

Species richness in boreal swamp forests of SE Norway: The role of surface microtopography

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Abstract

Question: What is the relative importance of environmental gradients and surface microtopography (variation in vertical level within sampling units) for fine-scale plant species richness in *Picea abies* swamp forests?

Location: 11 swamp forests in SE Norway.

Methods: We recorded species richness (number of species of vascular plants, mosses, *Sphagnum* and hepatics), depth to water table, soil base status and vertical range (microtopographic relief) in 2400 microplots, (each 1/16 m²), in 150 1-m² plots in the 11 swamp forests. Relationships between species richness and environmental predictors were modelled by GLMM.

Results: Moss and hepatic species richness increased with increasing microtopographic relief, most strongly for wet acid sites, in which similar trends were also found for *Sphagnum*. Relief was a poor predictor of vascular plant species richness.

Conclusions: Microtopographic relief is a good predictor of local species richness in *Picea abies* swamp forests, partly because larger vertical variability means higher within-plot habitat diversity with respect to the wet-dry gradient, and partly because qualitatively new microhabitats associated with steep slopes are added in drier sites. The relationship between species richness and microtopographic relief is context dependent, differing in complex ways among species groups and among sites with different environmental conditions.

Keywords: Bryophyte; Microsite; Peatland; *Picea abies*, *Sphagnum*.

Abbreviations: AIC = Akaike's information criterion; BIC = Bayesian information criterion; BLUP = Best linear unbiased predictions; GLMM = Generalised linear mixed model; LNMDS = Local non-metric multi-dimensional scaling.

Introduction

Species richness varies in space, in time, among different groups of organisms, and on different scales (Palmer 1994; van Groenendael et al. 2000; Pausas & Austin 2001). Although progress in understanding the mechanisms behind observed species richness patterns is hindered by difficulties with quantifying relevant process related factors (Eriksson 1993; Pärtel & Zobel 1999; van Groenendael et al. 2000; R. Økland et al. 2003, 2006), there is a growing awareness that patterns of species richness are context dependent – i.e. that 'a diversity of explanations exist for diversity' (Tilman 1999). Regardless if species richness patterns are system-specific or not, new insights into richness controlling factors may be obtained by studying relatively stable ecosystems in which the variation along ecological gradients is well known and in which demographic processes such as local colonisation, persistence and extinction (Fröberg & Eriksson 1997) are likely not to be of high importance on fine temporal scales.

The main determinants of species richness in a specific plot of given size are: (1) the size of the available species pool ('the species-pool hypothesis'; Taylor et al. 1990; Zobel 1992; Grace 1999); (2) the plot's position along main environmental gradients, which determines the habitat's suitability for each species of the species pool (Grime 1979; Grace 1999) and (3) within-plot environmental heterogeneity (Shmida & Wilson 1985; Callaway 1995), which via a ' β -diversity effect' (Veech et al. 2002) determines the number of qualitatively different habitats and hence the species richness in the plot (e.g. Økland 1996; Chen et al. 2004).

Swamp forests are biodiversity hotspots in the boreal forest landscape (Ohlson et al. 1997; Hörnberg et al. 1998; Økland et al. 2001b). Although most boreal swamp forests, over centuries or millennia, have been subjected to disturbances such as windthrows and forest fires (Ohlson et al. 2006) these ecosystems are relatively stable over decades or centuries, as shown by their tendency to accumulate species more or less

individually (R. Økland et al. 2003). Like other *Sphagnum* dominated ecosystems (Økland 1990a; Nordbakken 1996; Bragazza & Gerdel 1999), swamp forests display microtopographic variation on scales of metres associated with hummock-hollow structures (Paratley & Fahey 1986; Johnson 1996; Økland et al. 2001b) and on scales of centimetres associated with occurrence of specific microsites within hummocks (and hollows) (Ehrenfeld 1995a; Økland et al. 2001a). Boreal swamp forests are, therefore, well suited for studying the relative importance of environmental gradients and fine-scale (within-plot) environmental heterogeneity for local fine-scale plant species richness.

With the aim of testing the relative importance of position along main environmental gradients and within-plot microtopographic (vertical) heterogeneity for fine-scale species richness patterns of different plant groups, we re-analysed a large data set from SE Norwegian *Picea abies* swamp forests (Økland et al. 2001b). Previous studies have documented that species composition is determined by two main environmental complex gradients, (1) soil base cation and N-concentrations and (2) depth to the water table (Økland et al. 2001a, b), and that species richness in small plots varies along these gradients (Økland et al. 2001b).

Material and Methods

Study area

The study was carried out in Østmarka Nature Reserve, Akershus county, SE Norway (for details see Økland 1996; Rydgren 1997; Økland et al. 2001b). The bedrock consists of acid rocks of proterozoic age and is usually covered by thin quaternary deposits of glaciofluvial origin (Holmsen 1951; Sigmond et al. 1984). The area is covered by coniferous forests, which occur interspersed with topogeneous mires, swamp forests and many small lakes. Due to large topographic variation over short distances, the variation in forest types on mineral soil is extensive. Above-ground (fire scars) and below-ground (charcoal) traces of forest fires occur (Ohlson et al. 2006). The area has been selectively cut, most recently ca. 70 years ago. The climate is slightly suboceanic with annual precipitation of ca. 800 mm and annual temperature of 3.9 °C (1961-1990 means; Aune 1993; Førlund 1993).

Sampling design and recording species richness

Species richness (i.e. number of species) was recorded for the four taxonomic groups vascular plants, mosses (excluding *Sphagnum*), *Sphagnum* and hepatics, in each of 16 (0.0625 m²) microplots nested within each of 150

1-m² plots (the total number of microplots was 2400). Lichens were too sparse to allow analysis of species richness patterns. Plots were nested within 11 swamp forests, selected to cover variation among swamp forests in the study area. Within swamp forests, plots were placed by a restricted random procedure (for details of sampling design see Økland et al. 2001b). A species was recorded as present in a microplot when the vertical projection of its phytomass covered some part of the microplot.

Recording predictors of species richness

The 150 plots were divided into a nutrient-poor (1568 microplots in 98 plots) and a nutrient-rich (832 microplots in 52 plots) data subset to account for variation along the main environmental gradient related to soil base cation and N-concentrations. Økland et al. (2001b) demonstrated high importance of this gradient for species composition and richness by parallel Detrended Correspondence Analysis (DCA; Hill 1979) and Local Non-Metric Multi-Dimensional Scaling (LNMS; Minchin 1987) ordinations of the full species composition (212 species) of the 150 plots. Along the main compositional gradient (first axes in both ordinations), strongly correlated with total N-content and loss on ignition, two clouds of densely placed plots were separated by a sparse region that corresponded to organic content in peat (loss on ignition) of ca. 90% and 2.2% (by mass) of total N in the organic soil fraction.

A perforated plastic pipe was placed in each plot in which the distance to the water table was measured ca. every tenth day during the 1998 growing season (for details see Økland et al. 2001b). We used the median depth to the water table, i.e. the depth from the surface level of a microplot to the level exceeded for half the 1998 growing season, as a measure of a microplot's position along the gradient (Økland et al. 2001b).

The relative vertical level of the peat surface was recorded for all microplot corners as the vertical distance from a levelled steel frame (placed over the plot) to the surface (Økland et al. 2001b). Microtopographic relief was quantified by the vertical range, the difference between the largest and the smallest of the four vertical level values recorded for each microplot.

The frequency distributions of the two continuous variables were reasonably symmetric (indicating homogeneous variance distributions) and no transformations were performed prior to statistical analyses.

Statistical analysis

We used generalised linear mixed models (GLMM; McCulloch & Searle 2002; Venables & Ripley 2002), as implemented in the glmmPQL (GLMM by penalised

quasi-likelihood) function of R Software (Anon. 2007) Version 2.1.0 for Windows; package MASS (Venables & Ripley 2002). GLMM is an extension of generalised linear models (GLM; McCullagh & Nelder 1989; Venables & Ripley 2002) by which a nested data structure can be appropriately analysed by separating random and fixed effects.

GLMM models were built for the continuous response (= dependent) variable (microplot) species richness (*SpR*), which was recorded for each of the four species groups in each of the 2400 microplots (total $n = 9600$). GLMM models for *SpR* used *Plot* (factor variable with 150 levels) nested within *SwFo* (Swamp forest; factor variable with 11 levels) as random factors. Fixed effect predictors of species richness were: (1) Species group (*SpGr*; factor variable with four levels: 1 = vascular plants; 2 = mosses; 3 = *Sphagnum*, 4 = hepatics); (2) Soil base cation and N-concentrations ('richness', *Rich*; factor variable with two levels: 1 = 'poor' subset; 2 = 'rich' subset); (3) Depth to water table (*DWT*; continuous variable); (4) Vertical range (*VerR* = microtopographic relief; continuous variable). By inclusion of *SpGr* as a fixed effect predictor, model coefficients were obtained separately for each species group.

Modelling was based on the assumption that the processes determining the relationship between the dependent variable (species richness) and the continuous fixed effect predictors were the same over the entire study area. Accordingly, we fitted random intercept models by which plot-level variance of the intercept was estimated for random effect predictors at the two levels of the sampling hierarchy (swamp forest and plot within swamp forest). Because our focus was on major trends over the study area, we used the best linear unbiased predictions (BLUP; Pinheiro & Bates 2000) for interpretation of modelling results.

Since the response variable *SpR* was species counts we used GLMM with logarithmic link function and a variance that increases with the mean. Potential problems with under- or overdispersion (deviation of the scale parameter θ , the proportionality factor for the relationship between the mean and the variance from one, as required by the Poisson distribution; McCullagh & Nelder 1989) was implicitly handled within the PQL algorithm by fitting a quasi-Poisson distribution (Venables & Ripley 2002).

Fixed effects were evaluated by joint consideration of (1) Akaike's Information Criterion (AIC) and (2) the Bayesian Information Criterion (BIC) (Pinheiro & Bates 2000; Myers et al. 2002; Venables & Ripley 2002); a GLMM model of lower complexity (in terms of included fixed-effect predictors and their interactions) being preferred over a more complex model if the former had lower AIC and BIC. The best model was found to be

the full model, with all interactions included:

$$SpR \sim SpGr * Rich * DWT * VerR + \text{random}(1|Plot|SwFo)$$

Graphical inspection of plots of standardised residuals for the best model as function of continuous fixed effect predictors revealed no systematic relationships (e.g. Pinheiro & Bates 2000) and the full model was, therefore, accepted.

The full model contained estimates for 32 coefficients; four for each of the eight combinations of *SpGr* and *Rich*: an intercept, slopes for *DWT* and *VerR* and the interaction term *DWT:VerR*. To facilitate comparison between effects of continuous predictors between the species-group/soil richness combinations, the full model was re-run eight times using treatment contrasts (Crawley 2002; Venables & Ripley 2002), each time with a different species-group/soil richness combination as level one for each factor. This allowed direct testing of deviations from zero of the four coefficients for each species-group/soil richness combination.

Modelling results were interpreted by consideration of the sign, magnitude and significance of deviation from zero in *t*-tests (Venables & Ripley 2002) of coefficients, and by graphs of predicted species richness as function of vertical range for different combinations of depth to the water table and soil richness. GLMM model predictions of $\log(SpR_i)$ were back transformed before plotting.

Results

A total of 103 vascular plant species, 55 mosses (excluding *Sphagnum*), 13 *Sphagnum* and 35 hepatic species, respectively, were recorded. Microplot species richness (number of species per microplot) ranged from 0 to 14 (vascular plants), 13 (mosses), 5 (*Sphagnum*) and 9 (hepatics), respectively (Fig. 1). Species richness was higher for the nutrient-rich than for the nutrient-poor subset for all species groups except *Sphagnum* (Fig. 1).

Median depth to water table varied from -7.3 cm to 56.1 cm while vertical range (microtopographic relief) varied from 1 cm to 42 cm. The mean vertical range tended to increase with increasing depth to the water table.

According to the best GLMM model, vascular plant species richness was significantly, positively but not strongly, related to microtopographic relief in the poor subset only (Table 1, Fig. 2), while no significant relationship with depth to water table was found. In the poor subset *Sphagnum* species number was significantly positively related to vertical range and weakly related to depth to water table while the interaction term was strongly significant (Table 1). *Sphagnum* species richness thus increased considerably with vertical range for low depths to water table (wet

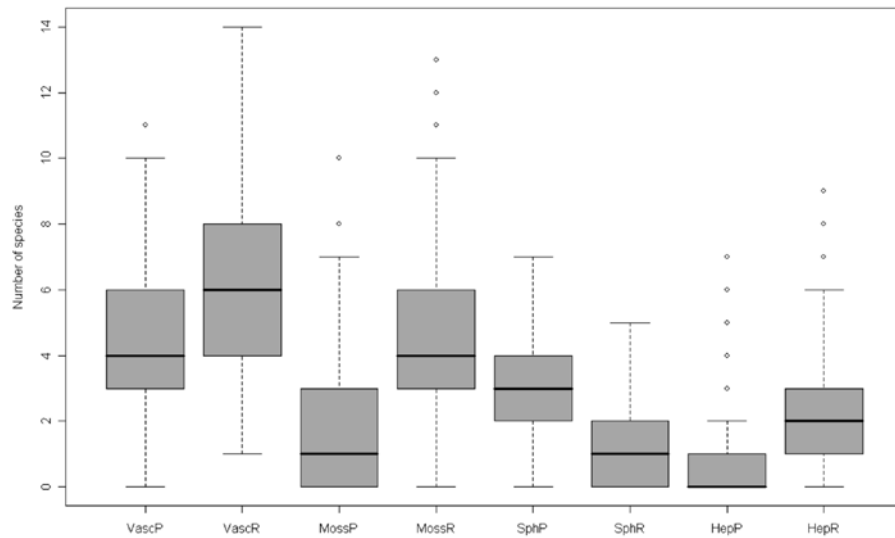


Fig. 1. Boxplot for species richness (number of species) in micro (1/16 m²) plots for the four species groups (Vas = Vascular plants, Moss = Mosses, Sph = *Sphagnum*, Hep = Hepatics) in each of the two subsets (P = 'poor', R = 'rich'). For each combination of species group and data subset the 25 and 75 percentiles is given by the grey box and the median is given by the horizontal line in the box. The horizontal lines joined to the box by dashed lines extend to 1.5 times the interquartile range; observations beyond this are shown as single points.

Table 1. Fixed effects of the final model: coefficients (by treatment contrasts; obtained in eight separate runs of the model, each time with a different species-group/richness combination as factor levels one, allowing direct estimation and testing of deviation from zero of the intercept, slopes and interaction for the group). The estimate is given for each coefficient together with the estimated standard error and a marginal *t*-test of deviation from zero. Coefficients significantly different from zero at the $\alpha = 0.01$ significance level are given in bold face. DWT = Depth to water table, VerR = Vertical range. Degrees of freedom = 9419.

Species group and soil 'richness'	Coefficient	Value	Standard error	<i>t</i> -value	<i>p</i> -value
Vascular plants, poor subset	Intercept	1.3976	0.0750	18.64	< 0.0001
	DWT	-0.0023	0.0030	-0.77	0.4427
	VerR	0.0094	0.0044	2.13	0.0334
	DWT:VerR	-0.0002	0.0002	-0.92	0.3555
Vascular plants, rich subset	Intercept	1.8454	0.0739	24.98	< 0.0001
	DWT	-0.0024	0.0037	-0.65	0.5138
	VerR	-0.0018	0.0044	-0.41	0.6824
	DWT:VerR	0.0000	0.0002	-0.07	0.9452
Mosses, poor subset	Intercept	-0.6585	0.0948	-6.94	< 0.0001
	DWT	0.0451	0.0038	11.83	< 0.0001
	VerR	0.0598	0.0059	10.17	< 0.0001
	DWT:VerR	-0.0011	0.0002	-4.60	< 0.0001
Mosses, rich subset	Intercept	1.0183	0.0802	12.70	< 0.0001
	DWT	0.0215	0.0043	5.02	< 0.0001
	VerR	0.0239	0.0050	4.75	< 0.0001
	DWT:VerR	-0.0008	0.0003	-2.92	0.0035
<i>Sphagnum</i> , poor subset	Intercept	1.2474	0.0812	15.36	< 0.0001
	DWT	-0.0079	0.0038	-2.08	0.0377
	VerR	0.0232	0.0058	4.02	0.0001
	DWT:VerR	-0.0020	0.0003	-6.39	< 0.0001
<i>Sphagnum</i> , rich subset	Intercept	0.0455	0.1169	0.39	0.6972
	DWT	0.0056	0.0091	0.62	0.5370
	VerR	0.0140	0.0113	1.24	0.2157
	DWT:VerR	-0.0026	0.0009	-2.92	0.0035
Hepatics, poor subset	Intercept	-2.1670	0.1505	-14.40	< 0.0001
	DWT	0.0504	0.0070	7.18	< 0.0001
	VerR	0.0948	0.0100	9.49	< 0.0001
	DWT:VerR	-0.0021	0.0004	-4.85	< 0.0001
Hepatics, rich subset	Intercept	0.0005	0.0969	0.00	0.9962
	DWT	0.0399	0.0061	6.57	< 0.0001
	VerR	0.0563	0.0070	8.11	< 0.0001
	DWT:VerR	-0.0026	0.0005	-5.71	< 0.0001

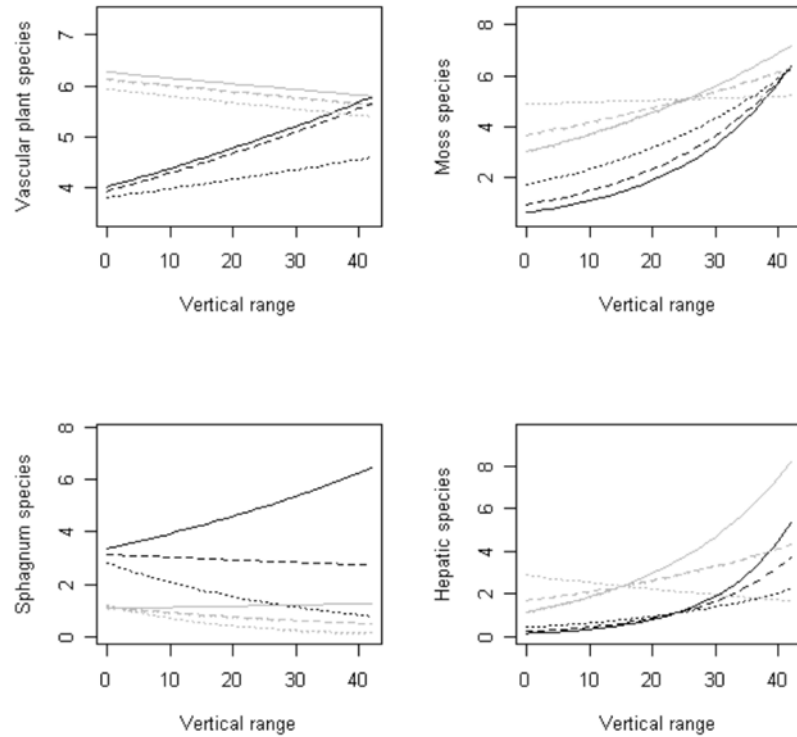


Fig. 2. GLMM model predictions for species number (in each of the four species groups) as function of vertical range (microtopographic relief). Black lines refer to the nutrient-poor, grey lines to the nutrient-rich subsets. Continuous lines refer to depth to water table of 3.8 cm (10-percentile), broken lines to median depth (13.0 cm) and dotted lines to 90-percentile for depth

depressions) and decreased with vertical range for high depths (elevated, drier sites). Microplots of the rich subset were poor in *Sphagnum* species (Fig. 2) and, apart from a significant, negative interaction term, no significant relationships were found.

Species richness patterns of mosses and hepatics were similar: all coefficients for continuous predictors were significantly different from zero and corresponding coefficients in the two soil richness subsets had the same sign. Species richness was positively related both to depth to water table (increasing from wetter to drier sites) and vertical range (increasing from level sites to sites with a pronounced microtopographic relief), but due to the negative sign of the interaction terms (Table 1), species richness was generally more weakly positively dependent (both species groups, nutrient-poor subset) or even negatively dependent (hepatics in rich subset) on vertical range for larger depths to the water table (Fig. 2).

Discussion

Our result, that depth to the water table is a significant predictor of species richness for several species groups, corroborates results of several previous studies. 1. The water table gradient is one of the main sources of variation in swamp forest species composition at local (within swamp forest) scales (Paratley & Fahey 1986; Jeglum 1991; Jeglum & He 1995; Økland et al. 2001b); 2. Rapid

species turnover takes place from the wettest to the driest parts (Økland et al. 2001b; Rydgren et al. 2003), hence: 3. Several qualitatively different habitats exist along the water table gradient (cf. Andrus 1986; Økland 1986, 1990b; Gignac et al. 1991). Compositional variation is, however, only accompanied by significant variation in species richness along the water table gradient for mosses and hepatics (and, to some extent, *Sphagnum*). This underpins the conceptual difference between species richness and species composition as descriptors of ecological communities (Austin 1999; R. Økland et al. 2006): a compositional gradient is paralleled by a richness gradient only if favourability for an entire group of species varies along it. The group preference of mosses and hepatics for drier sites in the swamp forest is discussed in detail by Økland et al. (2001b) who suggest two main causes: (1) intolerance of many species to waterlogging and (2) that the larger and faster growing *Sphagnum* species monopolise the wet habitat.

Our GLMM modelling results show that fine-scale ($1/16\text{ m}^2$) moss and hepatic species richness increase with increasing microtopographic relief, as expected because a more pronounced relief implies a greater diversity of habitats with respect to the gradient related to depth to water table (the ‘beta diversity effect’). Vascular plant richness does not, however, follow this pattern (no relationship was found), and for *Sphagnum* only a weak trace of a positive effect is found for low depths to water table (wet sites) in the poor subset. The weak relationship of

vascular plant species richness with microrelief indicates that the beta diversity effect does not apply to vascular plants in the investigated swamp forests; addition of new microhabitats along the moisture gradient is not reflected in establishment of more vascular plant species. A plausible reason for this is that vascular plants in mires and swamp forests have deeper roots (Metsävainio 1931) which give them access to water and dissolved nutrients over considerable vertical ranges. Furthermore, vascular plants which depend on seeds for establishment may find germination and establishment difficult in the (mostly) closed bryophyte carpets of swamp forests (Ohlson & Zackrisson 1992; Ehrenfeld 1995b; Hörnberg et al. 1997) so that species already established at a local site may tend to consolidate their positions by clonal encroachment instead of new species becoming established (R. Økland et al. 2003).

Mosses, and in particular hepatics, are small plants. Their local distributions are strongly influenced by processes that operate on very fine scales (Økland 1994; Økland & Bakkestuen 2004), likely to be manifested in richness patterns on scales close to these of microplots. The richness patterns observed for these groups may be due to addition of new habitats along the depth to water table gradient (the beta diversity effect) and/or addition of new, qualitatively different, microhabitats in microtopographically heterogeneous sites. Variation in the strength and shape of relationships between species richness and microtopographic relief between the poor and rich subsets and with depth to water table suggests that the relative contributions of these two processes to the observed pattern is context dependent.

The tendency for a larger increase in moss and hepatic species richness as function of microtopographic relief (as measured by vertical range, in cm) in wetter than in drier sites accords with predictions from the 'beta diversity effect hypothesis' because the compositional turnover per cm along the water table gradient (and hence the range of qualitatively different microsites within a plot with a given vertical range) is greater in periodically waterlogged sites than in sites that are never waterlogged (Økland 1986, 1989, 1990b; Økland et al. 2001b). Therefore, we consider the β -diversity effect as the major mechanism behind observed richness patterns with respect to vertical range for all bryophyte groups (except for *Sphagnum* species in rich sites where they are very sparsely present). The increase in moss and hepatic species richness with increasing vertical relief also in dry, poor sites in which compositional turnover with respect to depth to water table is low, does, however, provide the possibility that microtopographically heterogeneous, relatively dry sites in poor swamp forests contain microsites suitable for bryophytes that are qualitatively different from other microsites in the swamp forest

floor. Candidates for such microsites are steep slopes that extend for some centimetres over the forest floor ('pockets'; Økland & Bendiksen 1985; Økland 1996); crevices under roots, beside stones, etc., which are important habitats for many small bryophytes in swamp forests (Økland et al. 2001b) as well as in other forest types (T. Økland et al. 2003). Two mechanisms may explain the deviant species composition of such microsites from that of the more level surrounding sites (Økland 1994): that these sites are gaps of short duration, created by fine-scale disturbance and colonised by pioneer species (During 1979); or that they are persistent but extreme with respect to important environmental factors such as inclination, radiation, soil organic matter content, soil depth or soil stability, hence occupied by stress tolerators (Grime 1979). Lower suitability of such microsites for larger, usually faster growing dominant bryophytes (cf. van Tooren & During 1988; Økland 1995) including *Sphagnum* spp. agrees with the observed difference of *Sphagnum* from moss and hepatic richness patterns. With its vertical growth form *Sphagnum* species are better suited for growing on level ground (During 1979; Bates 1998) than in microsites associated with interrupted microtopographies.

Positive relationships between moss and hepatic species richness and microrelief are obtained for drier sites in the nutrient-poor subset while in the nutrient-rich subset none or even slightly negative relationships occur. Plausible reasons are the greater diversity of microhabitats suited for bryophytes in poor swamp forests, and the more rapid colonization of open microsites in nutrient-rich sites by the early arriving species, which may have higher growth rates (cf. Rydin 1997), from diaspores or by clonal encroachment (cf. Frego 1996; Rydgren et al. 1998).

Our results are consistent with the hypothesis that microtopographic relief is a good predictor of local species richness in *Picea abies* swamp forests, partly because a stronger relief is associated with higher within-plot diversity of habitats along the wet-dry gradient, and partly because qualitatively new habitats associated with near-vertical microsites are added. However, our results also show that the strength and sign of the relationship between species richness and microtopographic relief is strongly context dependent, differing in complex ways among species groups with different biological characteristics and different ecosystem functions, and among sites with different positions along main environmental gradients. Our results encourage searches for local (idiosyncratic) explanations for variation in species richness, based upon knowledge of ecosystem and species-group properties and local environmental variation, and underpin the notion of 'a diversity of explanations for diversity' (Tilman 1999).

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