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BIODIVERSITY RESEARCH

Biodiversity patterns of vascular plant species in mountain vegetation in the Faroe Islands

Anna Maria Fosaa

Lund University, Department of Ecology, Plant Ecology and Systematics, Sölvegatan 37, S-223 62 Lund, Sweden

Correspondence: Anna Maria Fosaa, Faroese Museum of Natural History, Department of Botany, Debesartrøð, FO-100 Tórshavn, Faroe Islands. E-mail: anmarfos@ngs.fo

ABSTRACT

Biodiversity patterns of vascular plant species were studied along altitudinal gradients in the Faroe Islands. Plants were sampled from five different mountains (150–856 m a.s.l.) at 50 m altitudinal intervals. Included in the study were 107 vascular plant species. In order to compare only altitudes with the same number of plots, three different analyses were carried out. One analysis included five mountains from 250 to 750 m a.s.l., one had three mountains from 150 to 750 m a.s.l., and the last one had two mountains from 750 to 850 m a.s.l. The patterns of biodiversity were evaluated on the basis of species richness as the total number of species at each altitudinal interval, as species turnover between altitudes and in relation to the Shannon-Wiener index. Similar patterns were found for species richness in the three analyses, although richness was higher along the whole transect when five mountains were included. For the Shannon-Wiener index, only small differences were found among the three analyses. A maximum was seen at 250 m a.s.l. and again at 500 m a.s.l. both in richness and in the Shannon-Wiener index. Maximum species turnover was found at mid-altitudes. Total vegetation cover followed the same pattern as richness. In addition to climate, the altitudinal variation of biodiversity may be affected by grazing.

Keywords

Islands, mountains, Shannon-Wiener index, species richness, species turnover.

INTRODUCTION

It has long been known that richness of vascular plant species decreases with increases in latitude and altitude (Begon *et al.*, 1996), and also that latitudinal and altitudinal gradients of species richness often mirror each other (Stevens, 1992; Rahbek, 1995). Altitudinal gradients are complex gradients and involve many different covarying factors, such as topography, soil, and climate (Austin *et al.*, 1996). Of these complex variables, which are difficult to separate, temperature and other climatic variables seem to be most important for describing decreasing species richness with altitude (Woodward, 1987; Körner, 1995), while soil parameters seem to be less important (Walker, 1995). As mountains are steep climate gradients, they should be perfect settings to study changes in species richness over relatively short distances, as most species have upper altitudinal limits that are set by various climatic parameters and by limitation of resources (Grabherr *et al.*, 1995; Körner, 1995; Lomolino, 2001; Theurillat *et al.*, 2003).

Understanding changes in richness of plant species along altitudinal transects is therefore valuable in the study of global climate change (Grabherr *et al.*, 1995; Sætersdal *et al.*, 1998; Gottfried *et al.*, 1999; Körner, 2000; Klanderud & Birks, 2003) because changing climate may lead to the migration of species.

Although we know that species richness decreases from low to high altitude (e.g. Odland & Birks, 1999), the pattern of changes has been found to be variable. Several studies have shown a monotonic decrease with altitude (e.g. Ohlmüller & Wilson, 2000; Austrheim, 2002). Others have found a hump-shaped relationship between species richness and altitude (e.g. Lomolino, 2001; Bhattarai & Vetaas, 2003). Still others have found both monotonic and hump-shaped relationships (Grytnes, 2003).

The variation in patterns has been reviewed by Rahbek (1995). He suggests that the differences between studies could partly be explained by the sampling regime and that the influence of area has often been ignored. To overcome this possible artefact, more standardized sampling is required (Whittaker *et al.*, 2001) and more studies are needed that compare the altitudinal patterns of species diversity (Lomolino, 2001). Species richness, which is usually expressed as the number of species in an area at different scales (alpha, beta and gamma diversity), has recently been reviewed by Whittaker *et al.* (2001), who seek a more precise definition of species diversity.

This paper is a study of the pattern of biodiversity along altitudinal gradients in the Faroe Islands based on sampling from five altitudinal gradients. This is done on the basis of species richness, species turnover and the Shannon-Wiener index. Biodiversity was studied in altitudinal intervals of 50 m along altitudinal gradients. Species richness was defined as the total number of species at each altitudinal interval and species turnover as gain and loss of species between altitudes.

In addition, the Shannon-Wiener index was used, which is one of the most common diversity indices to express species richness weighted by species evenness. It varies from zero in communities with only one species, to seven or more in rich forest communities (Barbour *et al.*, 1999). Diversity index and species richness are usually positively correlated (Eide *et al.*, 2001), although with exceptions. Environmental gradients exist where a decrease of species richness is accompanied by an increase in diversity indices (Hurlbert, 1971).

The aim of this study was to determine the patterns of biodiversity change along altitudinal gradients in the Faroe Islands and relate them to environmental parameters including grazing.

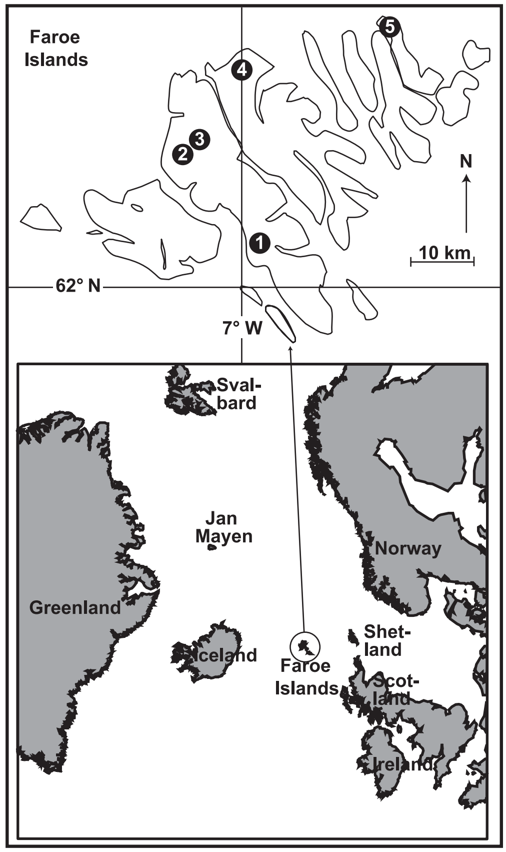

Figure 1 Location of the Faroe Islands and of the five studied mountains: 1: Sornfelli; 2: Mosarøkur; 3: Ørvisfelli; 4: Gráfelli and 5: Villingardalsfjall. See Table 1 for further details.

METHODS

Study area

The study area comprises five mountains on the three islands in the northernmost part of the Faroe Islands (Fig. 1) from 856 m a.s.l. down to 150 m a.s.l. The vegetation in the lowland temperate zone is dominated by dwarf-shrub vegetation with *Calluna vulgaris* and *Nardus stricta* and with *Hylocomiun splendens* in the moss layer, through the low alpine areas with moist grassland and a scarcity of dwarf shrubs, but still with *Nardus stricta* as the dominant species and *Hylocomium splendens* and *Racomitrium* spp. in the moss layer. In the alpine zone, *Racomitrium* vegetation is dominant, together with open grassland vegetation. In this zone, species such as *Salix herbacea* and *Bistorta vivipara* are common (Böcher, 1937, 1940; Hansen, 1967; Ostenfeld, 1905–1908). The whole area is grazed, mainly by sheep, with a stock density of between 34 and 49 sheep/km^2 (calculated from Thorsteinsson, 2001).

The climate in the Faroe Islands is oceanic, strongly influenced by the warm North Atlantic Current and by the proximity to the low-pressure track in the North Atlantic region. Consequently, the climate is humid, variable, and windy. The warmest months are July and August with a mean temperature of 11 °C (lowland) and the coldest is February with a mean of 4 °C (lowland). The mean precipitation in the Faroe Islands is 1500 mm annually (lowland). The precipitation reflects the topography of the islands, with the coastal areas receiving around 1000 mm per year, increasing to more than 3000 mm in the central regions (Cappelen & Laursen, 1998). The soils in the area are relatively nutrient poor (Olsen & Fosaa, 2002; Lawesson *et al.*, 2003). Soil pH increases with altitude, with a minimum value of 4.8 at low altitudes and a maximum of 5.8 at high altitudes. This is a result

Table 1 Details of the five mountains studied in the Faroe Islands. Names of localities, 1–5 refers to the numbers on the map, Fig. 1. Aspects include: N = north-facing slope; SW = south-west-facing slope and S = south-facing slope

	Names of localities	Length of transects (km)	Altitude (m a.s.l.)	Aspect	Size of island km^2	No. of species on islands	No. of species on transects
1	Sornfelli	3.7	749	N	373.5	221	60
2	Mosarøkur	4	756	SW	373.5	221	68
3	Ørvisfelli	1.2	783	N	373.5	221	62
4	Gráfelli	2.9	856	SW	286.4	207	66
5	Villingardalsfjall	1.3	841	S	41.0	136	66

of a more humus-rich soil in the lowlands and a less acid mineral soil at higher altitudes.

Field sampling

In July-August 1999 and 2000, the vegetation was sampled along five altitudinal transects, from the top (856 m a.s.l.) down to 150 m a.s.l. on five mountains on the Faroe Islands (Fig. 1). In order to include the entire variation of vegetation in terms of vegetation zones, the highest possible mountains were chosen, where the vegetation could be sampled with as little change in aspect as possible along the same transect.

The vegetation was sampled at 50 m altitudinal intervals within 100 m^2 quadrats (macro-plots). In each macro-plot, 8 smaller (0.25 m^2) quadrats (meso-plots) were placed randomly. The meso-plots were subdivided into 25 (0.01 m^2) micro-plots and the presence/absence of each plant species was noted for each micro-plot. In this way, the abundance of species, ranging from 1 to 25, was determined for each meso-plot. Thus, all altitudinal intervals compared on the five mountains had equal numbers of plots and the same plot size, except for those mountains that could not be sampled at the lowest altitude, due to topography, and those mountains that did not reach the highest altitude. The number of altitudinal plots varied from 12 to 15 macro-plots.

Due to variable slope, the length of the transects ranged between 1.2 km and 4.0 km and since only one macro-plot was sampled in each altitudinal interval, distances between macro-plots varied.

Data analysis

Species richness was determined as the total number of species in 100 m^2 (macro-scale) in each altitudinal interval, representing 8 meso-plots for each altitude on each mountain. This gives a maximum of 40 meso-plots at each altitude.

The Shannon-Wiener index is generally defined as:

$$SW = -\sum_{i=1}^{s} p_i \cdot \ln p_i$$

where s is the total number of species at the altitude and p_i is the proportion of all individuals in the sample that belong to species i. In this study, the number of individual plants has not been counted and p_i cannot therefore be computed according to its original definition. Instead, the abundance values (1–25), as previously defined, were used to compute values of p_i for each species, which were inserted into the equation above.

Species turnover (β) diversity was calculated as the gain and loss of species between altitudes according to the formula proposed by Wilson & Shmida (1984):

$$\beta = \frac{g(H) + l(H)}{\alpha(H) + \alpha(H-1)}$$

where $g(H)$ and $l(H)$ are the number of species gained and lost, respectively, from altitude $H-1$ to altitude H and $\alpha(H)$ is the species richness at altitude H.

RESULTS

The study included a total of 107 vascular plants. To avoid comparison between altitudes with different numbers of macro-plots, the data were split into three sets, identified as 'five mountains', 'three mountains', and 'two mountains', respectively (Table 2). The first of these includes all the plots from mid-altitudes (250 m a.s.l. up to 750 m a.s.l.). The second includes the plots from the lowest altitudes (150 m a.s.l. to 750 m a.s.l.) and the third includes the uppermost plots (750 m a.s.l. to 850 m a.s.l.).

In the data set from mid-altitudes on five mountains there were 55 macro-plots (100 m^2) with 104 species. The low-altitude data from three mountains had 39 macro-plots (100 m^2) with 92 species, and the high-altitude data from two mountains had 6 macro-plots with 25 species (Table 2). The number of species on each of the five mountains varied between 60 and 68 species.

Figure 2(a) shows that species richness decreases with altitude. It is seen that the curve with five mountains has the same shape as the curve with three mountains (Fig. 2a), but in general has higher richness than when only three and two mountains are included. Both curves show two maxima in species richness. The first is at 250 m a.s.l. with 65 species (five mountains) and 48 species (three mountains). The second maximum occurs at 500 m a.s.l. with 57 species (five mountains) and 43 species (three mountains). Above 500 m a.s.l., richness decreases more or less monotonically until the top of the mountains.

A linear regression was carried out between richness values and altitude. For each altitude, the total number of species on either three or five mountains was found and these numbers were regressed against altitude. For all five mountains (250 m a.s.l. to 750 m a.s.l.), the slope of the regression line was found to be $-0.045\ m^{-1}$ with a standard error of $0.011\ m^{-1}$ $(-0.045 \pm 0.011)\ m^{-1}$, which is significantly different from zero ($P < 0.01$). For three mountains, the slope was found to be $(-0.023 \pm 0.012)\ m^{-1}$, which also is significantly different from zero ($P < 0.05$). Thus, the decrease in richness from 250 m a.s.l. was statistically significant. Whether the increase from 150 to 250 m a.s.l. and the local maximum at 500 m a.s.l. are statistically significant is difficult to estimate with the few degrees of freedom available.

Similar results were found for the Shannon-Wiener index (Fig. 2b). In this analysis only small differences were found among the analyses for five, three and two mountains. The index varies from 2.8 at 150 m a.s.l. to 3.4 at 250 m a.s.l. and down to 1.9 at 850 m a.s.l. The decrease with altitude for five mountains had

Table 2 Details of the three data sets

	Five mountains	Three mountains	Two mountains
Number of meso-plots	55	39	6
Altitudinal range	250–750 m	150–750	750–850
Number of species	104	92	25

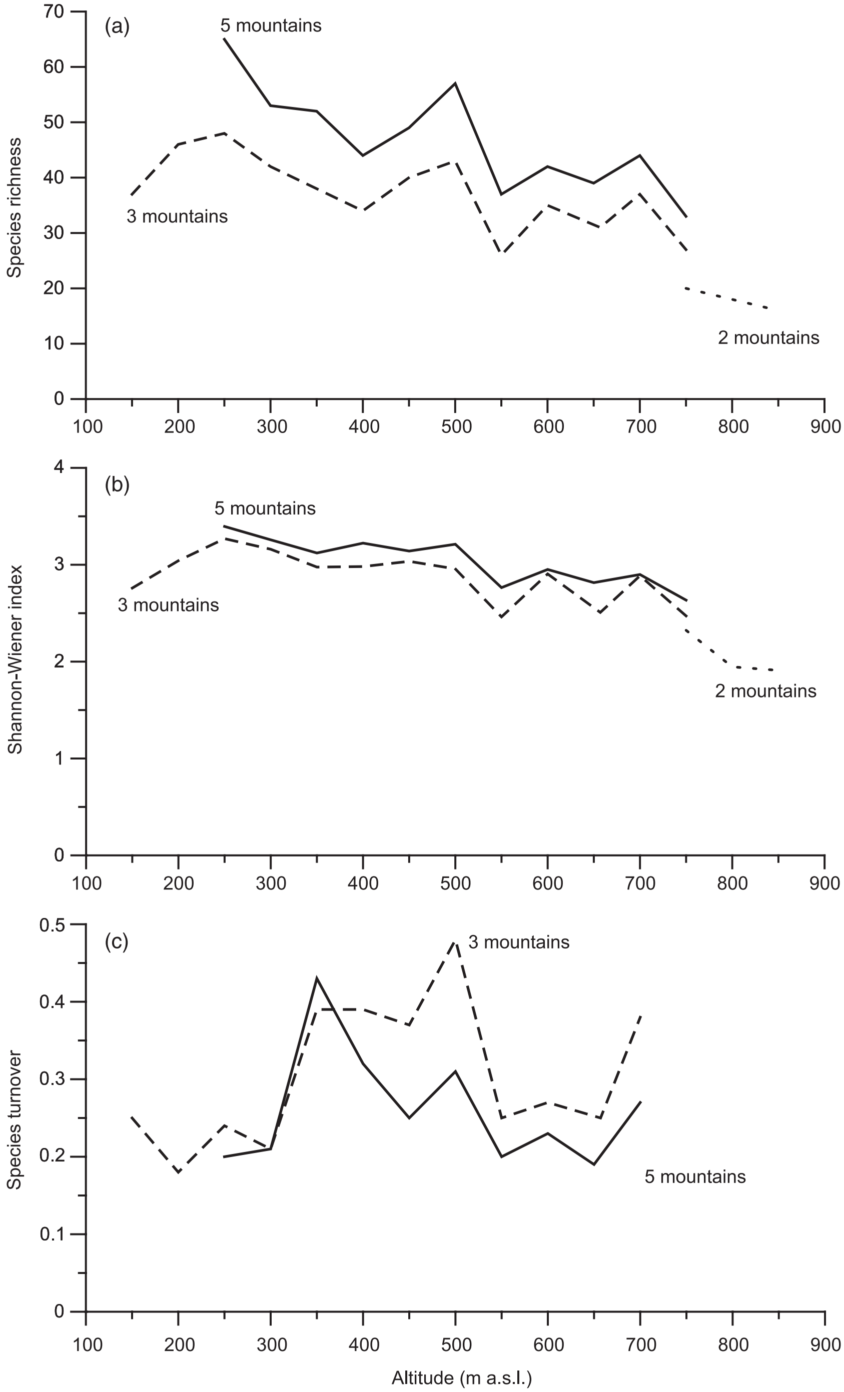

Figure 2 (a) The relationship between species richness and altitude from five mountains including all plots from mid-altitudes (250 m a.s.l. up to 750 m a.s.l.). From three mountains plots from the lowest altitudes (150 m a.s.l. to 750 m a.s.l.) are included and from two mountains the uppermost plots (750 m a.s.l. to 850 m a.s.l.) are included. (b) The relationship between the Shannon-Wiener index and altitude. (c) The relationship between species turnover and altitude.

a regression line slope of $(-0.0013 \pm 0.0002)\ m^{-1}$ and for three mountains $(0.0008 \pm 0.0003)\ m^{-1}$. These were significantly different from zero ($P < 0.01$ and $P < 0.05$, respectively).

Species turnover (Fig. 2c) was seen to fluctuate along the altitudinal gradient with the highest turnover between 300 and 500 m a.s.l. A linear regression analysis did not give regression slopes significantly different from zero.

A Pearson correlation analysis (Table 3) shows high correlations between richness and the Shannon-Wiener index. Both of these are negatively correlated with altitude and positively correlated with cover. Species turnover did not show a significant correlation with any other parameter.

DISCUSSION

The species richness data on vascular plant species from this study support the hypothesis that species richness decreases with altitude (e.g. Woodward, 1987; Körner, 1995). The three islands studied have different sizes and different numbers of species (Hansen, 1966, 1972) (Table 1). Despite these differences, earlier

Table 3 Pearson correlation coefficients between variables (Sh-W = Shannon-Wiener)

	Total cover (%)	Altitude	Richness	Sh-W index.
Altitude	−0.88†			
Richness	0.80†	−0.67†		
Sh-W index	0.73†	−0.61*	0.90†	
Species turnover	−0.33 n.s.	0.35 n.s.	−0.02 n.s.	0.09 n.s.

†Correlation is significant at the 0.01 level (2-tailed).
*Correlation is significant at the 0.05 level (2-tailed).

studies (Christensen & Hansen, 1998) found no significant difference in the flora of the three islands on the basis of similarity indices (Connor & McCoy, 1979). This is confirmed by the similarity among the five mountains, which are found to have about the same number of vascular plant species.

Despite the same total number of vascular plants on the five mountains, the altitudinal variation of biodiversity varied somewhat from one mountain to another (Fig. 3). The differences may be partly statistical and partly related to the different topography of the mountains (shape, slope and length of the transects) and consequently to a different area for the altitudinal intervals. From 250 m a.s.l. upwards, there is a statistically significant decrease in species richness equivalent to 4.5 species per 100 m on the five mountains. From 150 m a.s.l. there is a statistically significant decrease in species richness equivalent to 2.3 species per 100 m on the three mountains.

From other studies, one might expect maxima in species richness to be found at intermediate altitudes in the transition between two zonal vegetation types (Lomolino, 2001). This is consistent with the two maxima in species richness and diversity at around 250 m a.s.l. and again at around 500 m a.s.l. found for both five and three mountains in this study.

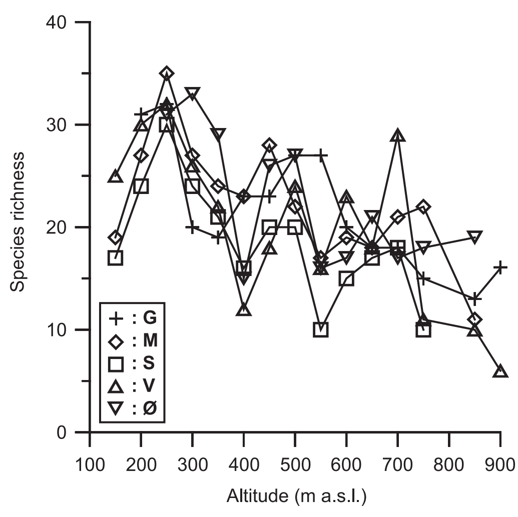

Figure 3 The variation in species richness in the altitudinal intervals on the five mountains. G: Gráfelli; M: Mosarøkur; S: Sornfelli; V: Villingardalsfjall; Ø: Ørvisfelli.

The maximum found at 250 m altitude is located where the temperate vegetation in the lowland (200 m) changes to low-alpine vegetation. The maximum at 500 m a.s.l. is similarly located close to the transition from the low-alpine zone to the alpine zone (above 400 m a.s.l.) (Fosaa, in press).

To evaluate these maxima, a comparison was made of species lost between the maximum found at 250 m a.s.l. and at 350 m a.s.l. It was found that many lowland species such as *Calluna vulgaris*, *Carex echinata*, *Narthecium ossifragum*, *Juncus squarrosus* and *Hypericum pulchrum* disappeared from 250 to 350 m a.s.l. Similarly, many *Carex* species such as *Carex demissa*, *C. pulicaris*, *C. echinata*, *C. nigra*, and *C. saxatilis*, and *Eriophorum vaginatum* disappeared from 500 to 600 m a.s.l.

The difference in the Shannon-Wiener index for five and three mountains is found to be small (Fig. 2b), while there is more difference in species richness between the two. This may be due to the fact that the diversity index and species richness are different variables and are not always comparable (Barbour *et al*., 1999). Richness is the number of species and diversity index is richness weighted by the evenness of the species. Evenness reaches a maximum when all species have the same number of individuals. In that case, the Shannon-Wiener index is as the logarithm of the richness. As a large positive correlation (Table 3) is found here between species richness and the Shannon-Wiener index, it appears that the variation in evenness of species is small. The small difference in the Shannon-Wiener index between three and five mountains is therefore most likely due to the logarithmic character of the Shannon-Wiener index.

As noted previously, the sampling method used requires a definition of the Shannon-Wiener index somewhat different from the original. In this data set, species abundance in each meso-plot can vary only by a factor of 25, while in reality the number of individual plants may vary considerably more. This may well enhance the evenness and thus also the Shannon-Wiener index, compared to the value it would have had if the number of individual plants had been used in the computation. It may also reduce the altitudinal variation of evenness and thus affect the altitudinal variation of the Shannon-Wiener index.

Species turnover showed the highest values between 350 and 500 m a.s.l. This maximum more or less overlaps with the low-alpine zone (200–400 m a.s.l.), which is the transition between temperate vegetation in the lowland and the alpine zone in the highland. (Fosaa in press). The obvious interpretation is therefore that this maximum is due to the loss of temperate species in this zone and the gain of more alpine species, in combination with relatively low species richness in these altitudes. Another possibility could be the patchy vegetation in the area, also proposed by Sklénar & Ramsay, 2001) for other mountainous areas.

The differences in richness from one mountain to another (Fig. 3) indicate that variables other than climate may control the decrease of species richness with increasing altitude on the mountains. Mountaintops are usually less disturbed by humans than lowlands, but disturbances due to natural causes such as high wind speed, high precipitation and thawing and freezing increase with altitude (Humlum & Christiansen, 1998; Christiansen & Mortensen, 2002).

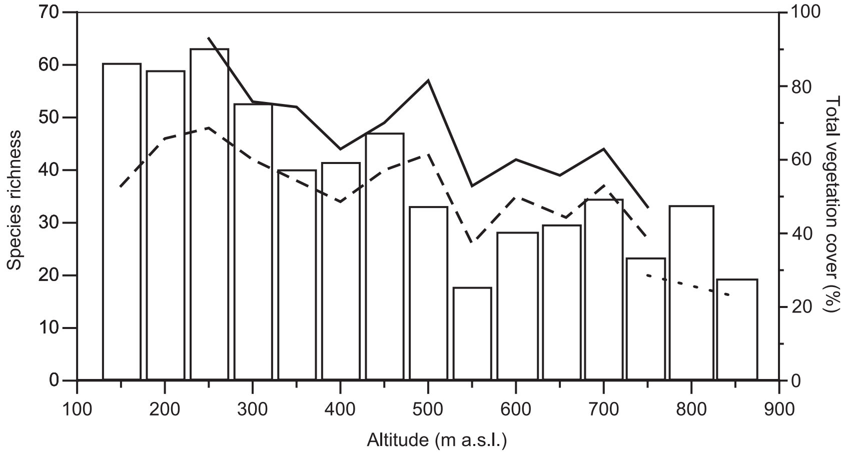

Figure 4 The relationship between total vegetation cover and species richness, based on plots from five and three mountains, respectively.

The studied mountains are grazed by sheep but there are no direct measurements of the intensity of grazing or its altitudinal variation. Moderate grazing in productive areas such as tall herb and grass meadows normally increases the biodiversity as grazing removes the biomass of taller species and allows smaller species, which are normally out-shaded, to persist. In less productive habitats, grazing will, however, reduce species richness (Austrheim & Eriksson, 2001). Thus, grazing can increase the difference between the low and the high altitudes.

In the alpine zone (above 400 m a.s.l.), the vegetation cover is low (Fig. 4). This, together with low temperatures, may explain the low values for richness and the Shannon-Wiener index at these high altitudes. The species richness in the alpine zone may thus be controlled by the number of safe sites where the vegetation can find shelter from wind and soil disturbances (Hansen & Johansen, 1982).

CONCLUSIONS

This study has showed that the diversity of vascular plant species on Faroese mountains decreases significantly with altitude. Two maxima are found that are identical with the transitions between the temperate and low-alpine zones and between the low-alpine and the alpine zones. This is seen in the disappearance of many low-altitude species. The importance of area is verified by the variance of biodiversity from one mountain to another. In addition to the influence from climate, the difference in biodiversity between the temperate zone and the alpine zone is affected by grazing. Moderate grazing can promote higher diversity in the temperate and low-alpine zone (productive habitats) and decreasing diversity in the alpine zone (less productive habitats). Also, the number of safe sites may control the biodiversity in the alpine zone.

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