



sommerfeltia supplement

2

R.H. Økland

Studies in SE Fennoscandian mires,
with special regard to the use of multivariate techniques
and the scaling of ecological gradients.

1990



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**Studies in SE Fennoscandian mires,
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The study presents the results from an integrated approach to hydromorphology, species distribution, and ecological conditions in SE Fennoscandian bogs and poor fens. Patterns of distribution are observed on spatial scales ranging from 0.25 m² to whole mires (1 km²), and the scope of the study extended to include the regional perspective. Detailed ecological studies are performed within a restricted part (0.3 km²) of one mire complex, N. Kisselbergmosen, Rødnes, SE Norway, while the distribution of plant species and hydromorphological mire types is studied within parts (1000 km²) of Akershus and Østfold counties, SE Norway. Patterns are interpreted by use of multivariate techniques, in particular ordination by detrended correspondence analysis (DCA). On the scale of one mire, four complex-gradients are shown to account for most of the vegetational variation. The relative merits of different sampling procedures and classification systems are discussed. On a broader scale, gradient relationships of vegetation, hydromorphology and species distributions can mostly be ascribed to variation in thermal and hygric factors, often operating in conjunction. Their effects on the vegetation are often mediated by differential water supply. Structuring factors in boreal mires are discussed, and interspecific interaction as well as abiotic factors are important. The importance of interactions is higher in the bottom layer in the field layer. On a fine scale, boreal mires are considered to conform to the patch dynamics theory of non-equilibrium coexistence of species. On a broad scale, boreal mires appear to be in a dynamic equilibrium with present climatic conditions east of the limit for the onset of erosion. The common conceptual basis for descriptive biogeography and vegetation ecology is emphasized. Arguments in favour of scaling ecological gradients in units of compositional turnover are forwarded, and the properties of one such scaling method, the nonlinear rescaling procedure in DCA ordination, is outlined. The advantage of an integrated approach to ecological problems is emphasized.

Keywords: Bog, DCA, Fennoscandia, Gradient scaling, Hydromorphology, Mire, Phytogeography, Vegetation.

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DISSERTATION CONTENTS

This dissertation is based upon the following nine papers:

- I Økland, R.H. 1986a. Rescaling of ecological gradients. I. Calculation of ecological distance between vegetation stands by means of their floristic composition. - Nord. J. Bot. 6: 651-660.
- II Økland, R.H. 1986b. Rescaling of ecological gradients. II. The effect of scale on symmetry of species response curves. - Nord. J. Bot. 6: 661-669.
- III Økland, R.H. 1986c. Rescaling of ecological gradients. III. The effect of scale on niche breadth measurements. - Nord. J. Bot. 6: 671-677.
- IV Økland, R.H. 1989a. Hydromorphology and phytogeography of mires in inner Østfold and adjacent part of Akershus, SE Norway, in relation to SE Fennoscandian mires. - Opera bot. 97: 1-122.
- V Økland, R.H. 1989b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. I. Introduction, flora, vegetation and ecological conditions. - Sommerfeltia 8: 1-172.
- VI Økland, R.H. 1990a. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. - Nord. J. Bot. 10: 79-108.
- VII Økland, R.H. 1990b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. - Nord. J. Bot. 10: 191-220.
- VIII Økland, R.H. 1990c. Regional variation in SE Fennoscandian mire vegetation. - Nord. J. Bot. 10: 285-310.
- IX Eilertsen, O., Økland, R.H., Økland, T. & Pedersen, O. 1990. Data manipulation and gradient length estimation in DCA ordination. - J. Veg. Sci. 1: 261-270.

The papers will be referred to by roman numerals, e.g., [VI, VIII].

INTRODUCTION

INTRODUCTION

The local ecology and regional differentiation of Fennoscandian mires have been major fields of major interest for most of this century, resulting in the release of several influential monographs [see IV, V]. These monographs have partly treated single mires or parts of mires in great detail, partly considered regional variation in mire vegetation and the distribution of mire plants. The interest in mires has, however, decreased strongly from the continental areas (Finland and Sweden) to the oceanic (W Norway). During the last two decades, international publishing practice has changed from comprehensive monographs to in-depth treatments of specific problems. Since the appearance of the last comprehensive monographs of Fennoscandian mire vegetation in the early 1970s, considerable developments have been made in the fields of mire hydrology and hydromorphology, mire chemistry, theoretical biogeography, as well as in the methodology for analysis of vegetational and biogeographical data. This opens the possibility for fruitful interactions between different branches of mire science when combined in a monographic, or at least an integrated approach.

Among important, largely unresolved questions in the mid 1980s, several can be mentioned. The terminology of water in mires and hydromorphological mire parts was in need of clarification (Malmer 1985). On the regional scale, the hydromorphological differentiation of mires westwards in Fennoscandia (towards more oceanic areas) was poorly known. This is exemplified by the lack of knowledge of the fate of the *limes norrlandicus* (Sernander in Du Rietz 1933), often considered the major borderline in Swedish vegetation, towards oceanic areas, or more precisely, when crossing the Swedish-Norwegian border. On the scale of one mire, a gap has emerged between the traditional methods of subjective classification as basis for description of ecological relationships, and the more recently developed multivariate methods based on randomized sampling. The detail of the vegetation-environment relationships inferred from subjectively based studies of Fennoscandian mire vegetation appears unmatched in the history of phytosociology. But a long list of hypotheses could not be answered by the traditional methodologies, and have been left unanswered. Examples of such questions are: (1) The hypothesis of a set of three major ecoclines as sufficient to explain the local vegetational variation in Fennoscandian mires: a nutrient (poor-rich) gradient, a mire expanse - mire margin gradient, and a gradient in depth to the water table. (2) The existence of a discontinuity in the nutrient gradient, the mineral soil water limit (Thunmark 1940), and a corresponding discontinuity in vegetation, the fen plant limit (Sjörs 1947). For an extension of the list, see [IV, V]. It might be beneficial in several respects to combine the traditional selective sampling of vegetation with randomized sampling in one study, for an evaluation of the potential of the traditional methods for inferring ecological relationships of vegetation, and for testing some of the hypotheses emerging from the use of these methods. Interest also centered on the analysis of patterns at several spatial scales within the framework of one study.

Numerical techniques are now standard tools in the analysis of ecological data, in particular for extracting gradient structure in species abundance data. From the first appearance of such techniques in the 1950s, a rapid increase in the number of different numerical techniques occurred during the 1960s and 1970s. The 1980s have led to a considerable rationalization among the techniques as results of extensive testing on

simulated data sets [see VI] and experience from practical applications. The few studies of Fennoscandian mire vegetation by multivariate techniques, have used data collected by the traditional subjective sampling techniques (see [VI], and the recent works by Heikilä (1987) and Singaas (1989)) or multivariate methods no longer considered appropriate [see VI]. There are many examples of extra-Fennoscandian treatises on mire vegetation by use of appropriate multivariate techniques [see V]. None of these have, however, changed the fundamentals of mire ecology, and the existence of three main coenoclines in mires is still considered as valid (e.g., Vitt & Slack 1984).

The development of detrended correspondence analysis (DCA; Hill 1979, Hill & Gauch 1980), available as easily accessed data programs, has had considerable impact on the development of vegetation ecology in the 1980s. Shortly after the release of DCA, the superiority of the method was claimed in several studies (Gauch et al. 1981, Gauch 1982a, 1982b). The method soon became the state-of-the-art method for ordination. The potential of the correspondence analysis (CA) concept (including DCA) was further improved by the development of the integrated set of methods implemented in the CANOCO program package (ter Braak 1987c), including variants in which some of the ordination axes may be constrained by supplied environmental variables, the effects of selected variables may be partialled out, etc. An attractive option for scaling of gradients in units of compositional turnover, the option for nonlinear rescaling, was also available with DCA. The potentials of the CA concept, including DCA, suggested the application of these methods to Fennoscandian mire data in order to approach several among the still unresolved problems in Fennoscandian mire science.

The problem of appropriate scaling of ecological gradients attracted my interest early in the study. Gradients are most often scaled in units of physical or chemical parameters. However, all transformations of one scaling may be equally valid, and the final choice of scaling may therefore be essentially arbitrary. It has been argued that a biologically more sound way of scaling ecoclines (terminology of gradients follows Whittaker (1967)) is in units of compositional turnover (Wilson & Mohler 1983, [I, II]). DCA ordination provides a scaling in units of compositional turnover, as axes (coenoclines) are rescaled in S.D. units which can be interpreted in terms of a unimodal species response model (Hill 1979, [II], Økland 1990). DCA ordination can be formulated as an iteration process of successive weighted averaging regressions and calibrations, also including two correction steps (ter Braak 1987b, ter Braak & Prentice 1988, Økland 1990). The axes are extracted one by one in the iteration process. Upon convergence, sample scores are the weighted averages of the species scores. Rescaling is carried out as a subsequent step after convergence has been reached. The rationale of the method is as follows: Denote the trial sample scores at convergence $\{x_j\}$, $j = 1, \dots, n$, and the trial species scores $\{u_i\}$, $i = 1, \dots, m$. Calculate the within-sample plot variance of species scores, weighted by y_{ij} , the abundance of species i in sample j :

$$v_j = [\text{SUM}_{i=1, \dots, m} y_{ij}(u_i - x_j)^2] y_j,$$

where y_j is the total abundance in sample j . Now the ordination axis is divided into a number of overlapping segments, and the running mean of v_j is calculated for all segments. The species ordination is then contracted and expanded, segment by segment, until the mean v_j is 1 within each segment along the axis. The units so obtained are termed S.D. units. Hill (1979) assumed equivalence of (1) the mean variance of the optima (scores) of species in the samples, and (2) the mean squared tolerance of the species. This assumption is met when all species are randomly distributed with equal variances (Hill 1979). Then 1 S.D. unit corresponds to the mean species tolerance, and more or less corresponds to the mean

species standard deviation assuming Gaussian species response curves. The validity of this interpretation when the assumptions are not met, are not known (cf. Økland 1990).

Three main questions are related to the nonlinear rescaling procedure: (1) The validity of its assumptions; in particular the relevance of the unimodal (and the Gaussian) species response models to ecological data. (2) The relative performance of the nonlinear rescaling to other techniques for estimation of β diversity and ecological distance. (3) The influence of data set properties, data manipulation (weighting, etc.) and other parameter settings on the β diversity estimates from nonlinear rescaling.

The 1980s have seen a considerable increase in the interest in theoretical biogeography and vegetation ecology [IV, VIII]. Central to contemporary biogeography and ecology are the questions relating to the structuring processes responsible for the observed patterns of species abundance on different scales. Several theories have been forwarded, extremes emphasize the importance of competition (mostly associated with assumptions of systems in equilibrium), or the importance of destabilizing factors, associated with assumptions of non-equilibrium. The boreal mires have not been taken into account in the discussions of structuring forces in ecosystems, despite the very fine detail of published observations. A major challenge was therefore to approach current theories by combining field observations and multivariate analysis of patterns on different scales.

AIMS

The aims of this study fall into several groups:

(1) To investigate the basis for interpretation of the nonlinear rescaling procedure available in DCA, and compare this method with other techniques for estimation of β diversity.

(2) To perform detailed phytogeographical and ecological studies of patterns in mires, on scales ranging from the size of one mire complex down to 0.25 m², in the less well-known, suboceanic part of Fennoscandia, and to relate the patterns to regional variation in SE Fennoscandian mires.

(3) To compare traditional, subjectively based approaches with approaches based on randomized sampling and data analysis by multivariate techniques.

(4) To assess the importance of different structuring factors in Fennoscandian mires.

(5) To evaluate the fruitfulness of an integrated approach to vegetation ecology and phytogeography.

SUMMARY OF PAPERS

PAPER I

This paper is an evaluation of the relative performance of the procedure for nonlinear rescaling of gradients in DCA and four floristic dissimilarity measures as measures of ecological distance. The dissimilarity measures considered were complemented similarity ratio, percentage dissimilarity, the complemented cosine of the angle between species vectors, and euclidean distance. Theoretical limitations of the latter type of measures are pointed out. A simulation study was designed, using four coenoclines representing combinations of two coenocline lengths with two noise levels. Symmetric (Gaussian) species response curves were assumed. The linearity of the distance measures relative to true ecological distance and their robustness were evaluated. Nonlinear rescaling by DCA was generally superior in both respects, particularly with noisy data. The potential of nonlinear DCA rescaling for rescaling of gradients is discussed. The study shows unequivocal superiority of this method when species show symmetric, Gaussian curves. Arguments in favour of scaling gradients in units of compositional are reviewed.

PAPER II

In this paper, ecological response curves for 15 plant species relative to two scalings of a gradient in (median) depth to the water table at the mire N. Kisselbergmosen, Rødnes, SE Norway (the R699 data set of [V]) are presented. The two scalings used were (1) in cm below the surface of the bottom layer, and (2) in units of compositional turnover, as estimated by nonlinear DCA rescaling. The two scalings were related in a complex manner; compositional turnover was linearly related to depth to the water table in cm from 0 cm (median position of the water table level with the bottom layer) to 10-12 cm (the maximum water table reaching the level of the bottom layer), thereafter decreasing strongly. This implies a stronger impact on the vegetation by differences in water-table in temporarily water-logged hollows than in aerated hummocks. In the former, water not only influences the moisture of the peat, but also the period of inundation. Only one among the 15 species showed slightly multimodal response, the remaining 14 were unimodal. Response curves produced by the two scalings differed with respect to curve symmetry; being highest by nonlinear rescaling. It was concluded that response curves will be Gaussian if (1) the response is with respect to a dominant ecological factor, (2) the range of variation along a gradient is sufficient, (3) the distribution of samples is adequate, and (4) the gradient is scaled in units of compositional turnover.

PAPER III

This paper treats the application of Levins' (1968) measure of niche breadth to vegetation

data. It was shown the the outcome of niche breadth calculations is strongly dependent on the scaling of the gradient and the subsequent division of the gradient into discrete categories. As an example, abundance data for eleven *Sphagnum* species relative to a gradient in (median) depth to the water table at N. Kisselbergmosen (the R800 and R699 data sets of [V]) were used. Three partitions of the gradient, reflecting three different scalings, were established: (1) Samples assigned to 15 categories, each spanning a 2 cm vertical interval. (3) Assignment of samples to 15 categories, each spanning an interval of fixed β diversity as estimated by nonlinear DCA rescaling. (2) Combining features of (1) and (3).

Habitat niche breadth was shown to be dependent on four issues, the most important being the scaling of the gradient. Six problems with calculation of niche breadth, three of which previously addressed by Colwell & Futuyma (1971), were discussed: (1) the range of the niche breadth measure, (2) spacing of categories, (3) scale, (4) choice of gradients, (5) number of samples, and (6) comparability of studies. It was concluded that four conditions have to be satisfied for measures of habitat niche breadth to be biologically meaningful: (1) the gradients chosen have to be important for the species, (2) sample plots must be adequately distributed over the gradient, (3) the gradients must be scaled in units of compositional turnover, and (4) several demands must be satisfied for comparability of habitat niche breadth estimates between studies. A proposal was made for amendment of Levins' formula for habitat niche breadth to allow expression of niche breadth on an unbound scale in units of compositional turnover.

PAPER IV

Paper IV treats broad-scale distributional patterns. The investigation area comprised some 1000 km² in Østfold and Akershus counties, SE Norway, situated where the extension of limes norrlandicus into Norway meets a suboceanic climate. Distributions in this area were compared to distributions in SE Fennoscandia, compiled from the literature. Paper IV consists of two main parts, the first dealing with hydromorphological mire component types, the second with plant species.

Five size levels of mire components were recognized; in order of increasing size: mire subfeatures, mire features, mire segments, mire synsegments, and mire complexes. Mire component types were discerned at each level. Particular emphasis was put on the mire synsegment types, of which four were considered important in the investigation area: plateau raised bogs, kermi raised bogs, plane transitional mires, and sloping fens. By means of field observations and air photos of 215 mires, the local distribution and variability of synsegment types were described. Four important borderlines were established for the investigation area: (1) the lower/southern limit of kermis, (2) the limit of soligeneous water supply, (3) the limit of plane transitional mires and plane bogs, swallow-holes, surface erosion and other features associated with drainage of bogs and transitional mires, and (4) the limit for dominance of sloping fens. The SE Fennoscandian distribution of hydromorphological mire synsegment types and the regional pattern of the borderlines were mapped. Local as well as regional distribution of hydromorphological mire component types was shown to be determined primarily by the water balance, a complex with both hygric and thermal components, modified by topography. The sharpness of borderlines between hydromorphological mire components decreases westwards in S Fennoscandia as a consequence of increasing surface roughness. The local and regional distributional patterns

and the established relationships with the water balance, were used to evaluate competing hypotheses on the causes of regional distribution patterns, in particular theories on the origin and development of mire components. The importance of the limit of erosion (borderline 3 above), separating an eastern region with more stable and a western region with potentially unstable mires, is stressed.

Phytogeographical patterns in the investigation area were established by mapping 65 species (all possible to fit into a classification of the S Norwegian flora into phytogeographic elements) in 76 mires. Several subjective and numerical classification methods were used to classify the species according to local distribution. In addition, phytogeographical gradients were found by DCA ordination. The first ordination axis reflected relative importance of the western and northern phytogeographic elements, and could be interpreted in terms of an underlying humidity gradient. The local distribution was compared to the regional distribution. Positive relationships were established between local abundance and nearness of the investigation area to the centre of a species' range, between local habitat niche breadth and nearness to range centre, and between local abundance and local habitat niche breadth. This supports the validity of a unimodal (in paper [IV] termed Gaussian) response model for biogeographic scales, as suggested by Hengeveld & Haeck (1981) and Brown (1984). The applicability of the unimodal response model to broad as well as fine scales (cf. paper [II]) has implications for evaluation of strategies for biogeographic analysis. The properties of ordination methods, in particular DCA, were discussed.

Local distribution and distributional limits were discussed with reference to climatic, historical and biotic factors. The importance of competition in explaining the present distributional patterns of different plant groups was particularly addressed, based on the results of paper [VII]. The disintegration of *limes norrlandicus* when passing westwards into oceanic climates was demonstrated, as this phytogeographic limit actually consists of at least seven component borderlines which more or less coincide in C Sweden, but diverge when passing into the more oceanic climate and the broken topography of SE Norway. Criteria for vegetation zones and sections are briefly discussed.

PAPER V

Paper [V] is devoted to a detailed description of the hydrotopography, species distributions, vegetation and ecological conditions of an intensively studied area (termed the special area), comprising ca. 30 ha on the mire N. Kisselbergmosen, Rødenes, SE Norway. This is a bog and poor fen area, characteristic to the humid, suboceanic uplands of SE Norway [cf. IV]. A hydrotopographic mapping was made, including establishment of a detailed map of mire features and subfeatures, and construction of a map of the topography of the water table. The special area consists of seven catchments and two or three synsegments.

Broad-scale distributions of species were mapped in a contiguous 4 x 4 m grid. The species were classified into nine broad-scale distributional groups, or D-groups, reflecting more or less coincident species distributional limits. Six zones were discerned on the basis of the classification into D-groups. Peat chemistry was analysed in samples from mud-bottoms along five transects across zonal borders. The zonal patterns were explained as response to two broad-scale complex-gradients; (1) the mire expanse - mire margin gradient, and (2) a nutrient gradient. Mechanisms responsible for the variation along these gradients are thoroughly discussed.

Fine-scale patterns of species occurrence were studied by use of 800 randomly placed sample plots, each 0.25 m² (the R800 data set). These were analyzed with respect to the full vegetational composition (abundance given as percentage cover). Fluctuations of depth from the surface of the bottom layer to the water table were intensively studied during the period 1980-82. A simple relationship was established between change in depth to the water table from time *t* to time (*t*+1), precipitation, and depth to the water table at time *t*. Particular emphasis was put on studying parameters of the cumulative distribution functions of depth to the water table; between-year variation, interdependence of fractiles, and estimation of parameters from few observations. It was shown that the maximum water table, the 10 % fractile, the median depth, and the compensation level, could confidently be estimated from one or two observations, while the minimum level differed more strongly between years and between mire sites. These results, based on three-year observations in 79 sample plots, were used to estimate characteristic levels of depth to the water table for 699 of the 800 sample plots. These constitute the R699 data set. Species were classified into seven W-groups according to relationship with the water table, and five series were considered along this gradient. The existence of a fourth coenocline, associated with differences in peat-producing ability, was hypothesized. Mechanisms responsible for the variation along the two fine-scale gradients were discussed.

A subset of the R800 data set, the R654 data-set containing sample plots that were subjectively judged homogeneous (according to a set of criteria), were used together with 765 subjectively selected sample plots, also 0.25 m², to illustrate the composition of vegetation. For this purpose, the vegetation was classified into 32 site-types by a reticulate division of the ecological space spanned by the four gradients. The types resulting from this direct gradient approach to classification (Whittaker 1967, Økland & Bendiksen 1985) are closely approaching the associations in several Fennoscandian mire classifications (e.g., Sjörs 1948, Malmer 1962, Fransson 1972). The common philosophy of these earlier approaches to classification and the direct gradient approach can be traced back to Tuomikoski (1942). Direct comparison with units of the Braun-Blanquet approach was not possible, for reasons discussed. The relative merit of classification systems was briefly discussed. Successional relationships of the site-types were inferred from observed transitions and ecological measurements.

PAPER VI

The main topic of this paper is the identification of gradient relationships in the vegetation of the special area of N. Kisselbergmosen, using DCA and its constrained variant, DCCA. Three subsets of the R800 data set (R800, R699, and R634, only including samples from the mire expanse) and one subjectively sampled set, S153, were subjected to ordination. Each composite sample of the S153 sample set was based on a sample plot series from one site-type within a restricted area, species abundance was recorded as frequency in samples. A set of four explanatory variables, deriving from ecological measurements and vegetational patterns, were used to interpret ordination results in terms of the four gradients recognized in [V]. The subjective classification of [V] was further used to aid interpretation. The gradient analyses (DCA and DCCA) showed the existence of three coenoclines in the material, reflected in the first three axes of the DCA ordination of the R800 data-set: (1) the coenocline along the mire expanse: low to high median depth to the water table - mire margin gradient, (2) the poor-rich coenocline, dependent on a complex-gradient in substrate

chemistry (relationship between zones and chemical parameters established in [V]), and (3) a coenocline attributed to variation in peat productivity. The analysis thus partly confirms the assumptions of previous Fennoscandian mire scientists embedded in the numerous systems for classifying mire vegetation, that three gradients are the most important in the mire ecosystem. The mire margin - mire expanse gradient and the coenocline associated with depth to the water table made up one complex coenocline in the R800 data-set because only mire margin vegetation with high depth to the water table occurred in the special area. Among the characteristic levels of cumulative curves for depth to the water table, the maximum water table showed best correlation with the first DCA axis (coenocline 1). Furthermore, the ordination showed that one more coenocline, the one associated with peat-producing ability, had to be added to account for all fine-scale variation in vegetation. Ordinations based on other data subsets partly showed other complex coenoclines, which could be explained as responses to changes in the correlations between the explanatory variables. Techniques for sampling of mire vegetation were discussed.

A comprehensive review of studies using DCA was carried out in order to explain possible faults of the method as apparent in the mire ordinations. Two main faults, a tongue effect and an instability were described, and the reasons for their appearance discussed. It is concluded that despite these faults, DCA has some advantages over other ordination methods. Ordination and constrained ordination are considered as complementary approaches to ecological analysis, useful for different purposes.

PAPER VII

Paper [VII] takes the interpreted DCA ordination of the R800 data set from N Kisselbergmosen as the basis for a detailed study of diversity and habitat niche relationships of the 39 most frequent species; 22 vascular plants, 9 *Sphagnum*, 5 hepatics, and three lichens. The autecology of these species was described and illustrated graphically by use of DCA ordination diagrams, axes 1 and 2, and 1 and 3, reflecting the three complex-gradients described in [VI].

The variation in alpha diversity along coenoclines was described. Much higher beta diversity of the bottom layer than of the vascular plants in the field layer, was demonstrated by separate DCA ordinations of layers. This indicated that the bottom layer reacts to finer grains in the environment than does the field layer.

Habitat niche breadth was analyzed using the approach recommended in [III]. Habitat niche breadth was strongly correlated with overall species abundance (frequency in the data set), and separable into a frequency-independent and a frequency-dependent component. The former was used for further analysis. Frequency-independent habitat niche breadth decreased from vascular plants to hepatics, and further from hepatics to *Sphagnum* spp. Habitat niche overlap was calculated and analyzed similarly. On the basis of the results of diversity and niche studies, also taking data on plant strategies into account, the following conclusions relating to interactions between species were inferred: Interactions are important in the bottom layer; particularly among the *Sphagnum* spp., but also among hepatics. Interactions among vascular plants are unimportant, except in hummocks. Interactions between layers are considered unimportant, except as responses to structural properties of the other layer.

The niche breadth and overlap approaches and the interpretation of niche metrics in terms of interspecific interactions was discussed. The information expressed in niche overlap indices can be obtained directly from the habitat niche breadth, the occurrence of species

along gradients, and the alpha diversity. Thus niche overlap calculations are superfluous. Improved sampling procedures that can increase the utility of niche breadth measurements, were suggested. It was concluded that interpretation of niche metrics must take advantage of available information of all kinds, and that interspecific interaction cannot be inferred from niche breadth data alone.

Four kinds of structuring factors were found to operate in boreal mires: (1) interspecific interactions, including competition, facilitation and priority of colonization, (2) destabilizing factors, including disturbance and fluctuations, (3) stress, and (4) chance. Boreal mires are considered to conform to the patch dynamics theory of non-equilibrium coexistence.

PAPER VIII

This paper treats regional aspects of SE Fennoscandian bog and poor fen vegetation from a perspective of regional gradients. The distribution in bogs was outlined for all species occurring in bogs only in part of their SE Fennoscandian area. These species showed several different distributional patterns, and nine hypotheses that have been forwarded as solutions to the regional fen plant problem were evaluated. The general pattern of fen plant regionality in SE Fennoscandia was ascribed to species being more demanding near their distributional limits, combined with the distribution of habitable sites.

All available published material of vegetation samples was used to outline the regional variation in vegetation. A classification into carpets, lawns and hummocks similar to the direct gradient approach in paper [V] was used. Four regional vegetational gradients were identified: (1) W-E, (2) S-N, (3) SW-NE, and (4) NW-SE. Patterns of variation along these four gradients were related to different underlying climatic gradients; (1) is primarily related to humidity (precipitation surplus), (2) is primarily determined by temperature, while (3) and (4) are determined by combinations of humidity and temperature. The effect of climatic gradients on the mire vegetation is hypothesized to a large extent to be mediated by influence on the ground water regime and the water supply. This hypothesis is strengthened by reference to the interpretation of hydrological borderlines in paper [IV]. The decisive factor for the SW-NE gradient is probably the frequency of ground water table fluctuations, high in SW, low in NE. The NW-SE gradient is likely to be caused by differences in water supply and ground-water flow rates, high in NW, low in SE. The main gradient in carpets was S-N (SE-NW), indicating dependence on the constancy of high water tables. The main gradient in lawns was SW-NE (W-E). On the scale of one mire, lawns are situated in the zone of periodic inundation of the bottom layer (just below the maximum water table; cf. paper [V]). The floristic variation in lawns is likely to be associated with dependence on periodic inundation. The frequency of inundation increases from NE to SW. The main gradient in hummocks was partly SW-NE, partly S-N. The indirect impact of the ground water on hummocks, only influencing the moisture of the peat and the depth to the water table, opens for the higher relative importance of thermal factors (S-N variation). The previous claims for a strong SW-NE gradient in Fennoscandian mire vegetation as a whole were thus shown to imply an oversimplification.

PAPER IX

This joint paper, based on four data-sets with subsets, from four different ecological investigations, addresses the influence of different kinds of data manipulation on the gradient length estimates by nonlinear DCA rescaling. The length of the first DCA axis, measured in S.D. units, invariably increased when the range of the abundance scale was increased, that is, when the scale favoured the quantitative aspect of the data. This was caused by changes in the kurtosis of species response curves under weighting of the data by use of a power function. Estimated gradient length decreased when infrequent species were removed, because these species have narrower tolerance than the more frequent ones, and hence, that the mean tolerance of the species remaining in the analysis was increased. Unfavourable properties of the option for downweighting of rare species in DCA were discussed, and a new downweighting formula was proposed. The advantages of the nonlinear rescaling procedure for estimation of gradient length and ecological distances were stressed. The fact that the length of axes produced by ordination methods other than DCA and gradients with other scalings can be estimated with rCCA (rescaled canonical correspondence analysis, ter Braak 1986, 1987a, Økland 1990), taking the original sample scores or gradient positions as constraining variables, was noted.

DISCUSSION AND GENERAL CONCLUSIONS

Most of the more specific conclusions of the study emerge from the individual papers. This chapter is therefore devoted to a brief concluding discussion of some methodological and general topics.

SCALING OF ECOLOGICAL GRADIENTS

A major aim of this study has been the demonstration of the advantages of scaling gradients (ecoclines) in units of compositional turnover. In summary, the following arguments in favour of such a scaling deserve particular attention:

(1) Almost no environmental gradient is made up by one factor only, and no single parameter normally accounts for all the biological variation along a gradient [I].

(2) In cases where one factor satisfactorily accounts for all variation along a gradient, the biological response is too complicated to be represented by simple transformations [I]. This is demonstrated by the gradient in depth to the water table at N. Kisselbergmosen in [II]. Although this single factor explains the variation along the carpet-hummock coenocline satisfactorily, the variation in compositional turnover along the gradient is most complex, due to the existence of zones along gradients with different impact of the underlying environmental factor on the vegetation. Only scalings in compositional turnover can account for such zones and integrate the biological response to the underlying complex-gradient in one scaling. On this basis, I cannot agree that all scalings of ecoclines are essentially arbitrary, as claimed by Wartenberg et al. (1987) and Minchin (1989), among others.

The nonlinear scaling in S.D. units has the intuitively appealing feature of the analogy with the Gaussian curve, making the interpretation of distances in S.D. units easy. The nonlinear rescaling procedure does not, however, assume Gaussian responses. The parameter used for rescaling, v_j , is meaningful whenever species have distinct optima, that is when species responses are unimodal and symmetric (cf. ter Braak & Barendregt 1986, ter Braak & Looman 1986, Minchin 1989). The interpretation of S.D. units in terms of the Gaussian curve should, however, be done with care when Gaussian response is not demonstrated.

In paper [II] it was shown that the symmetry of species response curves increased by nonlinear rescaling of the water table gradient. By nonlinear rescaling, gradients are rescaled to constant compositional turnover at each point along the gradient. That a response curve is symmetric after rescaling simply implies that the ascending and descending parts of the species' response have the same relationships to the average compositional turnover (averaging over all species), in the respective intervals. Minchin et al. (unpubl., in Minchin 1989) comment on this, stating that "DCA tends to rescale the gradient in order to maximize the number of apparently symmetric responses", and further claim that the observations in paper [II] that curve symmetry increases upon rescaling "simply reflects this bias of DCA, rather than providing independent support for the Gaussian model". In my opinion, this increase in curve symmetry reflects no bias of DCA, but merely the fact that zones exist along gradients, with stronger or lesser change in compositional turnover than the average. This is no bias, but an important property of the relationships of plant species and environmental gradients. The existence of such zones is the basis for hypothesizing the mechanisms by which the environmental factor influences vegetation. In

mires, the water acts directly on the plants below the hollow-hummock limit and indirectly above this limit. This difference explains the abrupt change in compositional turnover at this point [II, V, VI, VII]. On this basis, the high incidence of symmetric unimodal curves after nonlinear rescaling [II] is considered a valid property of vegetation. The fact that not all asymmetry is removed by nonlinear rescaling is due to the differential impacts of the underlying gradient on different plant species or groups of plant species. The general symmetry of response curves with respect to the depth to the water table gradient at N Kisselbergmosen, indicates that water table impacts all species in more or less the same way in all zones along the gradient.

The data from N Kisselbergmosen appears from [II] to be in good accordance with the underlying model of DCA in general, and of nonlinear rescaling in particular. The dependence of the ecological analysis and the niche relationships in [VI] and [VII] on gradients nonlinearly rescaled by DCA is therefore well justified. Limitations and potential pitfalls in the interpretation of S.D. units and the comparison of gradient length estimates between studies are now well-known [IX]. Two questions still await investigation: (1) The performance of nonlinear rescaling relative to other measures of β diversity under less restrictive model conditions than tested in [I]. (2) The interpretation of S.D. units in terms of species tolerances relative to a response model less restrictive than the Gaussian model.

NUMERICAL TECHNIQUES

This study has used DCA as the only approach to ordination, in general with satisfactory results, as judged by interpretability in terms of explanatory variables. The unimodality of species responses relative to the underlying complex-gradients, and the existence of several very pronounced gradients in the vegetation (and corresponding underlying complex-gradients in the environment) are likely to be major reasons for the good performance of DCA in this study. The outline of faults of DCA in [VI] will hopefully help preventing misinterpretation of artifactual patterns produced by DCA. However, this is not meant to discourage the development of improved ordination techniques. None among the presently available ordination methods produce better results with all realistic data-sets, and artifacts may also occur in MDS (Minchin 1987, Økland 1990, Økland & Eilertsen, in prep.). Even if MDS produces generally more reliable ordinations in terms of gradient recovery, there are several advantages of DCA still not available with MDS that may change the overall judgment in favour of DCA (Økland 1990). These are the scaling of axes in DCA, the joint ordination of species and sample plots, and the integrated framework of correspondence analysis techniques; also including partial and constrained ordination. Improvements in ordination methodology are likely to occur by broadening the conceptual framework around MDS, including improved scaling of axes, etc. Meanwhile, ordination should be approached by using both DCA and MDS. Congruent configurations strongly indicate that a realistic ordination has been achieved.

THE OUTCOME FOR THE TRADITIONAL APPROACHES

The multivariate analysis [VI] largely confirmed the results obtained by more traditional

methods [V]. But besides removing the subjective bias inherent in the traditional approach, the multivariate approaches contributed to produce a more many-sided picture of the complex patterns of variation in boreal mires. This can be illustrated by some examples: (1) The interpretation of correlations between explanatory variables in the randomly sampled data sets in [VI], determining the degree to which environmental gradients form complex-gradients, and in which combinations. (2) The result in [VI] that maximum water table explains the position along DCA axis 1 (the coenocline associated with depth to the water table) best among the available parameters, indicating that the duration of water cover at the level of the bottom layer is more important for the vegetation than other aspects of water table fluctuation. (3) The observation that the β diversity of the bottom layer is much higher than that of the field layer [VII]. The list could have been extended.

The multivariate analyses have demonstrated with clarity that several of the choices inherent in traditional Fennoscandian mire methodology have been based on sound intuition: (1) The coenoclines treated, and their interpretation in environmental terms. For instance, Malmer (1962) classified mire vegetation relative to the same 4 gradients as demonstrated to be the most important in the special area of N Kisselbergmosen. (2) The choice of scale for investigation, mostly being 0.25 m², is apparently a good compromise between homogeneity and representativity, allowing for recognition of broad-scale as well fine-scale patterns in vegetation. (3) The emphasis put on use of the full species composition. This study has fully demonstrated that the species of the bottom layer, including the hepatics and the lichens, are important components of the mire ecosystem [IV, V, VII], and that they have high potentials as indicators of ecological conditions.

STRUCTURING FACTORS IN FENNOSCANDIAN MIRES AND THE INTEGRATED APPROACH

The questions of structuring factors in Fennoscandian mires were approached on two spatial scales; the scale of hydromorphological mire components (and species distributions relative to these, [IV, VIII]), and the fine scale of segments of vegetation (0.25 m²; [V, VI, VII]). In both cases, the analysis benefited strongly from being part of a broad-scope integrated study. Broad-scale patterns often have counterparts in fine-scale patterns and vice versa. Several examples can be used to illustrate this:

In paper [VII] it was argued that the vegetation of boreal mires conform to the patch dynamics theory of non-equilibrium coexistence of species. This result, one of the main conclusions of this study, was supported by several sources of independent evidence; habitat niche breadth relationships [VII], observations of relative importance of naked peat in different site-types [V], plant strategies [VII], species richness gradients [VII], and ecological measurements, particularly relating to fluctuations of the water table [V] and their impact on the vegetation [II, VI]. On the level of structural groups of plant species, the importance of interspecific interactions is shown to differ considerably; from negligible in vascular plants to high in *Sphagnum* [VII]. These observations on a fine scale formed the basis for interpreting broad-scale patterns of plant species distributions in [IV]: vascular plants were thus not likely to be restricted by competition, while the converse might be true for *Sphagnum*.

The relative importance of different structuring factors on the fine scale was established for a part of one mire [V, VI, VII]. In particular, the importance of water in mires and the water table fluctuations, were noted. It was shown in [V] and [VII] that

water may act as a strong destabilizing factor on the fine scale, for instance by water erosion of peat, ice erosion, and drought (lack of water). The probability of regressive development of vegetation following local catastrophic events under the present climatic conditions at N Kisselbergmosen, was discussed in [V]. This detailed knowledge of fine-scale relationships was shown in [IV] and [VIII] to have strong relevance to the broad and the regional scales. For instance, results of the fine-scale study could be used to predict regional variation in the probability of occurrence of catastrophic events (e.g., the distribution of erosion [IV]) and in water table fluctuation patterns [VIII].

The final aim of this study eventually became showing the strong interrelationships of the many facets of boreal mires; in the first place the way the plants depend on the environmental conditions and on each other, but also the way local and regional phenomena have a common ecological basis, and the strong interdependence of patterns occurring on different spatial scales. One consequence of this is the conclusion of [IV] that descriptive biogeography and descriptive vegetation ecology must be considered two aspects of one branch of biological science.

Hopefully, this study has shown the advantages of an integrated approach in ecology.

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