



Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: are the patterns determined by environment or by land-use?

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Abstract

This study presents a quantitative partitioning of the variance in floristic data from grazed semi-natural vegetation of summer farms in Røldal, western Norway. The data consist of 189 taxa recorded in 107 4 m² sample plots within 10 summer farms with different land-use histories. Thirty-five environmental variables were recorded, including altitude, slope, radiation, geology, soil chemistry, and past and present land-use. A series of (partial) canonical correspondence analyses (CCAs) were used to partition the total variation into within-farm and between-farm components, and to investigate the explanatory power of different groups of environmental and land-use variables at the two scales. The results show that: (1) although local gradients are of overriding importance for floristic composition, landscape-scale processes also contribute significantly to the observed patterns; (2) the measured land-use and environmental factors account for comparable amounts of compositional variance at the two scales; and (3) even if the relative contributions of the two classes of explanatory variables are comparable, details differ, showing that broad-scale environmental and land-use patterns are not just scaled-up versions of the fine-scale patterns or vice versa. These results support a multi-process view of vegetation patterns.

Introduction

The effects of large grazing animals on grasslands have been intensively studied throughout the world, but the results have been partly contradictory. Grazing has been shown to both increase (Belsky 1992; Montalvo et al. 1993) and decrease (McIntyre and Lavorel 1994) plant diversity. Grazers may affect floristic composition (Peart and Foin 1985; Marrs et al. 1988), vegetation structure (Diaz et al. 1994), neither of these (Glenn and Collins 1992), or both (Diaz et al. 1992; Noy-Meir et al. 1989). Responses to changes in grazing pressure may be small and slow (Diaz et al. 1994) or large and rapid (Smith and Rush-ton 1994; Pettit et al. 1995). As a result of such discrepancies, the importance of grazing on vegetation

has been much debated (Huntly 1991; Hulme 1996; Olf and Ritchie 1998). Milchunas and Lauenroth (1993), in a world-wide meta-analysis of 236 studies of grazing / no grazing contrasts, show that the compositional and structural responses are, to a large extent, determined by the overall productivity and the evolutionary history of the study systems. Thus, the relative importance of land-use and environment for grazed natural communities may differ between systems.

Developments in ecological theory emphasise the scale-dependence of ecological patterns and processes (O'Neil et al. 1986; Pickett et al. 1989). This means that patterns in local richness and composition in natural communities cannot be understood in terms of one single process - instead we may need to consider

the relative contributions of several non-mutually exclusive processes that may operate at different temporal and spatial scales (Power 1992). Zobel (1992, 1997) visualises these processes as a series of filters acting on the community at the continental, regional, local, and community scales. Far from being simple ecological factors, grazing animals may affect vegetation in several different ways, through direct biomass consumption, trampling, urination, defecation, and by acting as dispersal agents (Olf and Ritchie 1998), and have been shown to impose pattern on vegetation on scales ranging from individual plants (Wielgolaski 1976; Anderson and Briske 1995) via vegetation patches (Bakker et al. 1983; Steinauer and Collins 1995) and vegetation types (Glenn et al. 1992; Milchunas et al. 1998) to regions (Glenn et al. 1992). In order to describe and understand the relative importance of grazing animals and environment in natural ecological systems, it is therefore necessary to elucidate the patterns at several different scales.

The sub- and low-alpine regions of Norway have been utilised as extensive summer pastures for large herds of domestic livestock since prehistoric times (Reinton 1955, 1957 & 1961; Kvamme 1988; Kvamme et al. 1992). Whilst in the mountains, the animals are allowed to range freely during daytime, but are gathered at night into barns or enclosures at summer farms for milking and shelter. These summer farms are surrounded by semi-natural grasslands and ruderal communities that differ both in species composition and general appearance from the surrounding alpine heaths or low-alpine forests (Resvoll-Holmsen 1920; Nordhagen 1943; Vandvik and Birks 2001a). Although the economic importance of summer farming has declined drastically over the past few decades, summer farms are still a characteristic feature of the Norwegian upland landscape. Their vegetation and species richness vary in response to environmental factors such as geography, altitude, moisture, and productivity, and land-use factors such as history, land-use regime, and grazing pressure (Austrheim et al. 1999; Vandvik and Birks 2001a, 2001b). The summer farms are scattered throughout the landscape, and the semi-natural grasslands and ruderal communities found on them may be seen as ecological systems that are shaped and maintained by the interacting effects of the historical land-use system and the contemporary environment. Given the insularity of these habitats, an obvious question is how much of the total variation in summer-farm vegetation occurs at the within-farm and between-farm scales, respec-

tively. As the importance of different environmental and land-use factors may vary with spatial scale, another question of interest is how much of the between-farm variation can be attributed to environment and land-use after within-farm patterns are accounted for, and vice versa.

Borcard et al. (1992) present a quantitative statistical method for partitioning the variance in compositional data into independent components, using a series of (partial) canonical ordinations (ter Braak 1988). This method allows one to estimate the independent contributions of different (groups of) variables, as well as the covariance between them. The method has been much used to investigate the relationships between spatial and environmental components of compositional variation in a variety of research fields including palaeoecology (e.g. Ammann et al. (1993); Birks and Lotter (1994)), biogeography (e.g. Heikkinen and Birks (1996); Ohmann and Spies (1998)), and ecology (e.g. Økland and Eilersen (1994); ter Braak and Wiertz (1994); Borcard and Legendre (1994); Baar and ter Braak (1996); Aude and Lawesson (1998); Roche et al. (1998)). This method of partitioning variance has recently been extended to more than two groups of explanatory variables, by combining the matrices into various sets in a series of analyses (Magnan et al. 1994; Jones and Juggins 1995; Gasse et al. 1995; Quinghong 1997; Lotter et al. 1997; Anderson and Gribble 1998). While most applications have focused on space vs. environment, or space vs. time vs. environment, any groups of explanatory variables can be analysed. As Pinel-Alloul et al. (1995) point out, this statistical approach is therefore conceptually linked to the recent developments in ecological theory that seek to explain community patterns in terms of the interactive effects of several different processes operating over a range of temporal and spatial scales (Zobel 1992, 1997).

In this paper we use the approach of Borcard et al. (1992) to investigate how environment and land-use relate to the compositional variation in summer-farm grasslands at the *within-farm* and *between-farm* scales. This is done in three steps: (1) the total variance in the floristic data-set from summer farms is partitioned into within-farm and between-farm components, (2) the potential explanatory power for groups of variables representing environment (soil chemistry, soil biology, physical factors) and land-use (land-use history, grazing pressure) for within-farm and between-farm patterns is quantified, and (3) in a

full variance partitioning the pure contributions of, as well as the shared components or covariances between, the groups of environmental and land-use variables at the two scales are quantified.

Methods

Study area

The study area in Røldal, western Norway, is at 650–850 m above sea level (a.s.l.) and is surrounded by mountains reaching 1600–1700 m a.s.l. Annual precipitation is ca 1350 mm (Førland 1993) and July mean temperature ca. 12 °C (Aune 1993). The climate is sub-oceanic, with high autumn precipitation and a relatively small amplitude in annual temperature (ca. 18 °C). The climatic forest-limit in the area is at 800–900 m a.s.l., and the sub-alpine forest is dominated by birch. Tall-herb and tall-fern vegetation occurs on the steep hillsides, while the open vegetation around the summer farms and above the forest limit consists mainly of dwarf-shrub heath (Odland 1981; Vandvik and Birks 2001a).

Sampling and data collection

Ten summer farms, within an area of ca. 10 × 20 km, representing a chronosequence from farms in use today to farms abandoned ca. 10, 20, and 40 years ago were selected for study. For each farm, data on land-use and grazing pressure were obtained from interviews, and altitude and geology were compiled from maps. The size of each summer farm was measured in the field as the average distance from the centre of the farm (barn, milking shed, or other assembly point for the animals) to the border between the semi-natural summer-farm grassland and the surrounding heath or woodland vegetation.

In July and August 1992 2 × 2 m plots were placed subjectively in order to sample the major floristic variability of each farm, including both the grasslands and the surrounding vegetation. The cover-abundance of each species was recorded using the Domin scale (Dahl 1957). Nomenclature follows Lid (1985) for vascular plants, (Smith 1978, 1990) for bryophytes, and Krog et al. (1980) for lichens. The slope and aspect of each plot were measured, and potential solar beam irradiation (Oke 1987) calculated. The distance from the plot to the farm centre (see above) was included in the analyses as a estimate of plot-scale graz-

ing pressure. In order to standardise this variable between farms, the distance was divided by farm size. The resulting variable, relative distance to farm centre, varies between 0 and 3. Soil chemical analyses were based upon air-dried soil passed through a 2 mm sieve. Loss-on-ignition, total nitrogen (Kjeldahl method), pH, and extractable phosphate, sodium, potassium, calcium, and magnesium were measured, and cation exchange capacity and base-saturation were calculated using standard procedures (Røeberg 1984). Phosphate and cation concentrations were log-transformed, and nitrogen expressed as N:LOI, which was considered to be a simple but useful index describing the ecologically relevant *available nitrogen* in the soil (see Vandvik and Birks (2001a) for details).

Numerical methods

The vegetation-environment relations were examined using the computer package CANOCO 3.12a (ter Braak 1987), using strict convergence criteria, default settings, and down-weighting of rare species. A preliminary detrended correspondence analysis (DCA, Hill and Gauch (1980)) with detrending by segments and non-linear rescaling showed that the main floristic gradient in the data was 4.9 standard deviations. Non-linear responses are expected along such a gradient, and unimodal-based methods (CA, CCA, partial CCA, DCA, DCCA) were therefore used.

To yield ecologically interpretable variance components, the explanatory variables were grouped into the following six subsets: (1) A matrix of categorical (or dummy) variables representing *farm identity* of the 10 summer farms, (2) The *relative distance* to farm centre, (3) The *physical* characteristics of the plots (altitude, slope, radiation index, bedrock geology), (4) Soil chemical variables that are mainly affected by *soil biology* (decomposition rate, etc.) namely soil organic content, phosphate, and nitrogen, (5) Soil chemical variables that are most closely associated with *soil reaction* (pH, cations, base-saturation, and cation exchange capacity), and (6) *land-use history* (years since abandonment, sheep grazing). Within groups 3–6 the forward selection option in CANOCO with statistical testing by unrestricted Monte Carlo permutation tests for each added variable (ter Braak 1990; ter Braak and Verdonschot 1995) was used to exclude variables that did not contribute significantly ($p > 0.01$) to the explained variance. This was done to avoid over-estimation of the explained variance in the data (Borcard et al. 1992; Økland and

Table 1. Summary of the groups of variables, their abbreviations, and the variables included in each group after forward selection. Variables are relative distance (RD), altitude (ALT), slope (SLO), loss-on-ignition (LOI), nitrogen (N:LOI), phosphate (P), Calcium (Ca), cation exchange capacity (CEC), Sodium (Na), pH, sheep grazing (SHE), and years since abandonment (YRS). The variance explained is the variance accounted for when the group is used as constraining variables in a CCA, and the unique contribution is variance accounted for when the effect of all other groups are removed in a partial CCA. These entries are expressed as % of total inertia. P-values refer to the unique contribution (see text).

Variable group	Abbreviation	Significant variables	Variance explained (%)	Unique contribution (%)	P-value
Farm ID	F	10 Farms	12.1	7.4	0.01
Relative distance	D	RD	5.6	1.7	0.01
Physical factors	P	ALT, SLO	7.4	2.5	0.02
Soil biology	B	LOI, N:LOI, P	11.0	6.7	0.01
Soil reaction	R	Ca, CEC, Na, pH	10.5	4.9	0.01
Land-use	U	SHE, YRS	3.1	0.9	0.28

Eilersen 1994). The groups, variables, and their abbreviations are listed in (DCA, Hill and Gauch (1980)).

In order to investigate how successfully the measured environmental variables capture the main variation in the floristic data, the results of both detrended and undetrended versions of the direct and indirect ordination analyses were compared. Additionally, a partial CA with all environmental variables partialled out was performed in order to investigate patterns in the residual variation, and the results of this analysis was compared to the overall floristic patterns in the data. Spearman's rank correlations (PROC CORR) (SAS Institute 1997) of plot order along the axes of the various analyses were computed.

Standard CCAs were run with the six groups of variables one at a time, and with all groups combined, as constraining explanatory variables. The total explained variance in the data, as well as the fraction of this variance that the different groups can potentially account for, were thus quantified. Partial CCAs with each group of variables as constraining variables and all other groups as covariables were run to quantify the unique contribution of each group – or the amount of variance they explain when the effect of all other groups of predictors are allowed for. The statistical significance of this unique contribution was tested using Monte Carlo permutation tests within CANOCO, with 299 unrestricted permutations, and significance based on by the overall (trace) statistic (Table 3, analyses 2 – 7).

The explanatory power of the groups of environmental and land-use variables for within-farm and between-farm floristic patterns was analysed in two conceptually different ways. The first approach was to investigate the potential explanatory power of each

group of variables for within-farm and between-farm floristic patterns in five independent analyses. In each of these analyses the variance partitioning approach of Borcard et al. (1992) was applied to partition the variance for the 10 farms and the groups of environmental or land-use variables to yield the following variance components: (1) between-farm variance independent of environment, (2) shared between-farm and environmental variance or explained differences between farms (3) within-farm variance explained by the environment, and (4) unexplained variance ((Table 3, analyses 8 – 12). The second approach was to perform a series of analyses with different models that enable the separation of independent components of variance and covariance between all groups of environmental variables (Table 3, analyses 13 – 25). The statistical significance of the independent variance components in these analyses was tested as described above.

Results

Comparison of direct and indirect ordinations

Eigenvalues decrease from the unconstrained to the constrained ordinations (Table 2), indicating that a portion of the floristic variation is not accounted for by the measured environmental variables. For second and subsequent axes, this is much more pronounced for undetrended (CA/CCA) than detrended (DCA/DCCA) analyses, suggesting that part of the decrease may result from polynomial distortion (Økland 1999). The high species-environment correlations of DCA, along with the strong Spearman's rank correlation between axes 1, 2, and 3 in DCA/DCCA, suggest that

Table 2. Eigenvalues and species-environment correlations from undetrended vs. detrended and unconstrained vs. constrained ordinations, and from a partial CA with all environmental variables as covariables. Spearman's rank correlations of plot order on the unconstrained and constrained axes of undetrended and detrended ordinations, and on the unconstrained ordination and the partial CA ordination axes are also given.

	Axis			
	1	2	3	4
Eigenvalues				
CA	0.51	0.32	0.26	0.22
CCA	0.41	0.19	0.15	0.14
DCA	0.51	0.25	0.14	0.11
DCCA	0.41	0.18	0.12	0.07
Partial CA	0.26	0.15	0.13	0.11
Species – environment correlations				
CA	0.86	0.67	0.82	0.70
CCA	0.91	0.88	0.75	0.82
DCA	0.89	0.81	0.61	0.67
DCCA	0.91	0.88	0.86	0.85
Partial CA	–	–	–	–
Spearman's rank correlations[†]				
CA/CCA	0.96**	0.20	0.22	–0.65**
DCA/DCCA	–1.00**	–0.95**	0.54**	0.13
CA/PartialCA	0.12	–0.25*	–0.33**	0.26**

[†] Signs of coefficients reflect the arbitrary selection of gradient directions in CANOCO. * $p < 0.05$ ** $p < 0.01$

much of the variation in the vegetation is related to the measured environmental variables. Although the partial CA had a moderately strong first gradient, the relationship between this gradient and the unconstrained axes is weak (Spearman's rank correlation with axes 1–4 were tested, axis 1 only reported in Table 2) and there was no obvious interpretation of the floristic patterns in the ordination plots.

Overall vegetation-environment relations

The results from a CCA with all groups of explanatory variables included are shown in Figure 1. The first gradient (9.2% of the floristic variance) is a gradient of decreasing soil nitrogen, phosphate, and pH, and increasing distance to the farm and slope. Weeds and grasses predominate at the positive side of CCA axis 1, while heathland species are more common at the negative side. The gradient can be interpreted mainly as a within-farm gradient of decreasing manure and grazing influence from farm centres to the surrounding heathlands. The second axis (4.3% of the variance) is a soil richness/moisture gradient posi-

tively correlated to soil calcium, base saturation, pH, and organic content. This axis contains a component of between-farm differences, as it is negatively correlated to altitude and abandonment. There is also a relatively important third gradient (3.4% of the variance) in the data.

The explanatory power of each group of variables

When all groups of explanatory variables are included, the sum of the constrained ordination axes is 1.540 (Table 3, analysis 2). As the total inertia (TI) in the floristic data (sum of unconstrained eigenvalues = variance) is 4.433 (Table 3, analysis 1), the explanatory variables account for 34.9% of the floristic variance (1.540/4.433). Differences between farms account for 12.1% of TI, or ca. 1/3 of the explained variance (Table 3, analysis 2; Figure 2a). The groups of environmental and land-use variables differ considerably in their ability to explain the floristic variation. Soil reaction and soil biology account for more than 10% each, whereas physical factors account for 7.4%, distance to farm centre 5.6%, and land-use 3.1% (Table 3, analyses 3 – 7; Figure 2a). The variance explained by the different groups separately adds up to much more than their joint explanatory power (34.9%), indicating that there is considerable covariation or shared variance between the groups of predictors.

The groups partitioned into within-farm and between-farm components

The groups of environmental and land-use variables are partitioned into between-farm and within-farm components in five separate analyses (Table 3, analyses 8 – 12). These variance components, displayed graphically in Figure 2b, can be added horizontally to yield the total variance explained by each group – which is simply the components of Figure 2a. Within the farms, soil reaction and biology are clearly the 'best' groups, accounting for more than 10% each, whereas physical factors and distance account for 5.8% and 5.6%, respectively. Again, the variance explained by the groups independently adds up to much more than their joint explanatory power (Table 3, analysis 2; Figure 2b, within-farm variance) and there is obviously much covariance between the different groups at the within-farm scale. At the between-farm scale, the explanatory power of all groups is low. Land-use (2%) and physical factors (1.6%) are the

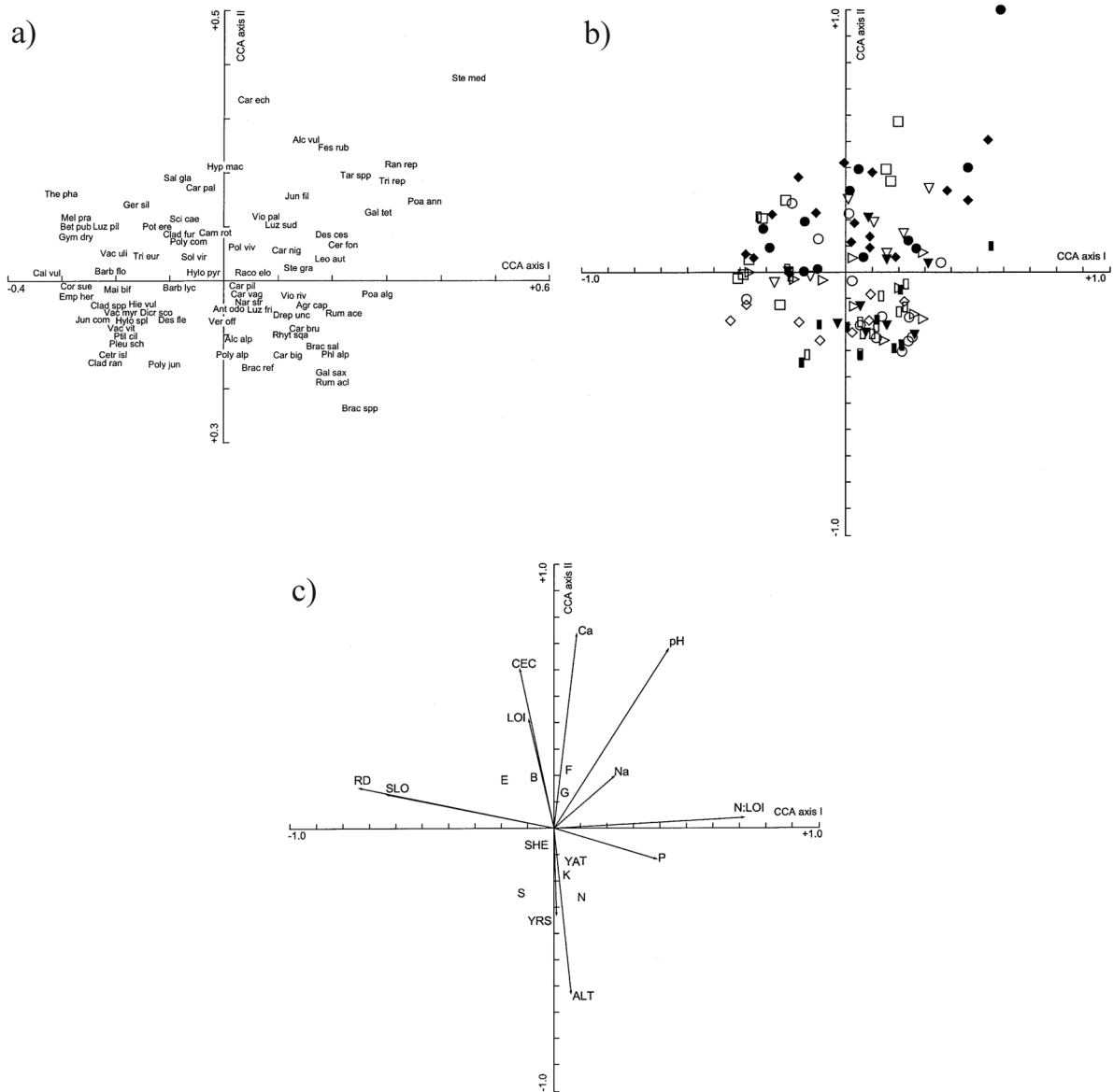


Figure 1. Ordination diagrams based on a CCA with all groups of explanatory variables included. Axes 1 and 2 explain 9.2% and 4.3% of the floristic variance, respectively. (a) Species. All species with more than three occurrences are shown. Abbreviations for species names are the 3 + 3 first letters of the names of vascular plants, and 4 + 3 first letters of names of bryophytes. Exceptions are *Poa alpigena* (Poa alg) and *Rumex acetosella* (Rum acf). For full species names, see Vandvik and Birks (2001a). (b) Samples. The ten farms are given different symbols, farms in use have filled symbols, and abandoned farms have open symbols. (c) Environmental variables. Abbreviations are explained in (Table 1), except for the capital letters A, B, E, F, G, K, N, S, T, and Y which represent farm centroids.

best groups, while soil reaction and biology each account for less than 0.5% of the differences between farms.

The explained variance partitioned into statistically independent components

The patterns of variance and covariance between all groups are quantified in analyses 13 – 25 of Table 3. A graphical display of the results is presented in Figure 2c. As in Figure 2b, the variance components can be added horizontally to yield the total variance ex-

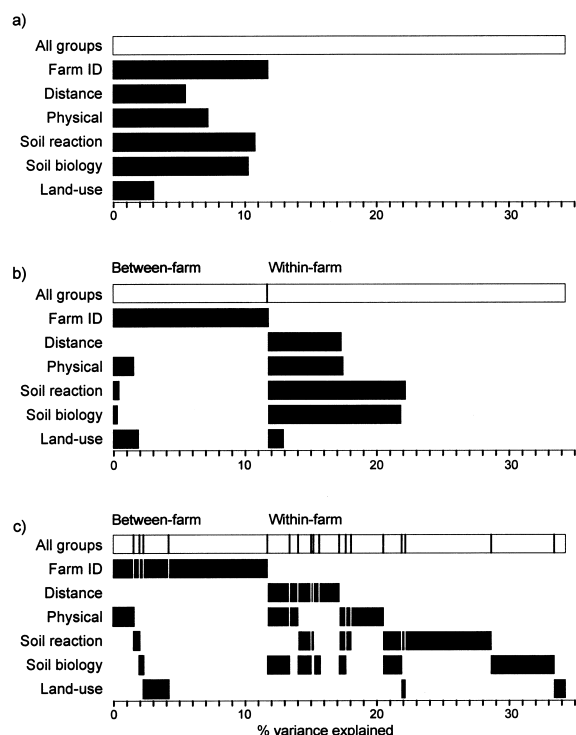


Figure 2. (a) Graphical representation of the amount of variance explained by all explanatory variables combined (open bar), and by each group of variables (black bars). The residual variance (65.7% of TI) is not shown on the figure. (b) The explained variance partitioned into within-farm and between-farm components (analyses 8–12, Table 3). For each group of variables, the explained between-farm variance components are the $A \cap B$ fractions in the Appendix or differences between farms that can be accounted for by the group of environmental or land-use variables. Accordingly, explained within-farm variance components are the $B \setminus A$ fractions. The variance components add up horizontally to the components in (Figure 2a). (c) The explained variance partitioned into independent components (analyses 13–25, Table 3). Hairlines delimit each independent variance component. For the groups of explanatory variables, vertically overlapping components are shared variances (explaining the same fractions of floristic variance, see text). The components can be summed horizontally to yield the variance components in 2b and 2a.

plained by the group. Additionally, the variance components can also be interpreted vertically. Overlapping components are shared variances, they explain the same fraction of floristic variance. For example, distance explains 5.6% of the floristic variance. A large fraction of this variance (3.9% of TI) is also explained by physical factors, soil biology and/or soil reaction (fraction $D \cap PBR$, analysis 22, (Table 3)). Distance and soil biology have a shared variance of 3.3% (fraction $D \cap B$, analysis 14, (Table 3)). 1.7% of this fraction is also shared by physical factors (fraction $D \cap P \cap B$, which can be calculated from

(Table 3)). This implies that these variables account for much of the same floristic patterns (parts of the strong farms-to-surroundings grazing and manure gradient, see Figure 1). The two groups of soil variables (soil reaction and biology) also explain large non-overlapping fractions of within-farm variance. At the between-farm scale, the physical variables (mainly altitude) and land-use account for different fractions of the variance, but the most important pattern to emerge is that two-thirds of the differences between farms (7.4% of the TI) cannot be accounted for by any of the measured variables.

Discussion

The overall gradient structure in the data (Figure 1) is difficult to interpret. Patterns at the within-farm and between-farm scales are confounded in CCA space, and the relative importance of land-use (distance, years), environmental variables that may be influenced by land-use to a greater or lesser degree (soil biology, soil reaction), and factors that are unaffected by land-use (physical characteristics such as altitude and slope), cannot be assessed as these variables covary along all interpretable gradients. Variance partitioning shows that all groups of variables contribute to the explained variance (Figure 2a, (Table 3)), confirming that both land-use and environment are important determinants for summer-farm vegetation. The patterns differ considerably between scales, however (Figures 2b and 2c). At the *within-farm* scale, all groups of variables account for appreciable but partly overlapping amounts of variance, suggesting that the vegetation is structured along strong within-farm gradients in soil reaction and productivity, physical conditions, and grazing effects. Despite differences in geology, altitude, slope, aspect, and land-use history, and the small spatial scale and insularity of these habitats, the investigated summer farms are remarkably similar: only 12% of the total compositional variance is found at the *between-farm* scale. Land-use and physical factors account for approximately 1/6 of the between-farm variance each, leaving 2/3 of the differences between farms unexplained.

Environment and land-use at the within-farm scale

All groups of environmental and land-use variables have high explanatory power for within-farm floristic patterns, and there is also considerable covariance be-

Table 3. Results of all CA, CCA and partial CCA analyses. A and B denote different combinations of groups of explanatory variables into subsets. Each row in the table is constructed by the following analyses: (1) a CCA with A as constraining variables giving the variance fraction A, (2) a CCA with B as constraining variables giving the variance fraction B, (3) a partial CCA with A as constraining variables and B as covariables giving the variance fraction A|B, (4) a CCA with (A+B) as constraining variables giving the variance fraction $A \cup B$. The variance fraction $A \cap B$ can be found by solving $(A - A|B)$ or $(A+B - A \cup B)$, and B|A can be found by solving $(A \cup B - A)$ or $(B - A \cap B)$. Entries are sums of eigenvalues $\times 1000$. Abbreviations for variable subsets and environmental variables included in each subset follow Table 1.

Analysis	A	B	A	B	A B	$A \cap B$	B A	$A \cup B$
1	–	–						4433
2	F	D P B R U	535	1210	330	205	1005	1540
3	D	F P B R U	249	1466	74	175	1291	1540
4	P	F D B R U	326	1428	112	214	1214	1540
5	B	F D P R U	487	1244	296	191	1053	1540
6	R	F D P B U	465	1321	219	246	1075	1540
7	U	F D P B R	139	1501	39	100	1401	1540
8	F	D	535	249	513	5	244	779
9	F	P	535	326	464	71	255	790
10	F	B	535	465	522	13	451	987
11	F	R	535	487	516	19	467	1002
12	F	U	535	139	447	88	51	586
13	D	P	249	326	147	102	224	473
14	D	B	249	465	106	144	320	570
15	D	R	249	487	196	53	434	683
16	F P B R	U	1440	139	1314	107	32	1480
17	F P B	R U	1135	621	859	276	345	1480
18	F P	B R U	790	971	509	281	690	1480
19	F	P B R U	535	1137	343	192	945	1480
20	D P B	R	763	487	593	170	317	1080
21	D P	B R	473	832	248	225	607	1080
22	D	P B R	249	1006	74	175	831	1080
23	P B R U	D F	1137	779	761	376	403	1540
24	P B R	U D F	1006	862	714	292	534	1540
25	P B	R U D F	681	1189	351	330	859	1540

tween the groups. For example, distance to farm centre accounts for 2/5 of the explained within-farm variance, but very little of this can be uniquely attributed to distance (Figures 2b and 2c, Table 1). This does not imply that these are redundant or unnecessary variables, but rather that the upland landscape of western Norway is mountainous, and access, slope, and insolation probably determined where summer farms were located in the first place. The land-use pattern in this rugged landscape is therefore constrained by physical factors. Once a summer farm is established, animals affect local vegetation by grazing and trampling but also through soil enrichment from dung and faeces, thereby creating a soil fertility/disturbance gradient (Vandvik and Birks 2001b).

Within-farm land-use effects are clearly important determinants of vegetation pattern (Figure 1). However, a considerable proportion (3/5) of the explained

within-farm floristic variance is not related to the spatial gradient (Figures 2b and 2c). One interpretation of this result could be that the physical environment and soils are of equal or greater importance for within-farm floristic patterns than grazing animal effects. However, relative distance is a coarse-grained variable that only captures the overall decrease in animal effects away from farms. It does not account for animal effects on smaller (patch) scales (Anderson and Briske 1995; Bakker et al. 1983; Steinauer and Collins 1995), or effects that do not change predictably with distance due to, for example, paths. The large unique contribution of soil biology (Figure 2c), and the importance of manure-related soil variables along CCA axis 1 (Figure 1) suggest that not all fertilisation effects are accounted for by relative distance. The same applies to disturbance effects, and the variance explained by relative distance should therefore be

viewed as a minimal estimate of animal effects on summer-farm vegetation rather than as a precise quantification.

Environment and land-use at the between-farm scale

Within the environmental variables, physical factors are the best group of explanatory variables for between-farm patterns (Figure 2). This can mainly be attributed to the altitudinal gradient related to CCA axis 2 (Figure 1). Several different ecological processes may affect compositional patterns along the altitudinal complex-gradient, including a decreasing intensity of biotic interactions as a result of decreasing overall productivity (Woodward 1988), decreasing nutrient mineralisation rates (Chapin et al. 1986), increasing overall ecological persistence (Montalvo et al. 1991), and regional dynamics (Shmida and Wilson 1985). Despite the great within-farm variability in soil conditions, the different summer farms are remarkably similar as far as edaphic conditions are concerned (Figures 2b and 2c). The overall conclusion based on our results is that site-specific environmental conditions are of little importance for vegetation development at summer farms within our study area.

Given the great impact that the spatial variance in grazing intensity has on within-farm patterns in summer farm vegetation (Figure 2b), (Vandvik and Birks 2001b), it could be hypothesised that changes in the same factor through time should initiate successional change in the vegetation. This is to some degree supported by the data: land-use history is the best group of explanatory variables at the between-farm scale (Figure 2). However, the magnitude of the response is small relative to the rapid successional changes that have been reported from abandoned lowland semi-natural grasslands in Norway (e.g. Losvik (1988); Norderhaug 1996) and elsewhere (e.g. Peart and Foin (1985); Marrs et al. (1988)). A second point concerns the direction of the change. One expected successional trajectory would be that under decreased grazing the summer-farm vegetation would gradually revert towards the 'natural' surrounding vegetation. This is, however, not supported by the data (no shared variance between history and relative distance Table 3, Figure 2c). An explanation for this could be two opposing effects that decreased grazing will have on summer farm soils. On one hand, less biomass is removed by animals, and more biomass is therefore decomposed at the site, resulting in a fertilisation effect.

On the other hand, the overall nutrient transport from the heaths to the summer farms ceases. Leaching is minimal as grassland soils retain nutrients very effectively (Uhlen 1978), and the net result is that the local soil enrichment brought about by summer farming is irreversible – at least at the time-scale investigated in our study (0–40 years). This is supported by our data, as there is no overall change in the summer-farm soils with time since abandonment (no shared variance between history and soils Figure 2c). Our results therefore suggest that abandoned summer farms will not gradually blend into the 'natural' sub-alpine heathland vegetation, but will remain distinct. Their future floristic composition and vegetation structure will depend on the available pool of species exhibiting traits that enable them to survive under the new soil fertility/disturbance regime (Prach et al. 1997; Zobel et al. 1998), as well as on the dispersal possibilities for these species within the landscape (Eriksson 1993; Poschlod et al. 1998).

The explanatory variables in this study were chosen specifically to capture differences between farms in physical, substrate, and land-use characteristics (Table 1). Environment and land-use history can only account for ca. 1/6 of the between-farm variance each, leaving 2/3 of the differences between farms unexplained. The obvious conclusion to draw from these results is that although environment and history have minor effects, the majority of the floristic variation at this scale results from chance events. Summer farms are island-like ecological systems, and a stochastic component in local immigration and extinction dynamics is expected. Stochastic variation at the between-farm scale would be further increased if animals are important dispersal vectors (Poschlod et al. 1998) and disturbance agents in the system, as they utilise the landscape unevenly.

Alternatively, some of the differences may result from deterministic factor(s) influencing the between-farm patterns that have not been measured. The natural vegetation of the sub- and low-alpine region is structured along gradients in altitude, microclimate, soil productivity, soil reaction, and moisture, and the measured environmental variables are assumed to represent this variation in a satisfactory way. Explanatory variables related to land-use and especially land-use history are generally more problematic to measure and express. First, human utilisation of a landscape is not an on-off effect. Land-use practices and intensity have varied greatly through space and time depending on human population size, land-owner

structure, economy, available technology, and agricultural policies (Reinton 1955, 1957 & 1961; Kvamme 1988; Edelman 1997). Thus our quantification of history into categories (Table 1) is a very crude simplification of a complex local land-use history. Second, grazers are selective in their feeding and resting behaviour at spatial scales ranging from individual plants via vegetation patches and to vegetation types (Wielgolaski 1976; Bakker et al. 1983; Sævre and Baadshaug 1984; de Leuw and Bakker 1986; Glenn and Collins 1992; Huntly 1991). Fine-scale pattern created by animals may therefore vary considerably in time and space even when the overall stocking rate and land-use regime are constant. Third, when a site is abandoned by the owner, grazing does not necessarily cease as there may still be free-ranging sheep or wild grazing animals in the area. The animals may prefer vegetation patches or types on abandoned summer farms to those in the surrounding heathlands, and the local variability in grazing animal effects may thus persist at abandoned farms even if the overall land-use intensity has decreased. All this suggests that land-use effects may be underestimated in our study. More precise quantifications of land-use history based on interviews and agricultural statistics have been attempted (e.g. Olsson et al. (2001); Losvik (1988); Kaland and Vandvik (1998)), but the above mentioned points make the reliability and utility of such data difficult to assess.

Methodological points

The amount of unexplained within-farm variance in the data-set is high (65.1% of TI). Such large fractions of unexplained variance may be interpreted as evidence for the existence of (1) important but unmeasured deterministic factors or (2) large fractions of random compositional variance in the data. However, it has recently been demonstrated that large fractions of TI may arise from purely statistical reasons (Økland 1999). As a consequence the 'fraction of TI explained' may not merit interpretation. Our approach is in accordance with these recent findings, in that we focus on the relative contributions of the different explanatory variables to the explained variance (within-farm vs. between-farm, environment vs. land-use), rather than on the explained vs. unexplained fractions.

Subdividing variance into many groups of explanatory variables has some disadvantages. For example, as the number of variance components to be estimated increases, statistical precision may be lost (Borcard

and Legendre 1994). Our successive subdivision of total variance (Figure 2a–c) may be seen as a compromise between statistical significance (greatest when the number of components is small, but problems with rounding errors, etc. arise as the number of components to estimate increases) and ecological interpretability (the covariance or shared structure between groups may be ecologically interesting).

The main aims of our study were to elucidate the overall patterns in the vegetation of summer farms, and to investigate the potential importance of different groups of environmental and land-use factors for these floristic patterns. Such pattern-seeking studies are necessarily based on observational field data, and as a result, the different explanatory variables are inextricably confounded. The potential value of observational studies depends critically on the application of adequate statistical techniques that take these features of the data into account (Haila and Margules 1996; Pinel-Alloul et al. 1995). The variance partitioning approach (Borcard et al. 1992) proved useful in this context, as it enabled us to clarify the complex variance-covariance structure within the data. Although the results cannot be used to determine causal relationships (Borcard et al. 1992; Anderson and Gribble 1998), or identify superfluous or missing explanatory variables, they can be used to identify potentially important factors that can later be investigated experimentally.

Conclusions

The results of this study show that although within-farm gradients related to grazing animal effects and soil fertility are of overriding importance for floristic composition at summer farms, landscape-scale processes also contribute significantly to the local patterns. The total variance explained differs greatly between scales, but the relative importance of land-use vs. environmental factors is still comparable. The two classes of explanatory variables are of roughly equal importance for within-farm as well as between-farm patterns. When the inherent difficulties in the measurement and expression of land-use factors are taken into account, these results suggest that, overall, land-use effects are of great, possibly overriding, importance for patterns at both scales. Although the relative contributions of the two classes of explanatory variables at the two scales are comparable, details differ, showing that the broad-scale environmental

and land-use patterns are not just scaled-up versions of the fine-scale patterns or vice versa. All this supports a multi-process view of vegetation patterns. The compositional patterns at summer farms result from the interactive effects of several different environmental and land-use factors operative at different spatial scales.

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