

PLANT SPECIES COMPOSITION OF BOREAL SPRUCE SWAMP FORESTS: CLOSED DOORS AND WINDOWS OF OPPORTUNITY

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Abstract. Previous studies point to biogeographic (i.e., evolutionary and demographic) and ecological (i.e., habitat differentiation and disturbance) processes as the most important causes of spatial variation in species richness and species composition (occurrence and abundance). We examined patterns of variation in vascular plant and bryophyte species composition among 150 1-m² plots distributed semi-randomly over 11 Norwegian boreal swamp-forest localities. Swamp forests are species-rich islands in an otherwise species-poor forest landscape. For each plot, 53 environmental variables were recorded. By using Canonical Correspondence Analysis (CCA), we found that ~20% of the explainable variation in species composition was due to swamp-forest affiliation, in addition to the ~35% that was due to environmental differences between swamp-forest localities. The uniqueness of the species composition of each swamp forest was also emphasized by analyses of compositional dissimilarity. Plots were significantly more dissimilar if situated in different swamp forests than if situated in the same swamp forest, after environmental differences had been corrected for. The lack of any significant relationship between compositional dissimilarity and geographical distance or swamp-forest area indicated that this pattern was not mainly due to recent successful dispersal and establishment events. We argue that the distinctness of swamp forests, in particular, those richer in species and soil nutrients, is due to a combination of factors among which randomness in establishment in gaps (“windows of opportunity”) and persistence of established clonal species are important. Furthermore, we argue that the probability for successful recruitment may have been higher in previous time periods than it is today. The unique combination of important determinants of the species composition in boreal swamp forests supports the view that there exists a diversity of explanations for diversity, and that these, to a large extent, are system and/or area specific.

Key words: bryophytes; ecological similarity; habitat islands; immigration history; spatial variation; swamp forest; variation partitioning; vascular plants.

INTRODUCTION

Ecologists have searched for general patterns in the distribution of species richness for decades (Hutchinson 1961, Shmida and Ellner 1984, van Groenendael et al. 2000). Explanations for high or low species richness can be divided into two indistinctly separated groups: biogeographic explanations that emphasize evolutionary and demographic processes and ecological explanations that emphasize ecological differentiation among species due to trade-offs in resource allocation (van Groenendael et al. 2000).

A key role for evolutionary processes in determining the available species pool has been deduced from the enhancement of species richness on broad scales by long-term continuity of evolutionary processes in a favorable environment (Zobel 1992, Eriksson 1993, Nekola and White 1999). Fine-scaled species richness pat-

terns have been ascribed to demographic processes such as local colonization, persistence, and extinction (Fröberg and Eriksson 1997) and to interactions between disturbance and dispersal (Jonsson and Esseen 1990). Species richness, low as well as high, is also often attributed to ecological processes. Richness-restricting factors include negative interspecific interactions (Tilman 1994) and environmental stress (Grime 1979), while richness-enhancing factors include a high number of niche dimensions and positive interspecific interactions (Callaway 1995). Disturbance, or the removal of biomass (Grime 1979), reduces richness in the short term, but may enhance richness in the long term when gaps are recolonized (Huston 1979).

There is currently a growing recognition that biogeographic and ecological processes are both important determinants of species richness (van Groenendael et al. 2000). Nevertheless, the contributions of different processes to observed species richness remain extremely difficult to quantify (Eriksson 1993, Pärtel and Zobel 1999, van Groenendael et al. 2000), and we still do not know the extent to which plant species richness is governed by general “laws,” or if there exists “a diversity of explanations for diversity” (Tilman 1999).

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PLATE 1. Typical view of a boreal swamp forest dominated by *Picea abies* (locality 11 of the present study). The foreground contains a wet, water-filled depression. Drier, elevated sites can be seen in the background. Photograph by Knut Rydgren.

Boreal swamp forests form islands of high biological diversity in the species-poor boreal forest landscape (Ohlson et al. 1997) (see Plate 1). Because of their high value for conservation (Hörnberg et al. 1998) and because the variation within and among swamp forests is poorly known, a study of plant species composition (i.e., patterns of occurrence and abundance) in relation to environmental conditions was initiated in SE Norwegian swamp forests in 1997 (Økland et al. 2001*b*). In that study, ordination analysis of vegetation data revealed two main, and one minor, vegetation gradients that were ecologically interpretable (by significant correlations with recorded environmental variables), appearing on the first, second, and fourth ordination axes. Even though an extensive, carefully selected set of 53 environmental variables were recorded for each vegetation plot, no environmental interpretation could, however, be found for the third ordination axis that separated plots according to swamp-forest affiliation. This result led us to ask if the plant species composition of swamp forests has a unique component and, in that case, if this unique component is due to factors other than present-day environmental conditions.

To answer these questions, we first quantified the variation in vegetation into variation that could be ascribed to a large set of carefully chosen environmental variables and the variation due to swamp-forest affiliation. Next we tested hypothesis A: Ecologically similar sites in different spruce swamp forests are not more different with respect to species composition than ecologically similar sites in the same swamp forest. Rejecting this hypothesis, the natural follow-up question was to determine if biogeographic processes such as dispersal, local colonization, persistence, and extinction, in a short time perspective of decades and centuries, are important determinants of the local species composition of swamp forests. We addressed this question by testing hypothesis B: The compositional similarity of ecologically similar sites in different spruce swamp forests does not decrease with increasing dis-

tance, because on these temporal scales the above-mentioned processes make compositional similarity decline with increasing spatial separation of sites (Nekola and White 1999). Both hypotheses were tested separately for vascular plants and bryophytes, because the generally wider total distributions of bryophyte species (Schuster 1983) suggest that biogeographic processes may be less important for them.

MATERIAL AND METHODS

The investigation area

We performed our study within 4 km² in the Østmarka Nature Reserve, Akershus County, SE Norway (11°02' E, 59°50' N, at 210–270 m above sea level). The bedrock is of proterozoic age; the landscape relief is broken, with structure on several scales, and with relative heights of 50 to 100 m, and occasionally 150 m, with N–S as the main direction of hills and valleys. Coniferous forests form a matrix in which topogeneous mires, swamp forests, and small lakes occur interspersed. The area has been selectively cut, most recently ~60 years ago. The climate is slightly suboceanic with annual mean precipitation of ~800 mm and annual mean temperature (1961–1990) of ~4°C (see Økland et al. [2001*b*] for further details).

Sampling

We selected 11 swamp-forest localities that were judged to represent the variation in size (160–5860 m²), topographic position (valley bottom, valley terrace, or plateau depression), nutrient status (topsoil pH = 3.88–6.00), peat depth (0–7.8 m), presence of springs, and age (paludification initiated between 10 000 and 2500 yr BP according to ¹⁴C-dated peat cores) of swamp forests in the study area. We allocated 150 1-m² plots to the swamp forests (7–22 to each forest according to its area) by a restricted random procedure in which springs, tall hummocks, outlets, and inlets were sampled in a more fine-grained manner than other areas in

order to represent such special site conditions adequately. All plot pairs were to be separated by at least 1 m. We determined the geographical position of each swamp forest as the means of x and y coordinates for all of its plots, relative to a local reference point. Distances between swamp forests ranged from 80 to 2340 m.

Presence and/or absence of soil- and peat-dwelling vascular plants (including lignified species <80 cm high), bryophytes, and lichens was recorded in each of 16 0.0625-m² subplots within each plot. Subplot frequency was used as a measure of species abundance. In total, 103 vascular plant, 103 bryophyte, and 6 (infrequent) lichen species were recorded in the 150 sample plots. The average species densities (per 1-m² plot) were 12.1, 14.1, and 0.01, respectively. Lichens were retained in the bryophyte data set to facilitate comparison with previous ordination results (Økland et al. 2001*b*), but their influence on the results was negligible (R. H. Økland, K. Rydgren, and T. Økland, unpublished data).

Fifty-three environmental variables in five groups, representing all factors known or suspected to be of high importance for differentiation of vegetation within and between swamp forests, were measured for each 1-m² plot (see Table 1 for a full account of the variables and the methods used for quantification): seven topographic and geographic variables (TG), eight tree influence variables (TI), nine water table variables (WT), eight water chemical and physical variables (WC), and 21 topsoil chemical and physical variables (SC). We transformed all variables to zero skewness and expressed them on a 0–1 scale prior to analyses in order to achieve homogeneity of variances (homoscedasticity) (Økland et al. 2001*b*).

Partitioning of variation in species composition on environmental variables and swamp forests

We applied the variation partitioning approach (Borcard et al. 1992, Økland and Eilertsen 1994) separately to the vascular plant and the bryophyte data sets. Canonical correspondence analysis (CCA; ter Braak 1986) was used for all (partial) constrained ordinations because of the high species turnover (length of detrended correspondent analysis [DCA] ordination axes 1 and 2 is >3 SD units; Økland et al. 2001*b*). The impact of rare species was kept low by downweighting by the median method according to Eilertsen et al. (1990). The CANOCO program package, Version 4.0 (ter Braak and Šmilauer 1998), was used for all multivariate analyses.

Compositional variation was partitioned on two sets of variables: (1) The reduced set $\{E_R\}$ with 23 and 22 variables for vascular plants and bryophytes, respectively, obtained from the set $\{E\}$ with all 53 recorded environmental variables (Table 1) by forward selection and Monte Carlo test (4999 permutations). Only variables with an independent contribution significant at the $P = 0.01$ level was included in $\{E_R\}$. The amount

of variation explained by $\{E_R\}$ was denoted \mathbf{E} . (2) The reduced set $\{S_R\}$ with 10 of the 11 binary swamp-forest variables (variable $s_i = 1$ for plots situated in swamp forest t , $s_i = 0$ otherwise; the eleventh variable was a linear combination of the other 10 and hence redundant), explaining an amount \mathbf{S} of variation. We used the sum of eigenvalues for all constrained ordination axes, obtained by using the reduced sets $\{E_R\}$ and $\{S_R\}$, respectively, as constraining variables in CCA analyses, as estimates for \mathbf{E} and \mathbf{S} .

All methods for assessment of the strength of vegetation–environment relationships rely on the untestable assumption that \mathbf{E} is a good approximation for the variation in species composition explained by the current environment. This assumption will be true if and only if the environmental factors with independent impact on the species composition and no others are represented by variables in $\{E\}$, and variables in $\{E\}$ are expressed on scales linearly related to compositional gradients. We hold the opinion that the 53 variables in $\{E\}$ are close to satisfying these ideal demands. The variables were carefully selected to include representatives for all complexes of environmental factors known from previous studies to be important for the differentiation of swamp-forest vegetation, as well as factors that are important in related ecosystems like mires and forests on mineral soil (see Økland et al. 2001*a, b*). The inevitable loss of some variation due to unmeasured variables is counteracted by the inevitable, moderate inflation of \mathbf{E} by the forward selection procedure: Selection of sets of moderately strongly correlated variables in $\{E_R\}$ was allowed by the inclusiveness criterion ($P < 0.01$), and the absence of a final backward elimination renders some overlap among the variations explained by variables in $\{E_R\}$ likely to remain.

The variation explained by $\{S\}$, not shared with $\{E\}$, $\mathbf{S}|\mathbf{E}$, was found by partial CCA (Borcard et al. 1992), using $\{E_R\}$ as covariables and $\{S_R\}$ as constraining variables. The other components of variation were calculated (see Økland and Eilertsen 1994 for an illustrated explanation) as

$$\mathbf{E} \cap \mathbf{S} \text{ (shared variation)} = \mathbf{S} - \mathbf{S}|\mathbf{E} \quad (1)$$

$$\begin{aligned} \mathbf{E}|\mathbf{S} \text{ (variation explained by } \{E\}, \text{ not shared by } \{S\}) \\ = \mathbf{E} - \mathbf{E} \cap \mathbf{S} \end{aligned} \quad (2)$$

$$\begin{aligned} \mathbf{E} \cup \mathbf{S} \text{ (total variation explained by } \{E_R \cup S_R\}) \\ = \mathbf{E} + \mathbf{S} - \mathbf{E} \cap \mathbf{S}. \end{aligned} \quad (3)$$

In accordance with the recommendation of Økland (1999), we report the relative variation explained (variation components divided by $\mathbf{E} \cup \mathbf{S}$) instead of the absolute fraction of variation explained (division by the total inertia, to which $\mathbf{E} \cup \mathbf{S}$ contributed 46.3%).

We obtained an estimate for the relative compositional distinctness (RCD) of swamp forest t (from the other 10 swamp forests) after variation due to ecolog-

TABLE 1. Environmental variables recorded in the 1-m² plots in the study swamp forest at the Østmarka Nature Reserve, Norway, their affiliation to group, significance of independent contribution to explaining variation in species composition of vascular plants and bryophytes, and the method used for quantification.

Variable	Significance†	Method for quantification‡
Topographic and geographic (TG)		
TG1, vertical range		The difference between the highest and lowest situated point in the 1-m ² plot
TG2, average slope	B	The average of the 40 measurements of slope (in degrees) made along the 25-cm edges of all 16 subplots
TG3, maximum slope 25 cm		The maximum of the 40 slopes measured for TG2
TG4, maximum slope 10 cm		The maximum measurable slope between two points in the 1-m ² plot, situated 10 cm apart
TG5, distance to mineral soil		The shortest distance from the center of each plot to mineral soil adjacent to the swamp forest
TG6, soil depth, from mean vertical position	V, B	The depth of soil/peat deposits from the average ground surface vertical level in the plot down to the mineral soil
TG7, soil depth, from median water table	B	The depth of soil/peat deposits from the median water table down to the mineral soil
Tree influence (TI)		
TI1, canopy cover, average	B	Percentage of canopy cover over the plot, as measured by a spherical densiometer; the average of measurements made in the four cardinal directions
TI2, Canopy cover, maximum		The maximum of the four measurements used for TI1
TI3, canopy cover, minimum		The minimum of the four measurements used for TI1
TI4, tree influence, living trees		The tree influence index of Økland et al. (1999), calculated from measurements of all mapped <i>living</i> trees rooted within a 7 × 7 m tree plot placed symmetrically around each 1-m ² plot, as well as all trees outside the former, sufficiently large and situated close enough to the 1-m ² plot to contribute to the tree index
TI5, tree influence, all trees	V	As TI4, but based upon all trees, i.e., standing and fallen dead trees and stumps in addition to living trees
TI6, basal area	V, B	A measure of tree density, measured at breast height by a relascope using the narrowest slit (relascope factor 1; Fitje and Strand 1973)
TI7, crown index	V	Percentage cover of needle or leaf mass for every tree in a 5 × 5 m plot placed symmetrically around each 1-m ² plot, summarized over all trees
TI8, litter index		Relative amounts of litter fall in the 1-m ² plot, estimated from measurements of all trees covering the plot
Water table (WT)		
WT1, snow cover	V	Snow cover (percent of ground in the plot still covered by snow) recorded on 23 April 1998, after a cold period
WT2, water table, 100% exceedance	V, B	Depth from the mean vertical ground surface level in the 1-m ² plot to the minimum groundwater table (as recorded in groundwater wells [one perforated plastic tube inserted into the peat in each plot], on average every tenth day) observed in the 1998 growing season (the 100% exceedance level)
WT3, water table, 90% exceedance	V, B	As WT2, but depth to the level exceeded for 90% of the time
WT4, water table, 50% exceedance		As WT2, but depth to the median water table
WT5, water table, 10% exceedance	V	As WT2, but depth to the level exceeded for 10% of the time
WT6, water table, 0% exceedance	V	As WT2, but depth to the maximum water table
WT7, water table, range		The range of water table fluctuations during the 1998 growing season
WT8, water table, top–minimum	B	As WT2, but depth from highest vertical ground surface level in the 1-m ² plot to the minimum water table
WT9, water table, low–maximum		As WT2, but depth from lowest vertical ground surface level to the maximum water table
Water chemical and physical (WC)		
WC1, water temperature May	V	Water temperature, measured 27 May 1998 by a probe inserted into the tube wells to a fixed depth 1–10 cm below the current water table
WC2, water temperature Aug	V	As WC1, but measured 26 August 1998
WC3, water pH May		Water pH, measured 27 May 1998 by a probe the same way as WC1
WC4, water pH Aug	V, B	As WC3, but measured 26 August 1998
WC5, electric conductivity May	V	Electric conductivity, measured 27 May 1998 by a probe the same way as WC1
WC6, electric conductivity Aug		As WC5, but measured 26 August 1998
WC7, dissolved O ₂ May		Dissolved oxygen, measured 27 May 1998 by a probe the same way as WC1

TABLE 1. Continued.

Variable	Significance†	Method for quantification‡
WC8, dissolved O ₂ Aug	V	As WC7, but measured 26 August 1998
Soil chemical and physical (SC)		
SC1, volume mass	B	Volume mass (g/dm ³) of topsoil (the upper 5 cm of the humus layer or, in peaty soil, the upper 5 cm below living bryophytes, determined in a composite sample of 5–10 subsamples collected just outside the border of the 1-m ² plot; the composite sample dried at 25°C and sifted with 2-mm mesh width before analysis at the Soil Laboratory of the Norwegian Forest Research Institute)
SC2, loss on ignition	V, B	Determined by ashing ~1 g of soil sample at 550°C in a muffle furnace
SC3, soil pH, H ₂ O	V	Measured in aqueous solution; one part (by volume) of the dried sample was mixed with 2.5 parts distilled water, the suspension was left overnight, and pH was measured the next day
SC4, soil pH, CaCl ₂		As SC3, but measured in 0.01 mol/L CaCl ₂
SC5, cation exchange capacity	V	The sum SC12 + ... + SC21
SC6, base saturation		100 × (SC12 + ... + SC15)/(SC11 + ... + SC15)
SC7, total N	V, B	Kjeldahl method; digestion of the dried sample with H ₂ SO ₄ and determination of N by flow injection analysis; expressed as percentage of total N in organic matter (measured values multiplied by 100/SC2)
SC8, extractable C		Determined by ICP-MS§ (~5 g of dried soil was extracted using 50 mL of 1 mol/L NH ₄ NO ₃ , the solution left overnight and filtered; the sediment washed with NH ₄ NO ₃ until volume of extract amounted to 250 cm ³), expressed as parts per million in organic matter (measured values multiplied by 100/SC2)
SC9, extractable P		As SC8
SC10, extractable S	V	As SC8
SC11, extractable acidity	B	Determined by endpoint titration to pH = 7.00 of the soil extract (see SC8) with 0.05 mol/L NaOH; the volume of titrant (NaOH) was corrected for the blank value of pure extractant
SC12, extractable Ca		As SC8
SC13, extractable Mg	VB	As SC8
SC14, extractable K		As SC8
SC15, extractable Na	VB	As SC8
SC16, extractable Ba	V, B	As SC8
SC17, extractable Fe	B	As SC8
SC18, extractable Mn	B	As SC8
SC19, extractable Sr	V, B	As SC8
SC20, extractable Zn	B	As SC8
SC21, extractable Al	B	As SC8

† Significance level, indicated by V and B for vascular plants and bryophytes, respectively, is $P < 0.01$.

‡ See Økland et al. 2001b for further details.

§ ICP-MS = inductively coupled plasma mass spectroscopy.

ical factors had been accounted for, RCD_i , as the eigenvalue of the constrained axis in a separate partial CCA analysis with s_i as (the only) constraining variable and $\{E_R\}$ as covariables.

Determining the compositional dissimilarity of ecologically similar sites, within and among swamp forests

The compositional dissimilarity (CD) between two plots j and k , with subplot frequencies x_{ij} and x_{ik} of species i ($i = 1, \dots, m$), was calculated by the Bray–Curtis coefficient (“Percentage” Dissimilarity; Økland 1990):

$$CD(j, k) = \frac{\sum_{i=1}^m |x_{ij} - x_{ik}|}{\sum_{i=1}^m x_{ij} + \sum_{i=1}^m x_{ik}}. \quad (4)$$

CD was calculated separately for vascular plants and bryophytes.

Ecological distance (ED; Whittaker 1952) was calculated as Euclidean distance in a conceptual ecological space with the two principal components as axes (PCA ordination of 150 plots with 53 transformed, centered, and standardized environmental variables; the fit of angles between variable vectors and correlations between variables optimized by correlation bi-plot scaling of axes). These two axes accounted for 44.2% of environmental variation (the first four PCA axes accounted for 30.6, 13.6, 7.9, and 6.3%, respectively; Økland et al. 2001b). Variables of the water table, water chemical, and soil chemical groups contributed most strongly to the first, while variables of the tree influence, topography, and, in part, water table groups contributed most to the second principal component (Table 2).

Provided that species are good indicators of the environment, the compositional dissimilarity between a pair of plots reflects the difference between these plots in ecological site conditions (Økland 1986). CD in-

TABLE 2. Ecological relationships of axes of PCA (of 53 environmental variables recorded for 150 plots) and DCA (of vascular plants and bryophytes separately, in 150 plots) ordinations.

Variable	PCA		Vascular plant DCA		Bryophyte DCA	
	PCA 1	PCA 2	DCA 1	DCA 2	DCA 1	DCA 2
TG6, soil depth	0.1578	-0.4076	-0.3860****	-0.0974	-0.2852****	0.1656**
T15, tree influence, all trees	0.4071	0.4703	-0.0890	0.3279****	0.0142	0.3289****
T17, crown index	0.0737	0.6486	0.1700**	0.2011***	0.2074***	0.1962***
WT6, water table, 0% exceedance	0.6868	0.5181	-0.0919	0.5703****	-0.0697	0.4910****
WC6, water pH Aug	-0.7305	0.3498	0.2511****	0.3234****	0.3295****	-0.0340
SC2, loss on ignition	0.8168	0.3122	-0.4860****	0.3098****	-0.4556****	0.2085***
SC4, soil pH, CaCl ₂	0.9248	0.1674	0.3893****	-0.4163****	0.4449****	-0.3383****
SC8, total N	0.8354	0.2637	0.4629****	-0.3028****	0.5043****	-0.2202***

Notes: For PCA, the tabulated values are the loadings of selected environmental variables (see Table 1 for explanation) on the axes, i.e., correlation coefficient r between each variable and axis. For DCA the tabulated values are Kendall's τ between variables and axes. The variable(s) most strongly related to the axes within each group of variables (see Table 1) are shown. For DCA axes, significance levels for H_0 ($\tau = 0$) against the two-tailed alternative are ** $P \leq 0.01$, *** $P \leq 0.001$, and **** $P \leq 0.0001$.

increases more or less linearly with increasing ecological distance till a threshold (at 2.0–2.5 SD units of compositional change along a vegetation gradient associated with the ecological gradient; Økland 1986). An approximate threshold value beyond which compositional dissimilarity no longer increased (linearly) with ecological distance was therefore determined. All further analyses were restricted to pairs of plots separated by ecological distances below this threshold (923 of the 1086 pairs from the same swamp forest, and 6693 of the 10 087 pairs from different swamp forests).

To facilitate testing of null hypothesis A, we used standard linear regression (Sokal and Rohlf 1995) to model the relationships between ecological distance (independent variable) and compositional dissimilarity (dependent variable) for the two sets (V and B refer to vascular plants and bryophytes, respectively) of plot pairs from the same swamp forest:

$$CD_V = 0.140(ED) + 0.486$$

$$(r^2 = 0.169, n = 923, P < 0.0001) \quad (5)$$

$$CD_B = 0.122(ED) + 0.418$$

$$(r^2 = 0.136, n = 923, P < 0.0001) \quad (6)$$

The fitted value of these regressions, $\widehat{CD}(x)$, is the *expected compositional dissimilarity of plots that are separated by a given ecological distance, x* . For any given pair of plots j and k , the *surplus of compositional dissimilarity* (relative to the expected value) was calculated as

$$sCD(j, k) = CD(j, k) - \widehat{CD} \quad (7)$$

The mean surplus of compositional dissimilarity for the swamp-forest pair tu , sCD_{tu} , was calculated as the average of $sCD(j, k)$ values for all n_{tu} plot pairs, j in t and k in u . The average of the sCD_{tu} values (for all $t = 1, \dots, 11$), using n_{tu} as weights, was used as an index of compositional distinctness of swamp-forest t , sCD_t .

Hypothesis testing

Kendall's τ was calculated to test the consistency of the two (RCD_t and sCD_t) measures of swamp-forest compositional distinctness for each plant group.

Hypothesis A, that ecologically similar sites in different spruce swamp forests are not more different with respect to species composition than ecologically similar sites in the same swamp forest, was approached by applying the two-sample T test (Sokal and Rohlf 1995) to the pool of $sCD(j, k)$ values, j and k not from the same swamp forests. Tests of H_0^A (i.e., the null for hypotheses A); $sCD = 0$ were made separately for each plant group (vascular plants or bryophytes), against two-tailed alternative hypotheses (H_1^A).

Hypothesis B, that the compositional similarity of ecologically comparable sites in different swamp-forest localities does not decrease with increasing distance, was approached by testing Kendall's τ between sCD_{tu} , the mean surplus of compositional dissimilarity for pairs of swamp forests t and u , and the geographic distance between these swamp forests, for significance of difference from $\tau = 0$ (H_0^B) against the two-tailed alternative hypothesis (H_1^B). The eight pairs of swamp forests for which sCD_{tu} was based upon <20 plot pairs were not included in the tests because the data were considered not to be sufficiently representative.

Possible ecological reasons for compositional distinctness of swamp forests were explored by calculating Kendall's τ between RCD_t or sCD_t and the mean position of plots from each swamp forest along the two main gradients in swamp forests in the study area, as summarized in environmentally interpreted DCA ordination axes. Furthermore, partial Kendall's τ (Legendre and Legendre 1998) were calculated between swamp-forest area and RCD_t or sCD_t to explore area-specific effects. Vascular plants and bryophytes were subjected to separate DCA (Hill 1979) ordinations (Økland et al. 2001b). Because ordination methods may occasionally distort the true gradient structure in a data

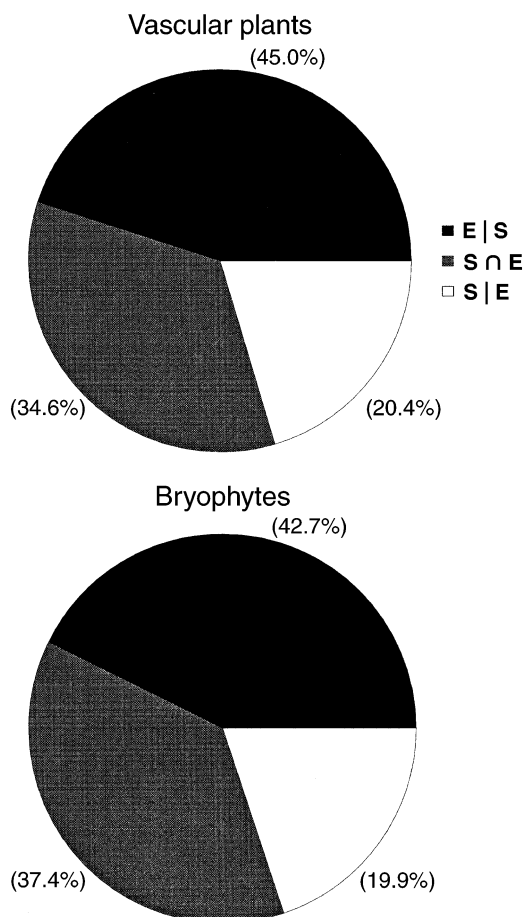


FIG. 1. Fraction of the total variation in vascular plant and bryophyte species composition explained that is attributable to environmental variables, swamp-forest affiliation, and both. $E|S$ = within swamp-forest variation in species composition attributable to current environmental factors, $S \cap E$ = among swamp-forest variation in species composition attributable to current environmental factors, and $S|E$ = among swamp-forest variation in species composition not attributable to current environmental factors.

set (Minchin 1987), the reliability of DCA was confirmed according to Økland (1996) by comparison with the axes of a four-dimensional local non-metric multidimensional scaling (LNMDs; see Økland et al. [2001b] for details). Corresponding axes 1 and 2 by the two methods were nearly identical (Kendall's non-parametric correlation coefficient [Sokal and Rohlf 1995] $\tau > 0.8$; $n = 125$, $P < 0.0001$). Pairs of corresponding DCA ordination axes for vascular plants and bryophytes were also strongly correlated (Kendall's $\tau > 0.7$; $n = 150$, $P < 0.0001$). The first axes (eigenvalues = 0.61 and 0.64 for vascular plants and bryophytes, respectively; gradient lengths = 5.07 and 4.76 SD units) reflected the main vegetation gradient from low to high soil pH and concentrations of N and other nutrients, the second axes (eigenvalues = 0.45 and 0.41; gradient lengths = 3.97 and 3.75 SD units)

TABLE 3. Surplus of compositional dissimilarity $sCD(j, k)$ of plot pair (j, k) , j and k situated in different swamp forests, over the expected dissimilarity of a plot pair from the same swamp forest that is separated by a similar distance in ecological space ($n = 6693$).

Plant group	$sCD(j, k)$ (mean \pm 1 SE)
Vascular plants	$0.1005 \pm 0.0019^{***.a}$
Bryophytes	$0.1512 \pm 0.0016^{***.b}$

Notes: Significance level for tests of hypothesis A (H_0 : mean $sCD(j, k) = 0$) against the two-tailed alternative is: $*** P \leq 0.001$. Different letters indicate plant group means (for a given ecological space) that are different at the $P \leq 0.005$ level according to a two-sample t test against the two-tailed alternative. Significance levels are based upon conservative estimates for the degrees of freedom; $df = 149$ for one-sample and $df = 298$ for two-sample tests.

reflected the gradient from wet to drier sites, as evident from Kendall's τ calculated between axes and environmental variables (Table 2). DCA ordinations were run with downweighting of rare species, detrending by segments, and nonlinear rescaling of axes.

RESULTS

Partitioning of variation in species composition

About one third of the total explained variation ($E \cup S$) in vascular plant and bryophyte species composition was due to environmental differences among swamp forests ($E \cap S$); about one fifth was explained by swamp-forest affiliation alone ($S|E$), while the remainder, somewhat less than half of the total explained variation (Fig. 1), was within swamp-forest variation in environmental conditions ($E|S$).

Compositional distinctness of swamp forests

The two methods for quantifying the compositional distinctness of different swamp forests gave consistent results (vascular plants: Kendall's $\tau = 0.600$, $n = 11$, $P = 0.010$; bryophytes: Kendall's $\tau = 0.574$, $n = 11$, $P = 0.015$).

Ecologically similar sites were found to be significantly more different in species composition if situated in different than if situated in the same swamp forests, for both plant groups (H_0^a , rejected; Table 3). The surplus of compositional dissimilarity (sCD) was significantly higher for bryophytes than for vascular plants (Table 3).

Compositional dissimilarity of ecologically comparable sites in different swamp-forest localities decreased slightly with increasing geographical distance for both species groups (vascular plants: Kendall's $\tau = -0.162$, $n = 47$, $P = 0.109$; bryophytes: Kendall's $\tau = -0.175$, $n = 47$, $P = 0.083$). H_0^b was therefore not rejected.

For both plant groups, swamp forests became significantly more distinct with respect to species composition along the main gradient from soils with low to soils with high pH and nutrient concentrations (Table 4). No relationship was found between compositional

TABLE 4. Kendall's rank correlation coefficients τ (and partial Kendall's τ) between two measures of swamp-forest compositional distinctness and swamp-forest characteristics (area and position along main gradients as summarized by DCA ordination axes).

Compared variable	Plant group	Measure of compositional distinctness	
		RCD _t	sCD _t
DCA 1	vascular plants	0.709**	0.418†
	bryophytes	0.709**	0.709**
DCA 2	vascular plants	-0.018	-0.309
	bryophytes	0.127	-0.091
Area DCA 1	vascular plants	-0.139	-0.216
	bryophytes	0.014	-0.139

Notes: Calculations were made separately for two plant groups ($n = 11$). Significance levels for tests of $\tau = 0$ against the two-tailed alternative are: † $P \leq 0.1$; ** $P \leq 0.01$. Measures of compositional distinctness are RCD_t, the relative variation in species composition explained by presence of a plot in swamp forest t ; and sCD_t, the mean surplus of compositional dissimilarity between plot pairs (j, l), plot j in swamp forest t and plot l in any other swamp forest. Gradients are DCA 1, running from low to high soil pH and low to high concentrations of N and other nutrients; and DCA 2, running from wetter, open sites to drier sites with or without high tree influence (see Table 2). The notation "Area | DCA 1" refers to correlation with area, with the variation due to DCA 1 partialled out.

distinctness and swamp-forest position along the second gradient related to wetness. Small swamp forests did not have more distinct species compositions than large swamp forests, when the strong correlations of area as well as compositional distinctness with nutrient status (mean DCA 1 score) had been partialled out (Table 4).

DISCUSSION

We find that ecologically similar sites in different spruce swamp forests differ more strongly with respect to species composition than ecologically similar sites in the same swamp forest regardless of plant group, and that a substantial amount of variation in species composition is attributed to swamp-forest affiliation while not being shared with the variation explained by measured environmental variables. These results place the ordination results of Økland et al. (2001b) that show that the species composition differs among ecologically similar swamp-forest sites, into a broader perspective and suggest that biogeographic processes are important determinants of species composition patterns, on some temporal (and spatial) scales.

Considerable variation in species composition among ecologically similar sites in different swamp forests is made possible by a large species pool (Ohlson et al. 1997), which is in turn ecologically conditioned by the high habitat diversity of swamp forests (Ohlson et al. 1997, Økland et al. 2001b) and by generally favorable conditions for plant growth in spruce swamp forests. Examples of such conditions are the ample sup-

plies of moving water, e.g., in wet flushes with spring horizons, and nutrients that are available in higher concentrations than in the surrounding forests (Økland et al. 2001a, b). The high importance of ecological processes is also demonstrated by the large amount of variation in species composition explained by environmental variables, both at the within- and at the between-swamp-forest scales.

Our result that the bryophyte species composition of ecologically similar sites in different swamp-forest localities is more distinct than the vascular plant composition does not accord with predictions from the overall distributions of species of the two plant groups. To the contrary, this result indicates that biogeographic processes are *more* important for bryophytes than for vascular plants on the spatial scales we address. Our result is, however, consistent with the dispersal and establishment strategies of the two plant groups. On scales of centimeters and years, most bryophytes and vascular plants in swamp forests propagate by clonal growth processes (Økland 1995a, Rydgren et al. 1998). Over scales of hundreds of meters (between swamp forests), bryophytes disperse by means of sexual spores as well as asexual diaspores (e.g., fragments), while vascular plants more or less exclusively rely on sexual diaspores. Because of their smaller size, bryophyte spores are more prone to dispersal over long distances than vascular plant diaspores (van Zanten and Pócs 1981). However, spores are ecologically unimportant on the time scales addressed in this study because establishment of bryophytes from spores in stable systems with high ground cover is extremely rare (Miles and Longton 1990, Økland 1995b), even after disturbance (Frego 1996, Rydgren et al. 1998). Most bryophyte species therefore disperse over longer distances by fragmentation of clones (Økland 1995b, Rydgren and Hestmark 1997) or by asexual diaspores that may be similar to vascular plant diaspores in size, but mostly lack the specializations of the latter to particular dispersal agents (Longton and Schuster 1983). Notably, the unspecialized bryophyte diaspores are likely to be inefficient means of long-distance dispersal in forested landscapes where dispersing winds are weak or absent (McDaniel and Miller 2000).

Variation in species composition and distributions is always preceded by successful dispersal and colonization, in recent or ancient times. The patterns of variation in compositional similarity observed in spruce swamp forests do not conform with the predicted outcome if biogeographic processes are continuously and highly important even in recent times. We do not observe any decline of compositional similarity with increasing spatial separation (Nekola and White 1999), the predicted manifestation of spatially autocorrelated species distribution patterns (Palmer 1988). Furthermore, we do not observe a positive correlation between the compositional distinctness of swamp-forest localities and their area. Such a relationship is the predicted

outcome of a spatial mass effect (Shmida and Ellner 1984) by which (forest) species are continuously supplied from the surrounding matrix (Harrison 1999) as a purely geometrical effect: The smaller the island, the larger is the circumference: area ratio, and the larger is the probability that a point on the island's surface is hit by a diaspore from the outside.

The lack of evidence for the continuously high importance of biogeographic processes of dispersal and colonization suggests that the studied boreal swamp forests differ from most other previously studied ecosystems with respect to relative importance of major determinants of plant species richness. This leads us to ask, as did McCune and Allen (1985), who found different trees to dominate old-growth forests in parallel river gorges, and Hörnberg et al. (1999), who found that the occurrence of a rare, patchily distributed forest type could not be explained by environmental factors, if historical biogeographic factors have to be invoked to explain present-day patterns.

Disturbances such as fire, and changes of disturbance regime by land-use change, can alter hydrology and tree-layer structure (Segerström 1997) and, in turn, affect swamp-forest understory species composition (Segerström et al. 1996). The intensity and frequency of disturbance are likely to be lower in swamp forests than in forests on mineral soil (Hörnberg et al. 1995, Ohlson and Tryterud 1999) except for tree uprooting which is likely to occur with similar frequency (Kuluvainen 1994). A typical characteristic of swamp forests is that all favorable sites for plant growth tend to be occupied. In particular, this is the case in the bryophyte layer, where only water-filled holes that are strongly prone to water and ice erosion remain permanently open (Økland 1989). Gaps created by other disturbance events are normally rapidly filled by ingrowth of the surrounding dominant species (Frego 1996, Rydgren et al. 2001). Vascular plant seeds, on the other hand, may germinate in bryophyte carpets (Eriksson and Ehrlén 1992). Generally, lower availability of microsites suitable for bryophyte than for vascular plant recruitment over broad spatial and temporal scales may contribute to the stronger bryophyte than vascular plant compositional distinctness of ecologically similar sites in different swamp-forest localities.

Lower probability of occurrence, in time and in space, of "invasion windows" (Eriksson and Fröberg 1996) in swamp forests than in forests on mineral soil and most other ecosystems may explain why compositional dissimilarity does not decline with spatial separation. If the long-term rates of species immigration to swamp forests were low, however, a species-poor flora mainly consisting of trivial species would be the result. This is, however, neither the case for younger (2000–4000 year-old) nor older (8000–10 000 year-old) swamp-forest localities (Økland et al. 2001b). Most likely, immigration rates were higher in the initial

phases of swamp-forest development. Nevertheless, the average colonization rate has certainly exceeded the average extinction rate in the studied swamp forests for most of their 10 000 year long developmental history. Our results accord with a scenario in which infrequent occurrence of gaps, recruitment limitation, and relatively low risk of competitive exclusion of established species are important elements. Macroscopic charcoal remains in peat show that the studied swamp-forest localities were more frequently affected by wild-fire in the 2000-year period before the immigration of *Picea abies* to the study area (A. Korbøl, unpublished data) ~2500 years ago (Hafsten 1992). This supports the hypothesis that gaps were created more frequently, and opportunities for recruitment were better, in previous time periods. The combination of invasion windows that are infrequently open and a high species richness is possible only when local extinction rates are low. The species pool of swamp forests contains a prominent element of clonal, long-lived genets with "remnant population dynamics" (Eriksson 1996). The long-term population dynamics of most swamp-forest plants is poorly known, but observations of wetland species on mires (Rydin and Barber 2001) indicate that established populations may persist for thousands of years. Furthermore, the Holocene migration of clonal forest herbs provides strong evidence for high frequency of occasional dispersal events (Cain et al. 1998). The more or less independent accumulation of species in different swamp forests over thousands of years may be visualized by a house, normally with closed doors, but with windows of opportunity that are occasionally open.

Highlighting the importance of recruitment limitation and processes that operate on long time scales, our explanations for the observed patterns resemble those given for high species richness in tropical rain forests (Hubbell et al. 1999, Tilman 1999). For cliff walls, which like swamp forests occur as spatially explicit habitat patches, there is also evidence for a low degree of spatial structure, but, in contrast to swamp forests, this is the result of lack of ecological differentiation and more or less random species assemblies (Haig et al. 2000). The spatial distribution of species richness in swamp forests deviates strongly from the spatially autocorrelated patterns described for contiguous ecosystems (Palmer 1988, Nekola and White 1999). The present study therefore supports a hypothesis that fragmented ecosystems differ from spatially contiguous ecosystems in species-richness distribution patterns. Furthermore, the studies performed so far in discontinuous ecosystems indicate that the pattern of variation in species richness and the relative importance of the processes that determine these patterns are, to a large degree, system and/or area specific. This accords with Tilman's notion (Tilman 1999) of "a diversity of explanations for diversity."

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