line the species richness is very low and randomness may be responsible for the high variance and steep increase in CA-sample scores.

5. Conclusions

Our study emphasises the different altitudinal patterns of species richness of vascular plants, bryophytes, and lichens. Although the main changes in species composition vary monotonically with altitude, species richness has a more complex relationship with altitude. Vascular plant species richness peaks immediately above the forest limit, possibly because the species in the forest have sink populations above the forest limit co-existing with alpine species in these areas. For bryophytes, the altitudinal gradient in species composition does not affect the species-richness pattern, probably because bryophytes respond to fine-scale environmental changes. Ground-dwelling lichens thrive poorly in the light conditions below the forest limit and species richness decreases towards the lowlands below the forest limit.

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