Distribution of Raunkiær's life-forms along altitudinal gradients in the Faroe Islands

Útbreiðslan av lívshættum Raunkiærs niðan eftir fjallasíðum í Føroyum

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Úrtak

Fyri at vita, hvar vøksturin í Føroyum skiftir frá at vera arktiskur til at vera tempereraður, kannaðu vit útbreiðsluna av lívshættum Raunkiærs niðan eftir fimm ymiskum fjallasíðum. Eisini kannaðu vit, hvønn týdning gróðrarlagið, LOI (gløðitap) og árligur miðalhiti hava fyri útbreiðsluna av lívshættum við hæddini. Okkara niðurstøða var, at tíðleikin av hemikryptofytum minkaði linjurætt við hæddini, tíðleikin av therofytum og geofytum vaks linjurætt við hæddini, og rásin, sum vísir tíðleikan av charmaifytum sum funktión av hæddini hevur skap sum parabil, við lægsta tíðleikanum á 400-500 m hædd. Tíðleikin av hemikryptofytum samsvarar eins væl við lága gróðrarlagið sum við hæddina, men therofytarnir samsvara best við lága gróðrarlagið. Chamaefytarnir samsvara best við tann árliga miðalhitan, men geofytarnir samsvara best við LOI. Kanningin vísir, at lutfallið millum hemikryptofytar og chamaefytar broytist við hæddini, sum vøksturin skiftir frá tempereraðum til arktiskt eyðkenni.

Abstract

To study the shift from temperate to arctic vegetation in the Faroe Islands, we quantitatively analysed the distribution of Raunkiær's life-forms along five altitudinal gradients. We further tested the importance of the non-climatic parameters of altitude, total vegetation cover and LOI (loss on ignition), and the climate variable of annual mean temperature in describing the abundance variation of life-forms. We found that as altitude increased, the abundance of hemicryptophytes decreased linearly; the abundance of therophytes and geophytes increased linearly; and the abundance of chamaephytes varied parabolically, with the lowest abundance around 400-500 m. The abundance variation of hemicryptophytes seems to be as well correlated with total vegetation cover as with altitude, while total vegetation cover was the best parameter to describe the variation in abundance of therophytes. Annual mean temperature was the most important parameter for describing the abundance variation of chamaephytes and LOI was the most important parameter describing the variation of geophytes. We concluded that the abundance relationship between hemicryptophytes and chamaephytes changed with altitude as the vegetation changed from temperate to arctic vegetation.

Introduction

In this paper, we investigate vegetation response along altitudinal gradients using functional types expressed as Raunkiær's life-forms.

The advantage of using functional types is that the diversity of species is reduced into a more manageable system, and there is minimal loss of relevant information. Such a system, where plant species are grouped together on the basis of similar attributes or functions into well-defined groups, can reveal similarities in the response of group members to environmental disturbance. Grouping of individuals according to similarities in attributes also makes it possible to compare areas with taxonomically different floras (Woodward and Cramer, 1996; Diaz *et al*., 1999). A variety of functional systems have been established (Nobel and Gitay, 1996). These are commonly based on autecological characteristics such as morphology, physiology and phenology, demography, etc., or a combination of several characteristics (Box, 1981; Grime *et al*., 1988; Kelly, 1996; Diaz, *et al.* 1997; Walker, 1997).

In recent years, plant functional classification has received much interest among ecologists studying the effect of global climate change on ecosystems (Diaz and Cabido, 1997; Gitay and Nobel, 1997; Hobbs, 1997). These classification systems have been used on a broad scale to describe global vegetation (Box, 1981; Prentice *et al.*, 1992), especially in climate change studies (e.g. IPCC, 2001), and, on a local scale, to describe the vegetation in a region (Diaz *et al*., 1997; Grime *et al*., 1997).

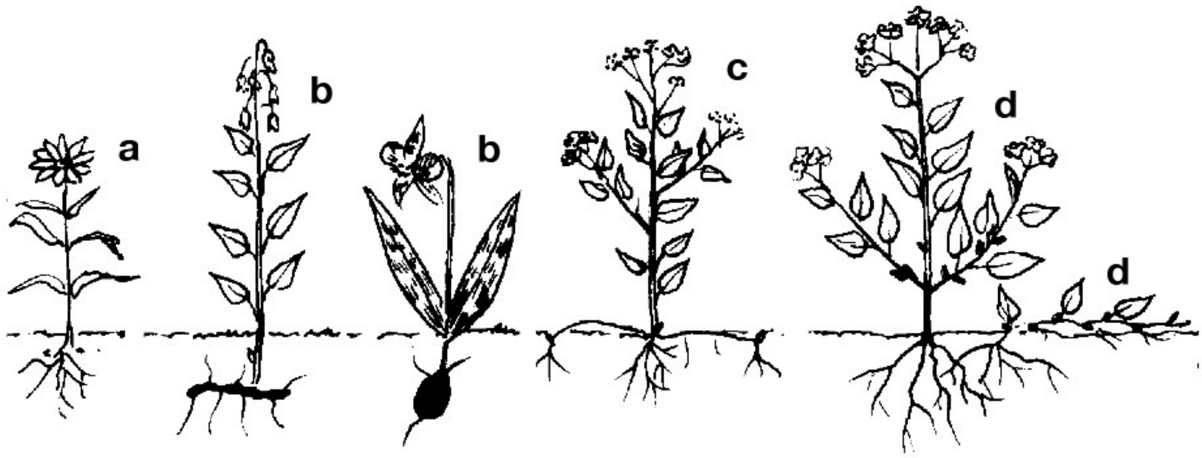
Altitudinal transects with steep climatic gradients are useful settings for studying the variation of functional types as a result of climate change. Various studies show that Raunkiær's life-forms vary along altitudinal transects (Gomez *et al*., 1993; Mark *et al*., 2000; 2001; Pavon *et al.*, 2000). This has also been shown for the Faroe Islands (Raunkiær, 1934; 1936; Hansen, 1972).

It is generally accepted that the effect of changing land use on most ecosystems is greater than the effect of climate change (Vitousek *et al*., 1997). Therefore, it is important that the effect of land use also be taken into consideration in a discussion of global climate change (Diaz *et al*., 1997). A number of different studies dealing with the effect of land use show that disturbances often promote certain life-forms and impede others (McIntyre *et al*., 1995; 1999; Hadar *et al*., 1999; Lavorel *et al*., 1999). Studies of land use change and its effects have used functional characteristics such as Raunkiær's life-forms (Raunkiær, 1934; McIntyre *et al*., 1995; Hadar *et al*., 1999).

Raunkiær based his functional classification on the position of over-wintering tissue, which is an indicator of the ability of a plant to survive unfavourable seasons (Raunkiær, 1934). Using this system, he was able to find relationships between climate and life-forms in whole floras in different parts of the world (Table 1).

In this study, we investigate the abundance variation of Raunkiær's life-forms along altitudinal gradients in the Faroe Islands. In general, the vegetation in the temperate zone is dominated by hemicryptophytes, however, the abundance of hemi-

Major life-forms	**Surviving buds**	**Main distribution area In relation to position of surviving buds and generalize distribution**
Therophytes	seed, annual plants	Open areas, deserts and steppes, decreases toward the poles
Geophytes	buried in the soil	Dry climate, steppes.
Hemicryptophytes	soil surface	Temperate and arctic climate
Chamaephytes	< 0.25 m above the soil surface	Temperate and arctic climate



a) Therophytes b) Geophytes c) Hemicryptophytes d) Chamaephytes

Table 1. *Definitions of life-forms according to Raunkiær (1934), the surviwing buds are in black on the drawings.*

cryptophytes changes to favour increasing numbers of chamaephytes in the arctic zone (Raunkiær, 1934). Vegetational studies of the Faroe Islands have indicated a shift from temperate vegetation in the lowlands to arctic vegetation in the highlands (Böcher, 1937; Hansen, 1972; Fosaa, 2004). Studies have also shown a change in life-form abundances along Faroese mountain slopes (Raunkiær, 1936; Hansen, 1972). In this study, we use quantitative methods to verify these results and to determine the altitude shift in vegetation zones. We also test the importance of climatic and non-climatic parameters on the abundance variation of life-forms.

Previous studies have given a general overview of changes in life-forms with altitude. These studies have, however, largely been qualitative and a number of questions remain unanswered: How do life-form abundances change with altitude in a quantitative manner? Is the shift from temperate to arctic vegetation abrupt or is there a broad tran-

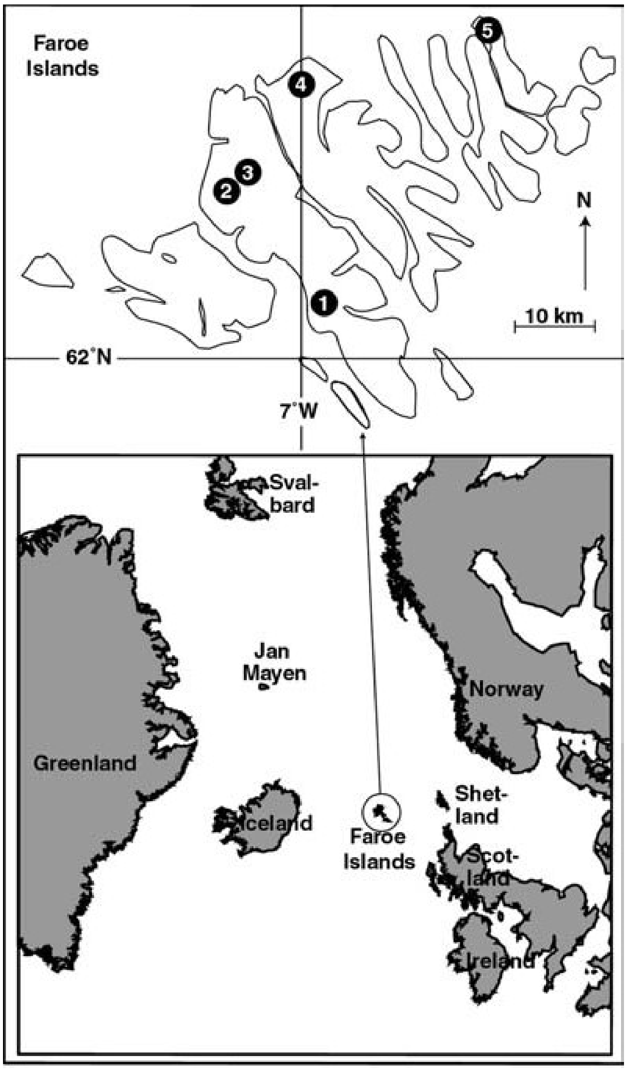


Fig. 1. Location of the Faroe Islands and location of the five studied mountains in the Faroe Islands: 1: Sornfelli; 2: Mosarøkur; 3: Ørvisfelli; 4: Gráfelli and 5: Villingardalsfjall.

sition? If so, then at what altitude? What parameters are responsible for the change? To what extent are these parameters climatic? The last of these questions stems from the original aim of our project, which was to evaluate how the vegetation might change in a global climate change scenario.

In order to answer these questions, we carried out quantitative sampling of the vegetation along altitudinal transects on five Faroese mountains. We also measured climatic and other environmental parameters on the transects. Here we report on the correlation between altitudinal change and life-forms in the Faroes and, in addition, the effects of climatic and other environmental parameters on Raunkiær life-forms.

Material and methods

Study area

In the summers of 1999 and 2000, we sampled the vegetation on five mountains in the Faroe Islands along transects from a high point of 856 m a.s.l. down to 150 m a.s.l. (Fig. 1). Two of the mountains had north-facing aspects; one faced south; and two had southwest-facing aspects (Table 2). The longest transect was 4.0 km, while the shortest was 1.2 km (Table 2). All the mountains are grazed by between 34 and 49 sheep/km^2 (Thorsteinsson, 2001). The dominant vegetation types on the five mountains are *Racomitrium* heath and open grassland vegetation in the alpine zone (400-856 m a.s.l.); moist heath vegetation in the low alpine zone (200-400 m a.s.l.); and moist dwarf shrub heath in the temperate zone (up to 200 m a.s.l.) (Fosaa, 2004).

Sampling

A total of 538 meso-plots were sampled on the five mountains. The vegetation was sampled at 50 m intervals of altitude from 10 x10 m quadrats (macro-plots). In each macro-plot, 8 smaller (0.5 x 0.5 m) quadrats (meso-plots) were randomly placed. The

Names of localities	*Latitude*	*Longitude*	*Length*	*Maximun Altitude*	*Aspect*
1 Sornfelli	62°04´10´´ N	6°57´25´´W	3.7 Km	749 m a.s.l.	N
2 Mosarøkur	62°11´05´´ N	7°10´52´´W	4.0 Km	756 m a.s.l.	SW
3 Ørvisfelli	62°12´32´´N	7°09´17´´W	1.2 Km	783 m a.s.l.	N
4 Gráfelli	62°18´41´´N	6°59´48´´W	2.9 Km	856 m a.s.l.	SW
5 Villingar-dalsfjall	62°22´53´´N	6°33´13´´W	1.3 Km	841 m a.s.l.	S

***Table 2**. Details of the five investigated transects.*

meso-plots were subdivided into 25 (0.1 x 0.1 m) micro-plots and the presence/absence of 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.
The total vegetation cover was estimated as the mean percent coverage of each meso-plot and the slope was measured. (Table 3).

One soil core (5 cm diam. x 10 cm deep) was sampled from each meso-plot after the vegetation had been removed.

Loss on ignition (LOI) was determined by ashing a soil sample at 550°C in a muffle furnace for three hours. The pH was determined with a Radiometer PHM 240 pH-meter after mixing dried soil with distilled water. (also see Lawesson *et al*., 2003)

Soil temperature at 1 cm depth, was also measured hourly at 50 m altitudinal intervals during the years 1999 and 2001 using TinyTag data loggers.

To calculate the characteristic values, we computed annual values for five key parameters: the annual mean temperature (T_{av}); the mean temperature of the warmest month (T_{max}); the mean temperature of the coldest month (T_{min}); growing degree days (GDD), and the number of days with snow cover. GDD was calculated by summing the temperature excess over 5°C for all hourly observations in a year and dividing by 24 (Molau and Mølgaard, 1996). Number of days with snow cover was determined by taking the number of days with daily temperature ranges below 0.5°C and the mean daily temperature below 1°C. The two year period of measurement was from September 1999 to August 2001 for all the mountains except one, where we used the yearly period August 2000 to July 2001 (Fig. 1, locality 2). Details of the measurements and the results have been reported by Fosaa *et al*. (2001).

Altitude (m)		Slope	Cover	pH	LOI	T(ave)	T(max)	T(min)	GDD	Snow cover
150	Mean	27	86	5.0	50.4	6.2	12.5	0.8	1036	59
	Std. Error of Mean	3	4	0.0	1.8	0.1	0.0	0.1	16	5
200	Mean	15	86	5.1	54.7	6.1	12.7	0.9	970	79
	Std. Error of Mean	2	5	0.1	1.0	0.1	0.2	0.1	11	5
250	Mean	4	87	5.4	40.8	5.6	12.2	0.6	892	96
	Std. Error of Mean	1	3	0.1	3.0	0.1	0.3	0.1	29	5
300	Mean	28	76	5.5	34.9	5.5	12.1	0.5	882	99
	Std. Error of Mean	2	5	0.1	2.0	0.1	0.2	0.0	9	4
350	Mean	29	67	5.3	27.0	5.3	11.7	0.4	830	106
	Std. Error of Mean	1	5	0.1	1.8	0.1	0.2	0.0	11	4
400	Mean	17	54	4.4	31.1	5.0	11.4	0.3	778	113
	Std. Error of Mean	2	6	0.3	3.9	0.1	0.2	0.0	13	4
450	Mean	21	69	5.0	24.5	4.7	11.0	0.1	726	121
	Std. Error of Mean	2	6	0.2	2.2	0.1	0.2	0.0	16	3
500	Mean	17	57	5.7	16.4	4.4	10.6	0.0	675	128
	Std. Error of Mean	2	5	0.1	1.3	0.1	0.2	0.0	20	3
550	Mean	30	30	5.7	12.0	4.1	10.2	-0.1	623	136
	Std. Error of Mean	2	5	0.1	0.4	0.1	0.2	0.0	23	3
600	Mean	22	55	5.7	13.5	3.9	9.9	-0.2	571	143
	Std. Error of Mean	2	6	0.1	0.9	0.1	0.2	0.0	27	3
650	Mean	30	47	5.9	11.3	3.6	9.5	-0.4	519	151
	Std. Error of Mean	3	6	0.1	0.8	0.1	0.2	0.0	31	4
700	Mean	25	45	5.7	15.1	3.2	9.0	-0.5	449	158
	Std. Error of Mean	3	4	0.0	1.6	0.1	0.2	0.1	37	4
750	Mean	15	42	5.2	11.5	3.7	9.1	-0.6	475	160
	Std. Error of Mean	2	5	0.3	0.8	0.2	0.2	0.1	29	3
800	Mean	18	56	5.3	15.6	2.9	8.6	-0.8	432	161
	Std. Error of Mean	2	8	0.2	1.6	0.1	0.3	0.1	41	5
850	Mean	3	27	5.9	14.9	2.9	9.4	-0.4	529	170
	Std. Error of Mean	1	9	0.3	0.6	0.1	0.1	0.2	5	4

Table 3. *Mean and standard error of the environmental parameters at all the altitudes studied.*

Data analysis

All plant species recorded were assigned to their respective life-form based on Raunkiær classifications following Ostenfeld's, (1905-1908) divison of the Faroese flora. To assess whether our data was representative for Raunkiær biological spectra for the Faroese flora, we calculated the number of vascular plant species belonging to each life-form type as a percentage of the total number of vascular plant species on all the five studied mountains. This was then compared with the distribution of Raunkiær's life-forms in the whole of the Faroese flora (Raunkiær, 1934), allowing us to determine if the life-form data from our study showed the same trends and, thus, is representative of the flora in the Faroe Islands.

Correlations between life-forms and the environmental parameters were tested using

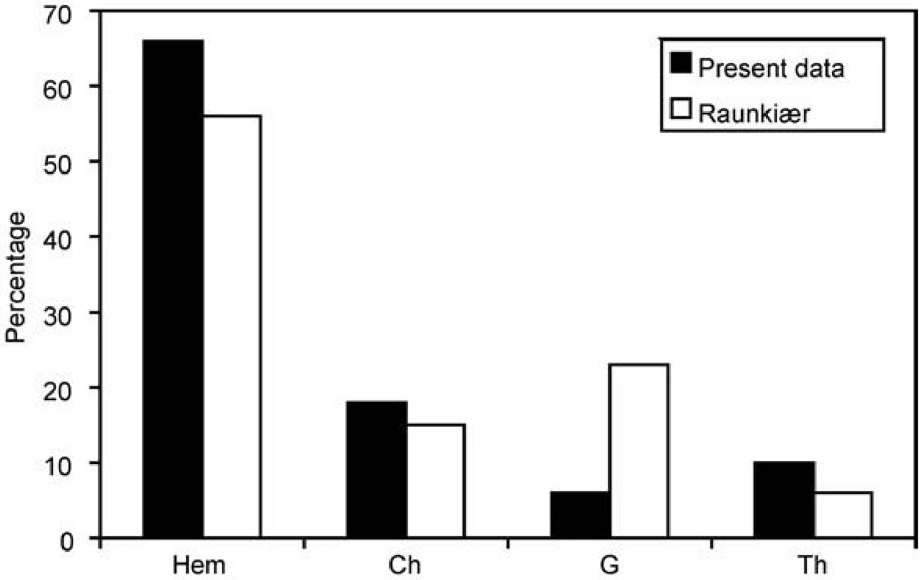


Fig. 2. *The biological spectra of Raunkiær's life-forms based on the total flora in the Faroe Islands compared to results from the present study. The life-forms are given as % of total number of vascular species for each of the four life-forms.*

Hem: Hemicryptophytes; Ch: Chamaephytes; G: Geophytes and Th: Therophytes.

the Pearson correlation test (Table 4) and the results used to determine which environmental variables should be included in the analysis by choosing the variables that were least correlated to one another.

The altitudinal variation was determined by plotting the weighted abundance of each life-form against altitude at 50 m intervals and identifying the best first or second order polynomium to fit the data from an ANOVA table. If the coefficient of the quadratic term in the second order regression analysis was significantly different from zero, the second order polynomium was selected; otherwise, the linear regression was selected. Life-form abundances, expressed as percentages, were determined by dividing the abundance of each life-form by the sum of all life-form abundances in each meso-plot. The correlation of life-form abundances with each environmental variable was determined using the same type of analysis.

Results

The occurrence of life-forms as a percentage of species number from this study and for the whole flora of the Faroe Islands based on Ostenfeld (1905-1908) is shown in Figure 2.

Hemicryptophytes were found to be the most species-rich life-form with an average value of 66% in our study in contrast to 56% in the earlier study (Raunkiær, 1936). Chamaephytes also had slightly more species in our study, 18% in contrast to 15% from previous studies. There were significantly fewer geophytes in our study, 6% in contrast to 23%, while therophytes were more numerous, 10% in contrast to 6% in older study (Fig. 2). Thus, we found the same trend in total flora as in the older studiy, with the exception of geophytes, which were markedly less. The reason why geophytes are less numerous in our study is that many are rare species or they grow in lowland habitats which are less represented in our study.

The relationship between the life-forms in 50 m altitudinal intervals are shown in Figure 3. Here we can see that hemicrypto-

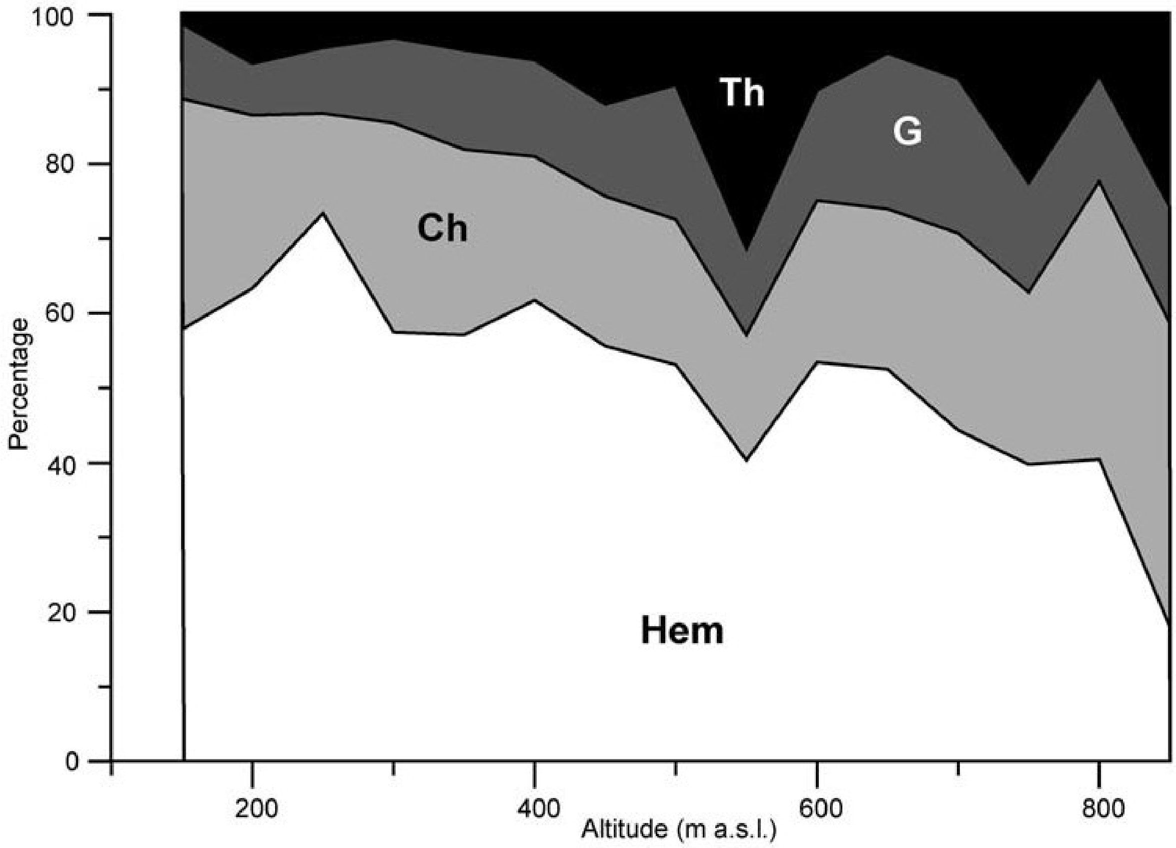


Fig. 3. *Relationship between abundance of life-forms on the five investigated mountains, in altitudinal intervals. For abbreviations see fig 2.*

phytes and chamaephytes are the most abundant life-forms.

The cross-correlation of variables are shown in Table 4. We find that both total vegetation cover and LOI were negatively correlated with altitude. All of the temperature-related parameters were also negatively correlated with altitude, except for snow cover. Using Table 4, and starting with altitude, the following sequence of variables would be slope, pH, cover, LOI, and the temperature-related variables. When fitting the life-form abundances against these variables, slope and pH did not yield significant fits, with one exception. Geophytes could be represented as a quadratic function of pH with a significance level $p=0.025$, but none of the other life-forms could be fitted significantly ($p<0.05$) to pH, and none could be fitted to slope. In the further analysis, we therefore use altitude, cover, LOI, and the temperature-related variables.

Since the temperature variables are not independent variables, we choose just one of these parameters, annual mean temperature, for further analysis (Fig. 6).

The analysis of altitudinal variation (Fig. 4 a-d through 7 a-d) indicated that abundance of all the life-forms, except for chamaephytes, varied linearly with altitude, hemicryptophytes decreasing linearly, while therophytes and geophytes increased with altitude. Chamaephytes had minimum abundance around 400-500 m a.s.l.

Correlations

	Altitude	Slope	Cover (%)	pH	LOI	T(ave)	T(max)	T(min)	GDD	Snow cover
Altitude (m)	1									
Slope (degrees)	0.015	1								
Cover total (%)	-.405(**)	-.109(*)	1							
pH	.169(**)	.111(*)	-0.042	1						
LOI	-.681(**)	-.248(**)	.543(**)	-.088(*)						
T(ave)	-.855(**)	-.133(**)	.294(**)	-.158(**)	.602(**)	1				
T(max)	-.728(**)	-.105(*)	.248(**)	-.169(**)	.506(**)	.884(**)	1			
T(min)	-.803(**)	-0.075	.301(**)	-.196(**)	.609(**)	.880(**)	.856(**)	1		
GDD	-.776(**)	-.114(**)	.224(**)	-.160(**)	.509(**)	.915(**)	.895(**)	.789(**)	1	
Snow cover	.760(**)	.124(**)	-.282(**)	.099(*)	-.513(**)	-.735(**)	-.491(**)	-.541(**)	-.765(**)	1

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

Table 4. *Pearson correlation matrix and significant values between the environmental parameters.*

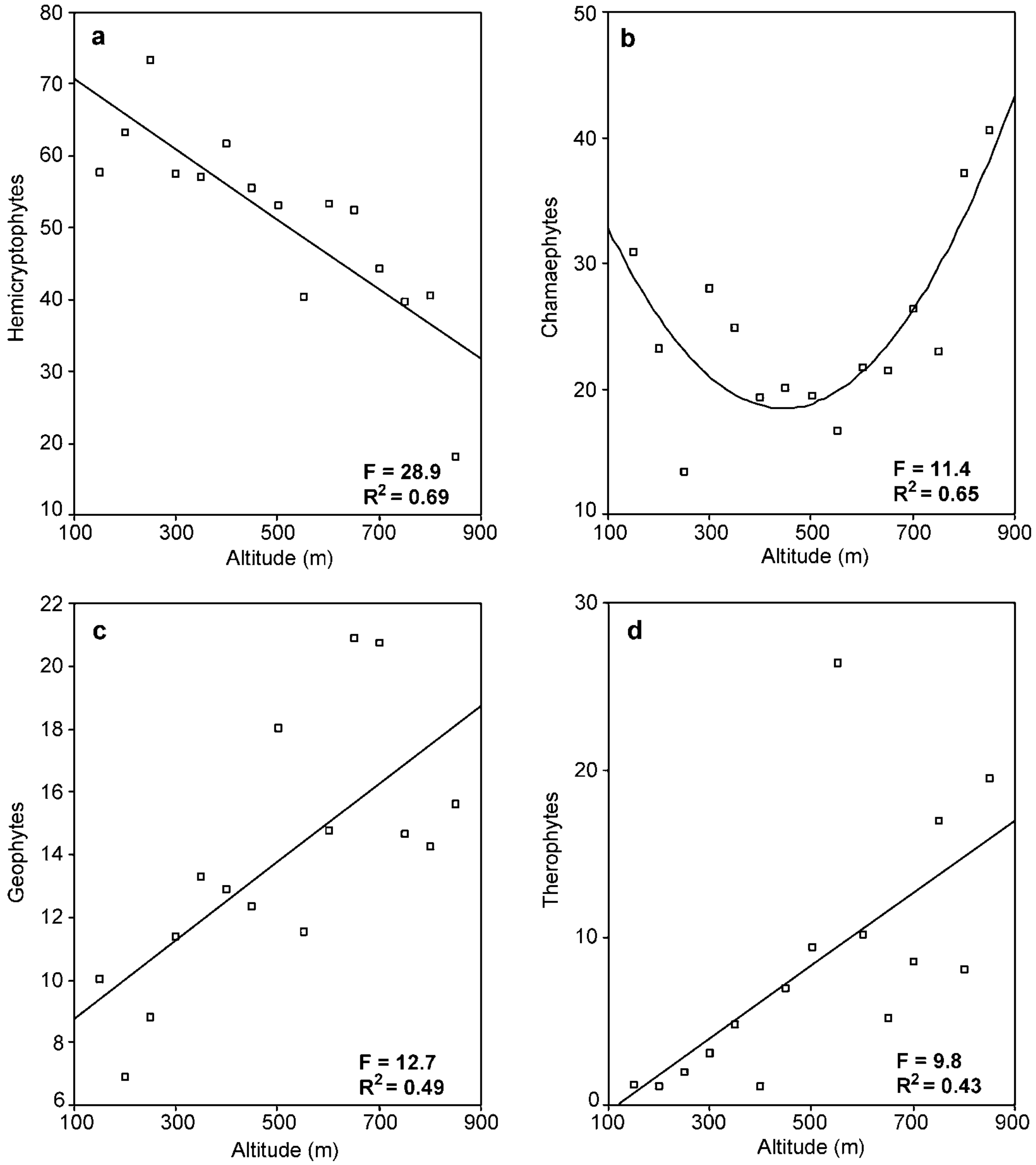


Fig. 4 a-d. *Scatter plots of the abundance of each of the four life-forms in relation to altitude. The best first and second order polynomium to fit the data is based on the highest F value from a one way ANOVA. R^2 for each analysis is also shown.*

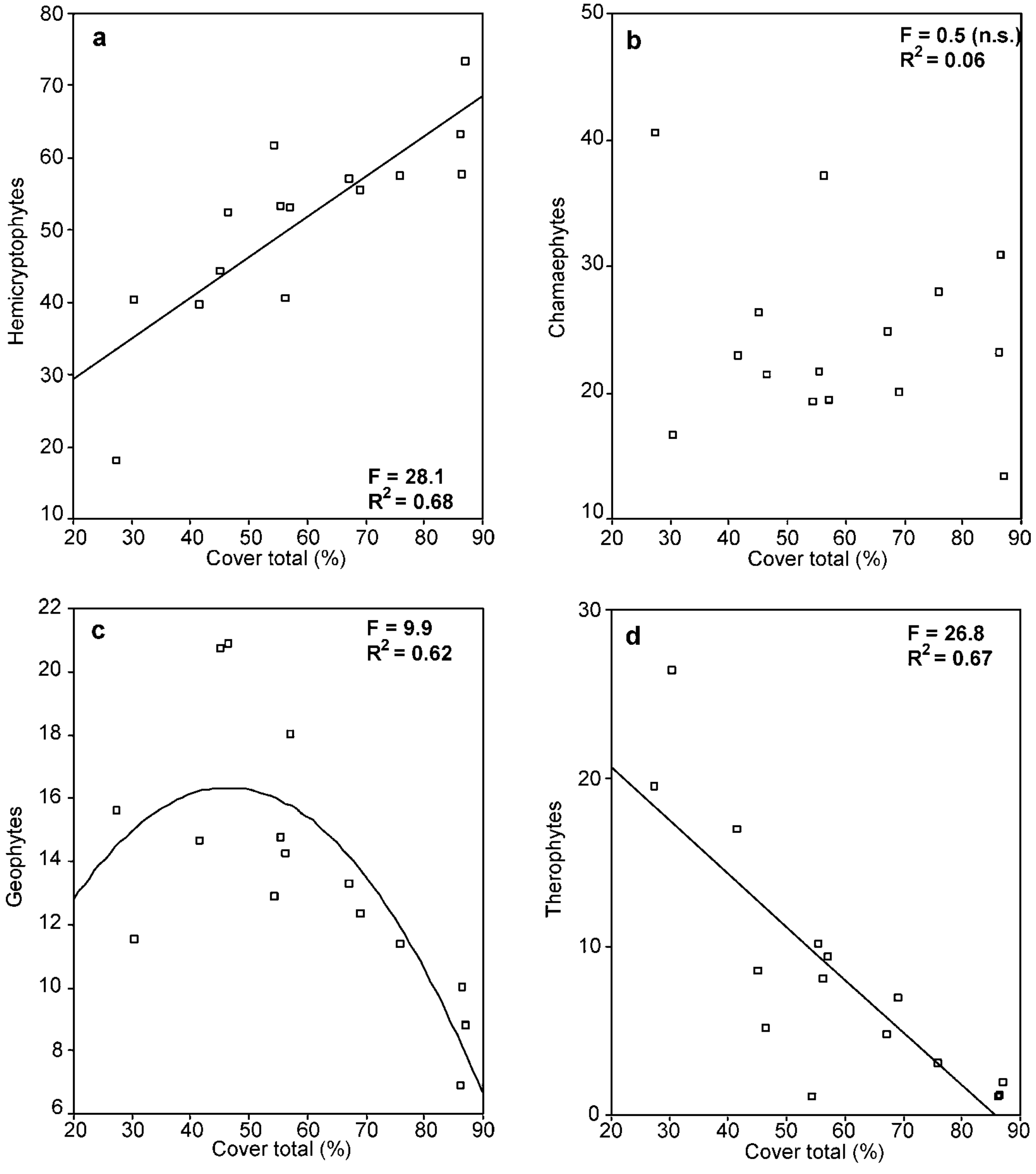


Fig. 5 a-d. *Scatter plots of the abundance of each of the four life-forms in relation to total vegetation cover. The best first and second order polynomium to fit the data is based on the highest F value from a one way ANOVA.* R^2 *for each analysis is also shown.*

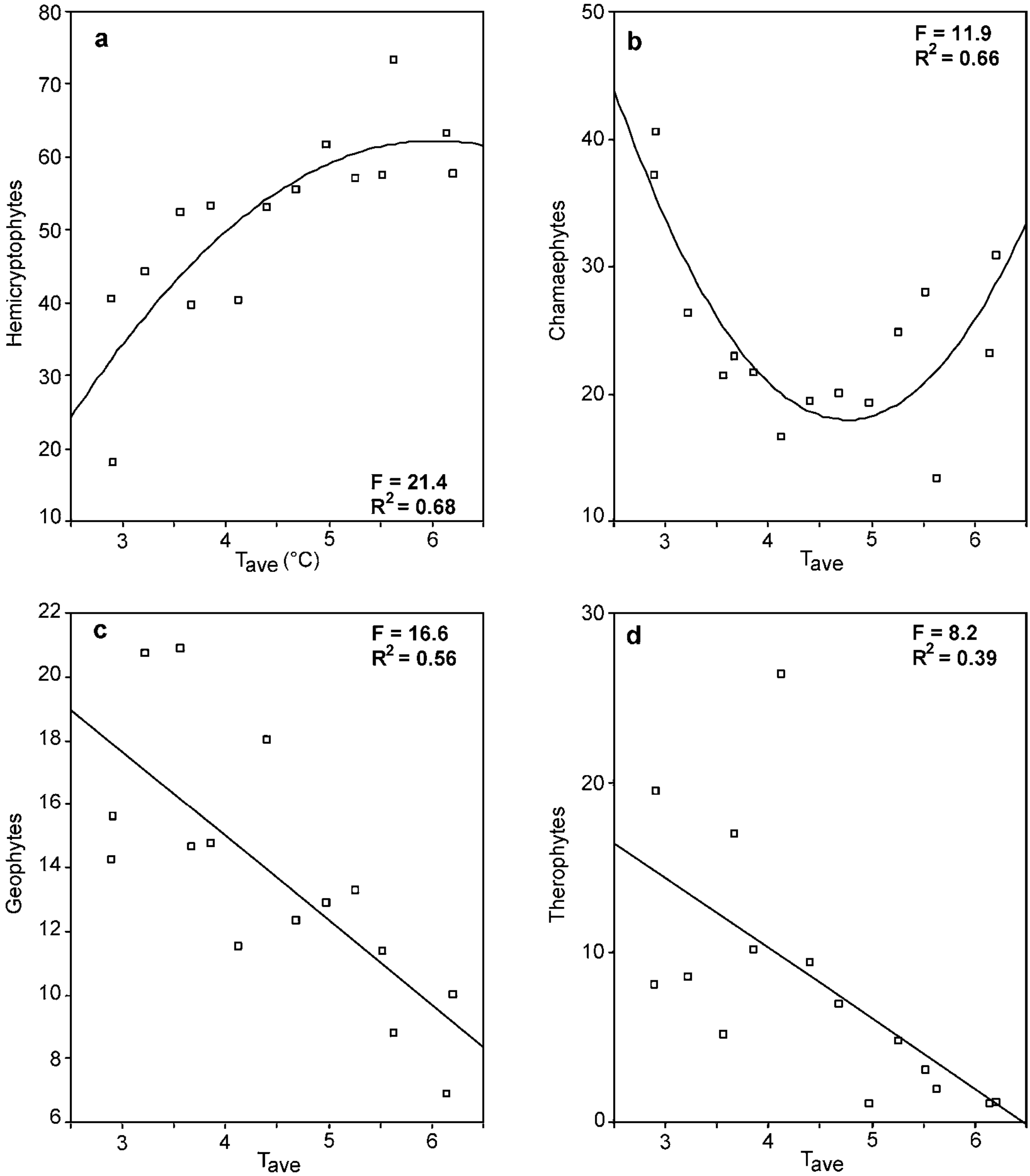


Fig. 6 a-d. *Scatter plots of the abundance of each of the four life-forms in relation to Tave. The best first and second order polynomium to fit the data is based on the highest F value from a one way ANOVA. R^2 for each analysis is also shown.*

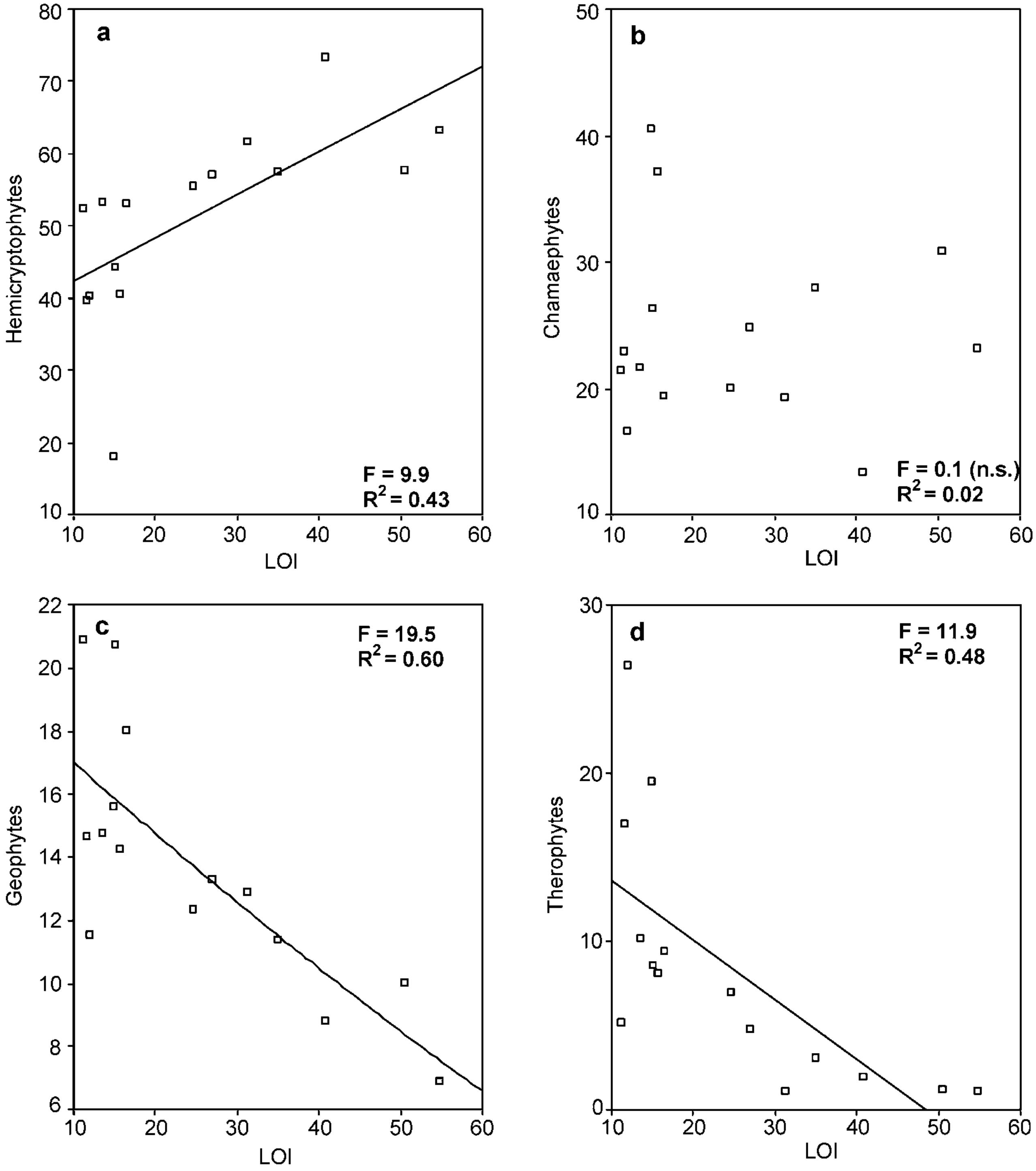


Fig. 7 a-d. *Scatter plots of the abundance of each of the four life-forms in relation to LOI. The best first and second order polynomium to fit the data is based on the highest F value from a one way ANOVA.* R^2 *for each analysis is also shown.*

To investigate which of the environmental parameters explained most of the variation, we compared the F values from the ANOVA tables (Figs. 4-7). Based on this criterion, total vegetation cover best explained the variation of hemicryptophytes and therophytes while temperature best explained chamaephyte variation and LOI gave the highest F value for geophytes.

Discussion

All the results are based on life-form abundances, which have been weighted so that the sum of all abundances for each meso-plot is 100%. This methodology has the drawback that the abundances of different life-forms are not independent. If some life-forms increase in relative abundance, others must decrease. Our main reason for choosing this strategy is the problem arising from the highly eroded areas that dominate parts of the Faroese mountainsides, associated with the decreasing vegetation cover with altitude (Table 3). By weighting the life-form abundances in the specified manner, we reduce the influence of vegetation-free areas on life-form abundance values.

Altitude does not appear to be the best parameter to account for the variation in abundance of all Raunkiær's life-forms along an altitudinal gradient. As seen from our results, total vegetation cover is correlated almost as strongly as altitude with the variation in abundance of hemicryptophytes, the most common life-form in the Faroe Islands. In relation to the other life-forms, we found that hemicryptophytes decrease linearly to the highest point on the gradient. This could, however, also be explained by the fact that total vegetation cover decreases similarily with altitude.

The decrease of hemicryptophyte abundance with altitude was also found in grazed areas at high altitude in Australia by McIntyre *et al.* (1995). They found that increasing soil disturbance resulted in a decreasing number of species with vegetative reproduction, but no effect was seen on species without vegetative reproduction. This was verified in our study with the negative correlation of total vegetation cover on the abundance of hemicryptophytes. In other studies, hemicryptophytes were found to be less tolerant of grazing than species with subterranean over-wintering buds (Hadar *et al.*, 1999; Sternberg *et al.*, 2000).

The most important parameter describing the distribution of therophytes is also total vegetation cover. Fellfields, screes and other areas with unstable soils such as patterned ground are widespread in the alpine zone in the Faroe Islands (Fosaa, 2004). In such unstable habitats, therophytes are the dominant life-form, with *Koenigia islandica* as the predominant species, commonly being the only species in our meso-plots. In the Faroe Islands, the mountains are grazed from the lowlands to the mountaintops, (Brattaberg, *pers. com.*). Increasing disturbances due to natural causes also result in decreasing total vegetation cover with increasing altitude (Table 3). Soil disturbance has been found to reduce the species richness (McIntyre and Lavorel, 1994), which is also consistent with our results. McIntyre *et al.* (1995) found that light grazing increases diversity, while heavy grazing result in a higher proportion of therophytes. The abundance of therophytes in the Faroes, increased significantly with increasing altitude, although the richness of this life-form decrease (Fig. 3). This result is consistent with Grime *et al.* (1988) and McIntyre *et al*. (1995) who found that therophytes increase in areas with low total vegetation cover and little competition from other species.

We found that chamaephytes had their lowest abundance between 400-500 m, and then increased with altitude. Geophytes increased linearly with altitude. The most important parameters describing the abundance variation of these two life-forms are annual mean soil temperature and soil loss on ignition, respectively.

Minimum chamaephyte abundance in the mid-mountain slopes can be explained by the disappearance of species such as *Calluna vulgaris, Empetrum nigrum, Vaccinium myrtillus* and *V. uliginosus* at the minimum abundance altitude (500 m), and increasing abundance of these chamaephytes above this elevation. It can, however, possibly also be the result of increased abundance of chamaephytes such as *Silene acaulis* and *Salix herbacea* above this same elevation.

Studies from other areas showed that geophytes are more resistant to grazing disturbance than both chamaephytes and hemicryptophytes, since their over-wintering buds are subterranean and they flower early, features which enables them to flower and set seed despite grazing (Hadar *et al*., 1999 and Sternberg *et al.*, 2000). In other studies, geophytes were also found to decrease with altitude (Danin and Orshan, 1990; Gomez *et al*. 1993; Pavón *et al*., 2000). Since geophytes in this study represent only 25 % of the geophytes occurring in the Faroe Islands (Fig. 2), it is difficult to draw any conclusions about this life-form.

Conclusion

Returning to the first question posed in the introduction: How do life-form abundances change with altitude in a quantitative manner? We found a linear relationship between altitude and three of the life-forms. Hemicryptophytes decrease linearly; therophytes and geophytes increase linearly; and chamaephyte abundance changes parabolically with a minimum at the mid-mountain elevation.

The second question posed was: Is the transition between temperate and arctic vegetation abrupt, or continuous, and, if the former, then at what altitude? We found a shift in the abundance distribution of chamaephytes at 400-500 m a.s.l. The relative abundance of chamaephytes increases in relation to hemicryptophytes above this altitude. This indicates a change from lowland temperate vegetation, with hemicryptophytes as the dominant life-form, to arctic vegetation in the highlands where chamaephytes are more abundant than at lower altitudes.

The third question was: What parameters are responsible for the life-form changes and to what extent are these parameters climatic? Both non-climatic and climatic parameters seem to be correlated with changes in relative abundance of life-forms. Chamaephytes are an exception to this generalisation, as they are not correlated to total vegetation cover or LOI.

The high abundance of therophytes in the alpine zone is seen to be due to low total vegetation cover, as therophytes are commonly found as the only life-form in unstable soils such as screes, fellfields and patterned fields.

We, therefore, suggest that the effect of environmental factors, such as soil disturbance, override the effect of climatic parameters for therophytes. Thus, disturbance of the soils due to reduced vegetation cover is most likely the best explanation for the high abundance of therophytes.

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References

Böcher, T.W. 1937. Nogle studier over Færøernes alpine vegetation. *Bot.Tid*. 44: 154-201.

Box, I.E. 1981. *Macroclimate and plant forms: An introduction to predictive modelling in phytogeography*. Dr W. Junk Publisher, The Hauge/ Boston/ London.

Danin, A. and Orshan, G. 1990. The distribution of Raunkiær life-forms in Israel in relation to environment. *J. Veg. Sci*. 1: 41-48.

Díaz, S. and Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8: 463-474.

Díaz, S., Cabido, M., Martínez Carretero, E. and Arnaíbar, J. 1999. Plant functional traits, ecosystem structure, and land-use history along a climatic gradient in central-western Argentina. *J. Veg. Sci.*10: 651-658.

Díaz, S., Marcelo, C. and Casanoves, F. 1997. Plant functional traits and environmental filter at a regional scale. *J. Veg. Sci.* 9: 113-122.

Fosaa, A.M., Hansen, B. and Gaard M. 2001. *Soil temperature in the Faroese Mountains. Data report. Faroese Museum of Natural History*. Tórshavn, Faroe Islands.

Fosaa, A.M. 2004. Altitudinal distribution of plant communities in the Faroe Islands. *Fróðskaparrit*, 51: 200-211.

Gitay, H. and Nobel I.R. 1997.What are functional types and how should we seek them? – *In*: Smith, T. M., Shugart, H. H. & Woodward, F. I. (eds.) *Plant functional types: their relevance to ecosystem properties and global change*. 3-19. Cambridge University Press, Cambridge.

Gomez, D., Sesé, J. A., Ferrández, J.V. and Aldezabal A. 1993. Altitudinal variation of floristic features and species richness in Spanish Pyrenees Alpine belt. *In*: *Island and high mountain vegetation: biodiversity, bioclimate and conservation*. Procedings of IAVS symposium Tenerife, Universidad de la Laguna, Serie Informes n^{o} 40.

Grime, J.P., Hodgson, J.G. and Hunt, R. 1988. *Comparative plant ecology a functional approach to common British species*. London, unwin Hyman.

Grime, J.P., Hodgson, J.G., Hunt, R., Thompson, K., Hendry, G.A.F., Campbell, B.D., Jalili, A., Hellier, S.H., Diaz S. and Burke, M.J.W. 1997. Functional types: Testing the concept in Northern England. – *In*: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds.) *Plant functional types: their relevance to ecosystem properties and global change*. 122-150. Cambridge University Press, Cambridge.

Hadar, L., Noy-Meir, I. and Perevolotsky, A. 1999. The effect of shrub clearing and grazing on composition of a Mediterranean plant community: functional groups versus species. *J. Veg. Sci.* 10:5. 673-682.

Hansen, K. 1972. Vertical vegetation zones and vertical distribution types in the Faeroes. *Bot. Tid*. 67:33-63.

Hobbs, R. J. 1997. Can we use plant functional types to describe and predict responses to environmental change? – *In*: Smith, T. M., Shugart, H. H. & Woodward, F. I. (eds). *Plant functional types: their relevance to ecosystem properties and global change*: 66-90. Cambridge University Press, Cambridge.

Intergovernmental Panel on Climate Change. 2001. *Climate change 2001: impact adaptation and vulnerability. Summary for policymakers.* Intergovernmental Panel on Climat Change. Cambridge University Press, Cambridge.

Kelly, C.K. 1996. Identifying plant functional types using floristic data bases: Ecological correlates of plant range size. *J. Veg. Sci*. 7: 3. 414-424.

Lavorel, S., McIntyre, S. and Grigulis, K. 1999. Plant response to disturbance in Mediterranean grassland: How many functional groups? *J. Veg. Sci.* 10: 661-672.

Lawesson, J.E., Fosaa, A.M. and Olsen, E. 2003. Calibration of Ellenberg indicator values for the Faroe Islands. *Applied ecology*, 6: 53-62

Mark, A.F., Dickinson, K.J.M and Hofstede, R.G.M. 2000. Alpine Vegetation, Plant Distribution, Life Forms, and Environmnents in a Perhumid New Zealand Region: Oceanic and Tropical High Mountain Affinities. *Arct. Antart. and Alp. Res*. 32: 240-254.

Mark,A.F., Dickinson, K.J.M., Allen J., Smith, R. and Wesr Carol, J. 2001. Vegetation patterns, plant distribution and life forms across the alpine zone in southern Tierra del Fuego, Argentina. *Australian Ecology*. 26: 423-440.

McIntyre, S. and Lavorel, S. 1994. Predicting richness of native, rare and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conservation biology*. 8: 521-431.

McIntyre, S., Lavorel, S. and Tremont, R. 1995. Plant life history attributes: their relationship to disturbance responses in herbaceous vegetation. *J. Ecol.* 83: 31-44.

McIntyre, S., Lavorel, S., Landsberg, J. and Forbes, T.D.A. 1999. Disturbance response in vegetation-toward a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.

Molau, U. and Mølgaard, P. 1996. *ITEX Manual International Tundra Experiment*. Danish Polar Centre

Nobel, I.R. and Gitay, H. 1996. A functional classification for predicting the dynamics of landscapes. *J. Veg. Sci*. 7: 329-336.

Ostenfeld, C.H. 1905-08. *The landvegetation of the Faeroes with special reference to higher plants*. Botany of the Faeroes. 3: 867-1026.

Pavon N., Hernández-Trejo, H. and Rico-Gray, V. 2000. Distribution of life-forms along altitudinal gradients in semi-arid valley of Zapotitlán, Mexico. *J. Veg. Sci.* 11: 39-42.

Prentice, I. C., Cramer, W., Harrison, S.P., Monserud, R.A. and Solomon, A.M. 1992. A global model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, 19: 117-134.

Raunkiær, C. 1934. *Life-forms of Plants and statistical plant geography*. Oxford: Claredon Press. 632 pp.

Raunkiær, C. 1936: *Life-form spectrum of some Atlantic islands*. Botaniske studier, hefte 4. J.H. Schultz forlag.

Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D. and Kiegel, J. 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *J. Appl. Ecol*. 37: 224-237.

Thorsteinsson, K. 2001. Hagar og seyðamark. pp. 1-88- Føroya Jarðarráð.

TinyTag - Gemini Data Loggers (UK) Ltd., Scientific House, Terminus Road, Chichester, West Sussex, UK.

Vitousek, P.M., Mooney, H.A., Lubchenco, J and Melillo, J.M. 1997. Human domination of earth's ecosystem. *Science*. 277: 494-499.

Walker, B.A. 1997. Functional types in non-equilibrium ecosystems. *In:* Smith, T. M., Shugart, H. H. and Woodward, F.I. (eds). *Plant functional types: their relevance to ecosystem properties and global change*. 3-19. Cambridge University Press, Cambridge.

Woodward, F. I. and Cramer, W. 1996. Plant functional changes and climatic changes: Introduction. *J. Veg. Sci*. 7: 306-309.