Causes of the large variation in bryophyte species richness and composition among boreal streamside forests

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Abstract

Questions: Boreal forests along small streams are bryophyte diversity hotspots because are moist, productive and relatively high pH. Do these factors also explain the large differences in species richness and species composition found among streamside sites? Do the species of species-poor sites represent nested subsets of the species of more species-rich sites? How do the results apply to conservation?

Location: Forests along small streams in mid-boreal Sweden.

Methods: Survey of the flora of liverworts and mosses and habitat properties, including calculation of a pH-index based on species indicator values, in 37 sites (1000-m^2 plots).

Results: The number of bryophyte species per plot ranged from 34 to 125. Neither soil moisture nor basal area of trees (a proxy for productivity) correlated significantly with species richness and composition, whereas pH-index and cover of boulders did. Species richness and composition were more strongly correlated with pH-index for mosses than for liverworts. The richness and composition of bryophyte species most frequently found on moist ground, stream channel margins and, most unexpected, woody debris were all more strongly associated with the pH-index than with other habitat properties. Although species composition was significantly nested, there was still some turnover of species along the first ordination axis.

Conclusions: To attain high numbers of species, streamside forests need to have boulders and at least pockets with higher soil and stream-water pH. The number of Red list species was weakly correlated with total species richness and the most species-rich sites contained many species found more in non-forest habitats. Hence, bryophyte conservation in streamside forests should not focus on species-rich sites but on the quality and quantity of substrate available for assemblages of forest species that are strongly disfavoured by forestry.

Keywords: Gradient; Habitat; Headwater stream; Liverwort; Moss; Nested subset; Niche; Ordination; PCA; pH; RANDNEST; Riparian forest; Species turnover; Substrate.

Abbreviation: LOWESS = Locally Weighted Regression Scatterplot Smoothing.

Nomenclature: Söderström & Hedenäs (1998); Söderström et al. (2000).

Introduction

A core issue of ecology is to understand the variation in species richness across landscapes. Since conservation efforts have to be limited to certain sites, concentrations of species (i.e. hotspots) have received much attention (e.g. Fleishman et al. 2000; Gjerde et al. 2004). A conservation strategy based on the protection of hotspots of species richness relies heavily on the assumption that these sites harbour all species in need of conservation, including rare ones, i.e. nestedness prevails; the communities of species-poor sites are subsets of communities of species-rich sites (Atmar & Patterson 1993). However, even when species occurrences are significantly nested, some target species may have their main habitat outside the hotspots (Simberloff & Martin 1991). Thus, to understand the distribution of species over the landscape it is also essential to quantify the role of species turnover along the gradient in species richness (cf. Leibold & Mikkelson 2002).

Mosses and liverworts, often combined into the, probably paraphyletic, bryophytes (Groth-Malonek & Knoop 2005) are important vegetation components in boreal forests (Longton 1992). Bryophyte communities can be species-rich (Frisvoll 1997), and the diversity in boreal forests often exceeds that of vascular plants at a scale of 0.1 ha, especially in old forests (M. Dynesius unpubl.; Berglund & Jonsson 2001). A landscape scale study of *Picea* dominated forests in middle boreal Norway showed that the main change in bryophyte composition on the forest floor (measured at a grain size of 100 m^2) is related to forest site type, reflecting gradients in water, productivity and pH (Frisvoll & Prestø 1997). One component of this change in species composition was that species richness was higher at moist, nutrient rich and high pH sites. A similar change in bryophyte community composition in boreal forest related to water, pH and nutrients (or productivity) has been demonstrated in other studies in both Europe (Kuusipalo 1985; Økland & Eilertsen 1993) and North America (Carleton

1990; Robinson et al. 1989). Also, for vascular plants of boreal forests these factors correlate positively with species richness (e.g. Zinko et al. 2005). Water availability has also been shown to be important for bryophyte communities to attain high species richness in other biomes (Pharo & Beattie 1997; Robinson et al. 1989; Frahm 1994). Boreal forests along small streams in northern Sweden have two to three times more bryophyte species than randomly located upland forests (plot size 0.02-0.1 ha) (Dynesius 2001). In North America streamside forests have also been pointed out as habitats rich in bryophyte species (Belland & Schofield 1994; cf. Heinlen & Vitt 2003). These results conform to the landscape pattern described above, as streamside forests are generally more moist, more productive and have higher pH than upland forests. Moreover, the stream channel adds a unique habitat for bryophytes which further increases species richness (Dynesius 2001).

Although boreal streamside forests are regarded as a general hotspot habitat for bryophytes, the number of species can differ considerably between sites (Dynesius 2001). In this study, we ask if the important correlates of species richness and species composition on the landscape level also explain the wide range in species richness among streamside sites. We also explore whether other factors could account for variation in bryophyte richness and composition among streamside forests. We combine ordination techniques and nestedness analyses to quantify the amount of species turnover along the gradients in species richness and composition. To increase the resolution we analyse different subsets of species grouped according to (1) systematic position (mosses and liverworts); (2) main habitat associations in the landscape; and (3) main substrate associations in the plots. Red-listed species are also analysed separately, since they are especially important for conservation. Finally we explore how the results could be applied to conservation priorities.

Methods

Study area and selection of sites

The 37 study sites are situaed in two loose clusters in the Swedish mid-boreal zone (*sensu* Ahti et al. 1968). A southern cluster with 28 sites was located in Medelpad and eastern Jämtland (62°40' N and 16°05' E, midpoint of the area) as part of a field experiment (see Hylander et al. 2005a). To obtain a more representative sample of boreal streamside forests, and to widen the range in soil composition and pH, we added nine sites. These were located in southern Västerbotten (63°55' N and 20°05' E) close to

Umeå to minimize travel distances. The closest sites between the two clusters are 190 km apart and the maximum distance between two sites within a cluster is 110 km. The entire area has been subjected to repeated glaciations and most of the parent material of the till is acidic granitic and metamorphic rocks (Fredén 1994). The southern cluster is situated above the post-glacial highest coastline whereas the northern is below this line, having more sedimentary deposits. The northern area also has somewhat lower soil pH. The study area is climatologically relatively homogeneous. The yearly precipitation is ca. 700 mm and the growing season is ca. 155 days (Raab & Vedin 1995). The mature forests mainly consist of *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce), with scattered *Betula pubescens* and *B. pendula* (birches) and *Populus tremula* (aspen). The forest land has been used for commercial logging for ca. 150 years with clear cutting being the prevalent method from around 1950 (Esseen et al. 1992). The streams included in the study are sufficiently small not to have been modified for timber floating, but some of them have been subject to low-intensity drainage measures.

A total of 19 sites in the southern cluster were randomly selected mature stands with intersecting small streams on the lands of a forest company (SCA). Plots were placed along the stream near the centre of each stand. Nine additional sites were randomly located along small streams in nature reserves in the same region. These southern plots were inventoried in July 1998. In the northern cluster, sites were selected from nine 5 km × 5 km squares randomly selected within a 50 km × 50 km area immediately northwest of Umeå. The midpoint of each 5 km × 5 km square was marked and the nearest stand of mature forest intersected by a small stream was located using maps and aerial photographs. Plots were placed along the stream in the middle of these stands and were inventoried in the autumn of 2000. The 37 stands all represented mature coniferous forests ca. 90 years or more old, which had been subject to selective cutting of varying intensity but most likely were never clear-felled.

Bryophyte inventory

In each stand we established a 1000 m² (50 m × 20 m) plot along the stream. The stream channel was included in the plot and crossed the midpoint of both short sides of the rectangle. Each plot was divided into five segments (10 m × 20 m) and all bryophyte species were listed for every segment. We collected many small samples of bryophytes to ensure correct identification of species, but despite this the following combinations of species were treated as one taxon each: *Chiloscyphus pallescens*

+ *polyanthos*, *Lophozia gillmanii + bantriensis*, *Pellia neesiana + epiphylla* and *Plagiothecium laetum + curvifolium*.

Habitat properties

Data on habitat properties were gathered at the 1000-m² scale. We estimated percent coverage of seven different bryophyte substrates by eye (1 to 7) and measured another three substrates using a tape. The undisturbed ground was divided into (1) wet; (2) moist; and (3) mesic according to definitions in Hägglund & Lundmark (1981). We also estimated the cover of (4) boulders (> 10 cm diameter) in the stream; (5) boulders on land not covered by ground vegetation; (6) crevices (i.e. depressions below or between roots, stumps, boulders etc.); and (7) exposed mineral soil in mounds and pits of tree uprootings. Woody debris was divided into (8) soft logs on land; (9) hard logs on land and in stream channels; and (10) soft stumps. If the tip of a knife could easily penetrate 1 cm into the wood it was considered to be soft. The surface area of logs was calculated using half the circumference and is reported in m². We also measured the basal area of trees using a relascope at two points (12.5 and 37.5 m from one short end of the plot) and calculated a mean value for *Pinus*, *Picea* and deciduous trees separately. We estimated, by eye, the percent cover of trees (the canopy), shrubs, bryophytes and vascular plant understorey. The width of the stream was measured at one representative place and the slope of the stream surface was measured using a rod and a level from its highest to its lowest point within the plot. The most important aspects of forest history in this data set were accounted for by including woody debris variables.

pH-indices

The variation in soil conditions (including pH) within topographically variable boreal landscapes is strongly associated with groundwater recharge and discharge (Giesler et al. 1998). Discharge areas, frequently found in streamside forests, have higher pH values and this is partly why streamside forests in general have many bryophyte species. However, pH varies between and within streamside forests because the influence of stream water and discharging groundwater varies as does the pH of the water. To make relevant and representative measurements of pH in large heterogeneous plots as those studied here would be difficult. An alternative procedure is to use the mean of indicator values for the species assemblage of the site as a proxy for real measurements. This method is described and discussed by Jongman et al.

(1995) and is generally considered to be an informative, semi-quantitative biotic index (cf. Diekmann 1995; Dupré & Diekmann 1998). We used substrate reaction values for bryophytes indicating acidity-alkalinity from Dierssen (2001) that were available for 99% of the species in our study. The indicator values are not equal to pH values. Instead, they represent delimited clusters of substrate pH. We converted the classes from Dierssen (2001) to numerical values (1 - 6) where 2 corresponds to highly acidic (pH 3.4 – 4.0), 4 to moderately acidic (pH 4.9 – 5.6) and 6 to basic (pH > 7) conditions. We constructed a pH-index by calculating the mean reaction value for all the bryophyte species found in a plot having their main substrate (see below) on moist ground, wet ground, stream channel margin and boulders in the stream (37.5 species per plot; range 13 - 69). We also calculated a pH-index using the values from Ellenberg et al. (1992) but since the two indices were strongly correlated ($r = 0.97$) we only report results for the pH-index calculated using the more comprehensive data of Dierssen (2001).

Macrohabitat and substrate associations

The species were classified into four mutually exclusive groups according to the macrohabitat in which they have their largest populations in the landscape (main macrohabitat) according to the literature (Hallingbäck 1996) and personal experience from the region. The habitats were forests, rocky outcrops, open mires and banks of roads and rivers; we later pooled the three open non-forest habitat categories.

For every species in every 1000-m² plot we recorded the substrate or substrates on which the species most commonly occurred. If, for example, a species was abundant on stumps and logs but only found once on a boulder only stumps and logs were recorded for that species in that particular plot. Each species was then assigned one main substrate, i.e. the substrate with the highest number of records in all 37 plots combined (see App. 1). In addition to substrates 1 - 7 listed above, the following eight categories were used: dry ground, stream channel margin, base of tree (of any species), bark on deciduous tree (*P. tremula*, *Sorbus aucuparia* and *Salix caprea* mostly > 1 m above ground), logs on land, logs in stream channel, stumps and dung or animal carcass).

Statistical analyses

Data from the two loose clusters of sites were pooled under the assumption that the species composition at the sites reflects differences in local habitat properties between sites rather than broad scale regional differences. Boreal bryophytes have wide distributions, and the two areas both lie within the range of all, except two, species encountered by us (Söderström 1995, 1996, 1998). Ordinations of the pooled data also show a clear overlap in species composition between the two areas. Furthermore, the results from a stepwise regression on total species richness, where geographical area was included, supported the validity of the assumptions for pooling the data (see below and Results section).

We performed locally weighted regression scatterplot smoothing (LOWESS regression; Trexler & Travis 1993) to explore how numbers of species within the different substrate and macrohabitat groups related to total species richness. In this way we could identify if some assemblages of species accounted more than others for the large variation in species richness among sites. The curves were constructed using the statistical package SigmaPlot (Version 9.0.1, Systat Software, Inc., Richmond, CA, USA)) and 50% of the total number of points was used to calculate each LOWESS regression point.

To construct a model of predicted total species richness from habitat properties we performed a stepwise multiple regression analysis with 13 independent variables: pH-index, cover of mesic ground, cover of land boulders, surface area of soft logs, surface area of hard logs, area of soft stumps, width of stream, stream slope, basal area of all trees, and of *Picea*, *Pinus* and deciduous trees, tree canopy cover and bryophyte cover. Some variables were logarithmically transformed to better meet the assumptions of normality. The following variables were still highly skewed after transformation and were omitted from the regression analysis: cover of moist ground, wet ground, exposed mineral soil, crevices, stream boulders, shrubs and understorey vascular plants. Another variable that also had a skewed distribution was amount of land boulders but since it showed high correlation with species richness we included it as a dummy variable and divided the data into two equal parts: high cover (0.3 - 12 %) and low cover (0 - 0.2 %). The variables were entered and removed in the following manner; at each step the independent variable not in the equation, which had the smallest probability of F was entered, if that probability was sufficiently small ($p < 0.05$). Variables already in the regression equation were removed if their probability of F became sufficiently large ($p > 0.10$) after including the new variable.

The procedure terminated when no more variables were eligible for inclusion or removal. We performed a second stepwise regression on total species richness to test if geographic area *per se* (i.e. if the plot belonged to the northern or southern cluster) added significantly to the model with the two variables that had turned out to be most important.

Correlation analyses were performed to explore the relationships (1) among habitat properties; (2) between habitat properties and species richness; (3) between habitat properties and species composition (i.e. PCA scores of sites – see below) and (4) between pH-index and the standard deviation of all species indicator values (not only those used in the pH-index) as well as between site mean and site standard deviation of indicator values for three of the species subgroups used to construct the pH-index (moist ground species, stream margin species and stream boulder species). For correlation analyses the non-parametric Spearman rank correlation test was applied to allow analysis of variables that were not normally distributed. For both regression and correlation analyses we used the statistical package SPSS (Norušis 1999). Invoking a larger set of comparisons increases the probability of type 1 errors, but since the prime purpose of the correlation analyses were exploratory we report significant correlations at $p < 0.05$ or, in some cases, $p < 0.01$.

We use indirect ordination methods to avoid the risk of masking important and for us unknown relationships between species composition and habitat properties (cf. Økland 1996). Principal Component Analysis (PCA) was performed because the length of the first ordination axis obtained by an initial Detrended Correspondence Analysis (DCA) was fairly short, not exceeding three standard deviations (ter Braak & Prentice 1988). If we had used smaller plots the gradients would probably have been longer (Økland et al. 1990). Separate ordinations were performed for all bryophytes, mosses, liverworts and for the five most species-rich main substrate species groups (each with 27 - 50 species found in the study, together comprising 70% of all species). The result from a PCA conducted with the statistical package PC-ORD (McCune & Mefford 1999) includes scores (co-ordinates) for the sites along the axes, eigenvectors for all species (the linear Pearson correlation coefficients between the species and the axes) and scores for the species calculated by weighted averaging. The ordinations were performed on species frequency data (0 - 5 of the 200 m^2 segments of each plot).

A species by site matrix is an illustrative way of presenting community data. In the most common case sites are sorted according to number of recorded species and the species according to frequency. If the matrix is

completely filled in one corner and empty elsewhere then the data is perfectly nested but, in real data, this is rare. The species by site matrix can also be ranked according to site variables other than species richness (Cutler 1991). Leibold & Mikkelson (2002) argued that the species by site matrix should primarily be ordered according to the scores of an ordination rather than species richness/species frequency, as they found cases where turnover along a gradient was masked in the scatter of the matrix. When sorted by ordination scores the matrix places sites with similar species composition close to each other. Species with similar distributional patterns over the sites are also placed close to each other. In this matrix it is possible to visually detect if some of the deviations are due to turnover along the first ordination axis (cf. Leibold & Mikkelson 2002). Another way to find out if there is a turnover in species composition along the first ordina-tion axis is to examine the eigenvectors for the species in the PCA output. In a perfectly nested matrix (with presence/absence data) all species have eigenvectors towards the species rich end of the gradient. Species with opposite direction of their eigenvector are either confined to or have higher abundance at the opposite end of the gradient, representing turnover.

The statistical test of nestedness was performed using the RANDNEST procedure described by Jonsson (2001). To test whether there was a significant nested pattern we calculated the discrepancy (d, Brualdi & Sanderson 1999) for each matrix, which is the number of occurrences that needs to be shifted to produce a perfectly nested matrix from the observed matrix. The null model, against which we evaluated each matrix, was a situation where species were distributed ran-domly across sites, with a probability of occurrence according to their observed frequency (for discussion on which null model to use see Jonsson 2001). The RANDNEST procedure generates a d-value from simu-lated null matrices (we performed 500 random matri-ces). The observed matrix is regarded as nested if the d-value is significantly lower ($p < 0.05$) than the mean d-value of the null matrices (assuming normal distri-bution of d for the 500 simulated matrices). We applied RANDNEST to all bryophytes and to the seven sub-groups separately (mosses, liverworts, moist ground species, stream margin species, stream boulder species, land boulder species and woody debris species). We made several tests ranking the sites (the species are not ranked in the RANDNEST test) according to PCA scores for the first axis, species richness and by some of the habitat variables that turned out to be correlated with the first PCA axis.

Results

Habitat properties

Some sites were well drained whereas other sites were dominated by wet, level ground dominated by peat mosses (*Sphagnum* spp.). *Picea* constituted on average more than 60% of the stem basal area (Table 1). Some sites had a relatively smooth surface whereas others had boulders, logs, crevices and uprootings. Correlations among habitat properties were generally weak (Table 2), except for easily interpreted cases such as boulders in stream and on land (positive), stream slope and stream boulders (positive), *Picea* and total basal area (positive), mesic ground and moist ground (negative).

Range in species numbers

The number of bryophyte species ranged from 34 to 125, with a mean of 75 species per 1000-m^2 plot. Moss and liverwort richness ranged from 21 to 80 (mean 47) and 10 to 46 (mean 28), respectively (Table 3). The ratio between the range and the mean was almost identical in the two groups (1.3).

Some species groups contributed more than others to the large differences in total species richness among sites. Species that occurred mainly in the stream margin contributed ca. 20, and species on moist ground ca. 15 of

Table 1. Range and mean of habitat properties among the 37 sampled boreal forest stands along small streams in northern Sweden. The data are from 1000-m^2 plots.

Habitat property	Range	Mean
pH-index[a]	3.0 - 4.6	4.1
Mesic ground (%)	0 - 78	18
Moist ground (%)	15 - 90	65
Wet ground (%)	0 - 56	6
Exposed mineral soil (%)	0 - 1.4	0.2
Crevice (%)	0 - 9.0	1.4
Land boulders (%)	0 - 12.0	1.0
Stream boulders (%)	0 - 10.5	2.1
Logs on land, soft (m^2)	0 – 16.2	4.0
Logs, hard (m^2)	2.3 – 88.4	27.1
Stumps, soft (m^2)	0.1 – 3.5	1.7
Width of stream (m)	0.3 - 3.0	1.3
Stream slope (%)	0 - 12.2	4.0
Total basal area (m^2 ha^{-1})	12.5 - 49.5	29.9
Picea (m^2 ha^{-1})	0.5 - 39.0	19.0
Pinus (m^2 ha^{-1})	0 - 30.0	5.3
Deciduous (m^2 ha^{-1})	0.5 - 27.5	5.6
Tree canopy cover (%)	30 – 90	64
Shrub cover (%)	1 – 40	14.5
Understorey cover (%)	50 – 90	77
Bryophyte cover (%)	30 - 100	80

[a] The pH-index is the mean indicator value (not pH-value) (*sensu* Dierssen 2001) at a site for all species growing on substrates which are strongly influenced by stream or groundwater (see Methods).

Table 2. Spearman's correlation coefficients among habitat properties in 37 streamside forests; significant correlations at $p < 0.05$ in bold. pH = pH-index[*]; MesG = Mesic ground; MoiG = Moist ground; WetG = Wet ground; Upro = Uprooting; Crev = Crevice; BouL = Boulder on land; BouS = Boulder in stream ; SocL = soft coarse logs; HacL = Hard coarse logs; SoSt = Soft stumps; WidS = Width of stream; SloS = Stream slope; BasT = Total basal area; BasS = Spruce basal area; BasP = Pine basal area; BasD = Deciduous basal area; CovT =Tree cover; CovS = Shrub cover; CovU = Understorey.

	pH	MesG	MoiG	WetG	Upro	Crev	BouL	BouS	SocL	HacL	SoSt	WidS	SloS	BasT	BasS	BasP	BasD	CovT	CovS	CovU
Mesic ground (%)	-0.29																			
Moist ground (%)	0.04	**-0.61**																		
Wet ground (%)	-0.27	-0.13	**-0.36**																	
Uprooting (%)	0.29	-0.32	0.17	-0.12																
Crevice (%)	**0.52**	-0.29	-0.15	0.16	**0.36**															
Boulder on land (%)	0.06	0.04	-0.11	-0.15	0.19	0.11														
Boulder in stream (%)	0.27	0.18	-0.10	**-0.33**	0.29	0.05	**0.69**													
Soft coarse logs (m²)	0.17	0.30	0.00	-0.31	-0.06	-0.25	0.21	**0.34**												
Hard coarse logs (m²)	**0.43**	-0.17	0.27	-0.26	0.18	0.19	0.06	0.08	0.10											
Soft stumps (m²)	-0.25	0.21	0.24	-0.31	-0.21	-0.28	0.12	0.23	**0.45**	-0.18										
Width of stream (m)	0.17	-0.15	0.13	**-0.43**	0.08	-0.25	0.16	0.30	0.17	0.08	-0.04									
Stream slope (%)	0.15	0.25	-0.20	-0.01	-0.07	0.07	**0.43**	**0.56**	**0.33**	-0.04	**0.35**	-0.15								
Total basal area (m².ha⁻¹)	0.22	0.07	0.14	**-0.33**	0.10	0.09	-0.01	0.07	0.27	**0.41**	0.27	-0.06	0.21							
Spruce basal area (m².ha⁻¹)	**-0.34**	0.29	0.15	-0.11	-0.10	-0.11	0.06	0.02	0.09	**0.34**	0.29	**-0.37**	0.14	**0.57**						
Pine basal area (m².ha⁻¹)	**0.33**	0.10	-0.26	-0.11	0.26	0.30	0.11	0.24	0.05	-0.02	-0.11	0.20	0.01	0.23	-0.23					
Deciduous basal area (m².ha⁻¹)	0.13	-0.09	0.17	-0.32	-0.16	-0.17	-0.17	-0.08	**0.35**	0.04	0.29	0.10	0.11	0.26	-0.09	-0.35				
Tree cover (%)	-0.13	0.09	0.18	-0.10	-0.03	-0.08	-0.03	-0.14	-0.09	0.00	0.17	-0.21	0.15	0.30	**0.44**	-0.26	-0.04			
Shrub cover (%)	0.20	-0.02	-0.12	0.18	0.12	0.24	-0.32	-0.05	-0.08	0.04	-0.15	-0.17	**-0.33**	-0.28	-0.13	-0.07	-0.02	**-0.40**		
Understory cover (%)	**0.36**	**-0.43**	0.18	0.19	0.15	0.20	-0.11	-0.04	-0.30	-0.11	-0.15	-0.20	0.11	-0.18	-0.41	0.04	-0.01	-0.05	0.00	
Bryophyte cover (%)	-0.14	0.32	-0.06	0.08	-0.14	0.02	-0.07	-0.14	0.11	**0.52**	0.02	**-0.39**	0.05	**0.38**	**0.74**	-0.18	-0.19	0.27	-0.03	-0.30

[*]pH-index calculated from indicator values (see Methods section).

the total difference of 91 species between the most species-rich and species-poor forests (LOWESS graph, Fig. 1a). In contrast, species growing mainly on tree bases, on mesic ground, on exposed mineral soil or in crevices contributed little or nothing to the difference. Therefore, species occurring mainly on mesic ground or tree bases together accounted for 20-30% of the species at species-poor sites but only 5-10% at species-rich sites (Fig. 1a). The groups of species from the non-forest macrohabitats (open mires, rocky outcrops and banks of roads and rivers) behaved similarly in relation to total species richness and therefore we pooled them (Fig. 1b). Forest species contributed strongly to the increase in total species number up to ca. 100 species. Above this level only species from non-forest habitats contributed. As many as 58% of the recorded species had their main habitat outside the forest (see App. 1) but because of their lower occupancy they represented only 32% of the species in the average 1000-m² plot. However, in the most species-rich plots forest species only constitute around half of the species (Fig. 1b).

Table 3. Total number of species encountered in the study, mean proportion of these species present in each plot, mean number per plot and ordination results for all and each of seven subgroups of bryophyte species (systematic groups as well as the five largest main substrate groups) in 37 streamside forests. Separate ordination analyses were performed for each group. The lengths of the gradients were obtained by DCA. Proportion of variance explained by the first ordination axis as well as number of species with positive and negative eigenvectors, respectively, were obtained from PCA. Positive eigenvectors denote species with an affinity to the high pH/ high cover of boulders end of the gradient, which coincided with the species-rich end of each PCA gradient. Spearman's rank correlation coefficient between site PCA scores (from the group-wise PCAs) and site species numbers of the group are given in the last column.

Group	Total number of species	Proportion per plot (%)	Mean (SE)	Length of gradient	Variance explained (%)	Eigenvectors # positive	Eigenvectors # negative	r_s[a]
All bryophyte species	258	29	75.1 (3.4)	1.97	13.4	164	94	0.903***
Mosses	174	27	46.8 (2.2)	2.07	13.1	116	58	0.911***
Liverworts	84	33	28.3 (1.4)	1.79	15.8	60	24	0.706***
Moist ground species	39	43	16.3 (0.7)	2.48	18.2	27	12	0.642***
Stream margin species	50	26	11.1 (0.8)	1.88	15.0	34	16	0.881***
Stream boulder species	27	18	4.4 (0.5)	2.22	20.8	20	7	0.803***
Land boulder species	35	17	6.2 (0.9)	2.98	28.0	34	1	0.961***
Woody debris species	29	43	15.4 (0.6)	1.44	17.4	25	4	0.957***

*** = $p < 0.001$; [a] PCA scores vs site species richness

Species richness and habitat properties

Total species richness was most strongly correlated with pH-index, but cover of stream and land boulders had almost equally high correlation coefficients (Table 4). In contrast, species richness did not correlate significantly with cover of moist or wet ground or with basal area of trees (a proxy for productivity). pH-index, cover of land boulders, surface area of hard logs (negative influence) and tree cover (negative influence) together explained two thirds of the variation in species richness (stepwise multiple regression, $R^2_{adj} = 0.69$). The coefficient of determination dropped to 0.58 in a two-variable model with only pH-index and cover of land boulders. When geographic position was included in the latter model it did not significantly improve the model ($p = 0.27$), but could substitute pH-index to some extent ($R^2_{adj} = 0.48$ for a model including geographic position and cover of land boulders).

Species numbers of mosses, non-forest species, stream margin species and moist ground species were most strongly correlated with pH-index whereas number of liverworts, forest species and boulder species were most strongly correlated with cover of boulders (Table 4). Number of woody debris species was not correlated with ground moisture and was only weakly correlated with surface area of logs (soft logs $r_s = 0.40$, $p = 0.014$) and tree basal area ($r_s = 0.47$, $p = 0.003$). Instead, pH-index was also the strongest correlate ($r_s = 0.55$, $p < 0.001$) for this group.
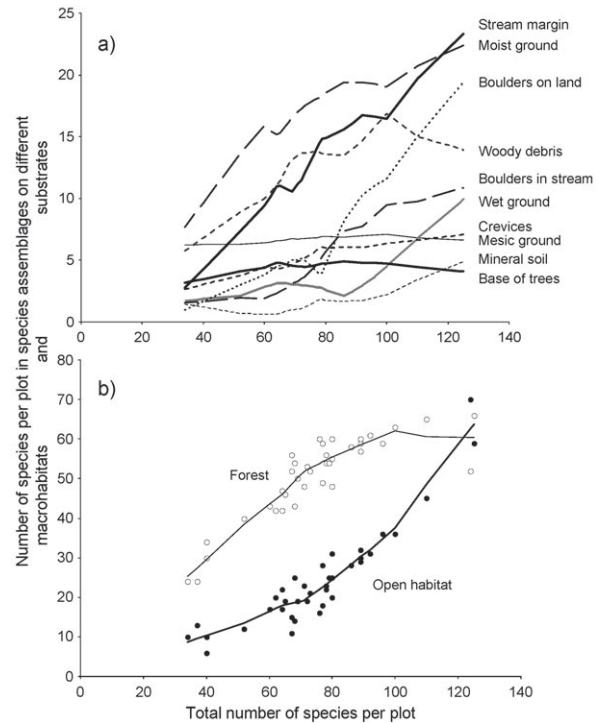
Fig. 1. Species richness of species associated with (**a**) different substrates and (**b**) different macrohabitats vs total species richness per plot based on data from 37 streamside forests. The graphs are constructed using Locally Weighted Regression Scatterplot Smoothing (LOWESS). All different species groups based on substrate affiliation were included except the three most species-poor (dry ground, dung and carcass and epiphytes on deciduous trees). Stumps, logs on land and logs in stream are grouped together as woody debris. The open habitats group included species mostly growing on rocky outcrops, open mires and banks of roads and rivers.

Table 4. Spearman's correlation coefficients between habitat properties and species numbers / first PCA-axis for different groupings of bryophyte species in 37 streamside forests. The positive end of the first ordination axis is defined as the high pH / high boulder cover / species-rich end. Only coefficients with $p < 0.01$ are reported ('–' denotes coefficients with higher p-values). The highest correlation coefficient for each grouping is shown in bold.

Species group	pH-index	Stream boulders	Land boulders	Crevices cover	Stream slope	Basal area *Pinus*	Basal area *Picea*	Basal area all trees	Surface area of logs[1]
All	**0.68 / 0.82**	0.67 / 0.51	0.59 / 0.44	– / 0.51	– / –	0.44 / 0.44	– / –	– / –	– / –
Mosses	**0.72 / 0.86**	0.63 / 0.47	0.55 / –	– / 0.52	– / –	0.42 / 0.46	– / –	– / –	– / –
Liverworts	0.48 / **0.55**	0.55 / 0.53	**0.57 / 0.55**	0.45 / –	0.45 / –	– / 0.45	– / –	– / –	– / –
Forest species	0.59 / **0.87**	**0.67** / 0.47	0.53 / –	– / –	– / –	– / 0.47	– / –	– / –	– / 0.44 (H)
Non-forest species	**0.64 / 0.72**	0.57 / 0.52	0.53 / 0.47	– / 0.43	– / –	0.45 / 0.42	-0.43 / –	– / –	– / –
Moist ground species	**0.49 / 0.94**	– / –	0.42 / –	0.45 / 0.58	– / –	– / –	– / -0.44	– / –	– / –
Stream margin species	**0.75 / 0.89**	– / –	0.49 / –	– / 0.55	– / –	– / 0.48	– / -0.43	– / –	– / –
Stream boulder species	– / 0.52	**0.76 / 0.62**	0.68 / 0.51	– / –	0.46 / –	– / –	– / –	– / –	– / –
Land boulder species	– / –	0.61 / 0.63	**0.77 / 0.76**	– / –	– / –	– / –	– / –	– / –	– / –
Woody debris species	**0.55 / 0.54**	– / 0.46	– / –	– / –	– / –	0.4 2 / 0.45	– / –	0.47 / –	– / 0.50 (S)

[1] (H) = hard wood surface area, (S) = soft wood surface area.

Species composition and habitat properties

The first axis obtained by the PCA with all species included accounted for 13% of the variation in species composition (Table 3). When all species were included, the species composition was strongly correlated with pH-index and weakly with cover of boulders and crevices (Table 4). For all subgroups, except boulder species, the species composition correlated most strongly with pH-index, but for liverworts the amount of land boulders correlated equally well (Table 4). Boulder species correlated most with amount of boulders. Very high positive correlation coefficients between the species composition and pH-index were found for mosses, forest species, stream margin species and moist ground species (r_s = 0.86-0.94, $p < 0.001$). Composition of woody debris species correlated almost equally well with area of soft logs as with pH-index.

Nestedness and turnover along the first ordination axis

The species composition was significantly nested in the entire data set, for mosses and liverworts separately, and for the five most species-rich substrate groups both when sorting sites by species richness and by ordination scores of the first axis (Table 5). Concerning habitat variables, the species by site matrix of all species and of mosses separately displayed strong nestedness when the sites were sorted by cover of boulders or by pH-index. Liverworts were significantly nested only when sites were sorted by cover of land boulders (Table 5).

The matrices for land boulder species and stream-margin species displayed two opposing patterns for how a species by site matrix changes when sorted according to species composition (ordination scores) instead of

species richness and frequency (Fig 2). Both were significantly nested when sorted by species richness/species frequency (Table 5). When the matrix of stream margin species was, instead, sorted by species composition some of the scatter from the first matrix (deviations from perfect nestedness) was grouped at the lower right corner of the gradient, revealing a clear turnover in species composition along this axis (Fig. 2b). In this matrix both the nestedness and the turnover became clearer. Most species at species-poor sites were also present in species-rich sites, but several stream margin species were confined to the species-poor sites. The turnover in this group related to pH-index, which was more strongly correlated to species composition than to species richness (Fig. 2b and Table 4). For land boulder species, no turnover was revealed and the correlations to habitat properties were similar between species composition and species richness (Fig. 2a).

All species, as well as the subgroups mosses, liverworts, moist ground species and stream boulder species, displayed a pattern of turnover similar to stream margin species. In these groups, quite a few species were confined to, or had higher abundances, in the low pH/species-poor part of the axis. For example, only 64% of the species in the entire data set had eigenvectors pointing in the 'high pH/species rich' direction of the first ordination axis (Table 3). Woody debris species, on the other hand, behaved like land boulder species and did not display turnover. Consequently, almost all species in these two groups had eigenvectors towards the 'high pH/species-rich' or 'much boulders/species-rich' end of the ordination axes (Table 3). For the groups displaying turnover, pH-index was generally more strongly correlated with species composition than with species richness. No such difference was evident for the groups not displaying turnover along the first PCA-axis.

Table 5. Results from nestedness analysis of bryophyte communities in streamside forests. The sites in the different species by site matrices were sorted according to species richness (# spec), the first PCA axis (PCA) or selected habitat variables (species are not sorted in this analysis). All habitat variables that produced at least one significantly ($p < 0.05$) nested matrix are included. These are pH-index (pH), cover of stream boulders (BouS), cover of land boulders (BouL) and cover of crevices (Crev).

Species group	Simulated $d \pm SD$[a]	# spec[b]	PCA[b]	pH[b]	BouS[b]	BouL[b]	Crev[b]
All species	1008.1 ± 21.6	8.6 ***	8.2 ***	3.6 ***	3.5 ***	4.6 ***	1.7 *
Mosses	630.9 ± 17.5	6.5 ***	6.0 ***	3.5 ***	3.0 **	2.8 **	0.2
Liverworts	360.9 ± 12.5	5.2 ***	3.2 ***	0.4	–0.2	2.4 **	-0.2
Moist ground species	205.3 ± 8.2	2.9 **	2.1 *	1.1	–0.9	-0.7	0.2
Stream margin species	182.9 ± 9.1	3.6 ***	2.8 **	1.0	–1.6	0.0	0.6
Stream boulder species	83.4 ± 5.8	3.2* **	3.0 **	–1.0	2.2 *	0.6	–2.7
Land boulder species	88.2 ± 7.1	2.2 *	2.4 **	–6.2	–2.4	0.0	–6.3
Wood species	109.0 ± 6.7	3.1 **	3.0 **	–0.2	–0.9	–1.6	–1.8

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; [a] The discrepancy from perfect nestedness in a matrix (Brualdi & Sanderson 1999). The observed discrepancies of each matrix sorted in several ways were compared with the mean discrepancy from 500 random simulations. [b] This value, often called *z*-value, denote how many standard deviations the observed value of *d* deviates from the simulated. Positive values denotes a stronger nestedness than the simulated.

Fig. 2. Species by site matrices for species having their main substrate on (**a**) land boulders and (**b**) stream margins. Note that the purpose with this figure is to illustrate the change in patterns revealed when sites and species are sorted in different ways and not to give an exhaustive presentation of species composition and species scores. Numbers denote 200-m^2 plot segment occupancy from 0 to 5. To the left the sites are sorted by species richness and the species by number of sites occupied and to the right both sites and species are sorted by ordination scores. Directions of gradients and Spearman's correlation coefficients between an environmental factor and species richness (left) and scores on the first ordination axis (right), are given below each matrix. S and N denote sites from the southern and northern cluster of sites, respectively, and E denotes the eigenvector for each species. *** denotes $p < 0.001$.

The pH-index and standard deviation of the indicator values of all the species in the plots (not only those used to calculate the pH-index) correlated strongly and positively ($r_s = 0.88$, $p < 0.001$), suggesting that there was a large variation in indicator values among the species present at sites with high pH-index, but not at sites with low pH-index. For stream margin species and stream boulder species there was a positive correlation between the mean indicator value and the standard deviation of the indicator values of the species in the groups ($r_s = 0.42$, $p = 0.01$; $r_s = 0.72$, $p < 0.001$), whereas for moist ground species this correlation was weak but significantly negative ($r_s = -0.33$, $p = 0.04$).

Red-listed species

Altogether, 12 red-listed species were encountered (Gärdenfors 2000). The number per plot ranged from zero (30% of the plots) to seven with a mean of 1.9. The seven species that were associated with logs comprised 90% of the records. Other substrates hosting red-listed species were land boulder (two species), stream margin (one species), deciduous trees (one species) and base of trees (one species). The number of red-listed species in a plot correlated positively, but relatively weakly, with total species richness ($r_s = 0.40$, $p = 0.01$) but did not correlate with the first PCA axis of all species ($r_s = 0.25$, $p = 0.13$). Among the measured habitat variables the strongest correlations with number of red-listed species were found for area of soft logs ($r_s = 0.52$, $p < 0.001$), total basal area of trees ($r_s = 0.48$, $p = 0.003$) and pH-index ($r_s = 0.40$, $p = 0.013$).

Discussion

Species richness and composition

Of the three habitat properties that correlate positively with bryophyte species richness over entire boreal landscapes (pH, productivity and moisture; e.g. Frisvoll & Prestø 1997) only pH-index correlated with species richness in this study of streamside forests. Stream boulder species was the only group in which species number correlated with ground moisture (negative correlation). However, this is probably caused by the lower cover of stream boulders in wet sites (Table 2). Productivity (measured as total basal area of trees) correlated only with number of woody debris species. This positive correlation is not surprising as the amount of substrate for this group is directly related to the production of tree biomass.

Two things are important for a streamside forest to attain high numbers of bryophyte species: many boulders and a relatively high pH in soil and water. Boulders raise species numbers because there are many epilithic (growing on stone) species in the boreal species pool (almost 25% of all species encountered in the study, Table 3) but also because boulders increase microtopographical and microclimatic heterogeneity. Boulders add both convex exposed habitats and dark, moist habitats on their north facing sides and in crevices between and under them. Bryophyte species richness is often positively correlated with microhabitat heterogeneity (Vitt et al. 1995; Vitt & Belland 1997; Mills & Macdonald 2004) or heterogeneity in habitat conditions such as moisture and light (Jonsson 1997).

How do we interpret the close relationship between pH-index and species richness? We provide three hypotheses for this: (1) spatial heterogeneity in pH; (2) a mid-domain effect; and (3) a historical/evolutionary imprint on the species pool. In our study, much evidence points in the direction of the habitat diversity hypothesis (e.g. Brown 1984; Rosenzweig 1995). Sites with high pH-indices also contain some projecting microsites with low pH such as stumps, logs, boulders and hillocks which are, in part, unaffected by the chemistry of the water and soil in the rest of the plot. The strong positive correlation between the pH-index and the standard deviation of the pH indicator values of all species in the plots also indicates a higher heterogeneity in pH in high-pH sites. Our results parallel those of Gould & Walker (1997) who found a close positive correlation between species richness of vascular plants and soil pH along an arctic Canadian river. The range of pH at their sites was correlated with mean pH, leading them to the conclusion that the habitat variability in pH was the main explanation for the richness patterns. Gough et al. (2000) also found that vascular plant species typical of low-pH sites were present in sites with generally high pH in Alaskan tundra vegetation but not *vice versa*. Zinko et al. (2005) showed significant nestedness and a strong positive correlation between a pH-index and species richness of vascular plants in a boreal forest landscape.

The heterogeneity in pH within sites might be a good explanation for the total species richness but seems a less likely explanation for the wide range in species richness (Fig. 1a) of, for example, stream margin species (being entirely affected by stream water) or moist ground species (having a negative correlation between mean and standard deviation of pH indicator values). In addition to heterogeneity in pH, we suggest that a mid-domain effect (Colwell & Lees 2000) in which there is more overlapping among pH-ranges of species in the high-pH end of the gradient may contribute to the positive relationship between pH-index and species richness. Our sites with "high" pH-index are in the middle of the pH-range found naturally while the low-pH-index

sites represent the acidic end, at which the number of species able to colonize is limited. This mid-domain effect may also contribute to the positive correlation between pH-index and its standard deviation found for several species groups, by limiting downward variation in indicator values at low-pH sites. The third explanation is that there may be, for historical reasons, a bias towards species with low tolerances for acidic conditions in the European species pool. Pärtel (2002) found that species richness of vascular plants was positively correlated with pH in regions were the species pool had its evolutionary origin in areas dominated by soils of high pH (such as Europe) and *vice versa*. These three hypotheses are not mutually exclusive. Extensive fine scale pH-measurements close to target species in plots differing in pH-index could be a way of quantifying their relative contributions.

Considering the strong correlation between species richness and species composition (Table 3) it was not surprising that the same habitat properties correlated both with species richness and species composition (cf. Table 4). However, pH-index was more closely related to composition than to species richness whereas the opposite was true for boulder cover, showing that there was more species turnover along the pH-gradient. Water chemistry has also previously been reported as being more important for bryophyte species composition than for species richness (Vitt et al. 1995; Wheeler & Proctor 2000). Species richness, on the other hand, has often been found to be positively correlated to heterogeneity of substrates (Vitt et al. 1995; Mills & Macdonald 2004). The correlations between the first PCA axis and basal area of *Pinus* and *Picea*, respectively, could be caused by a significant correlation between pH-index and these habitat properties in our data set (Table 2). A functional explanation for this relationship relates to the higher leaf area index of *Picea* compared to *Pinus*. The forest floor in *Pinus* dominated stands receives much more light compared to *Picea* dominated ones, improving the habitat for light demanding bryophyte species. The role of light is supported by the fact that species richness of non-forest bryophytes (presumably light demanding) was significantly correlated with these two variables whereas forest species richness was not (Table 4).

An important aspect that we have not been able to analyse in this study is to what extent colonization/ extinction processes account for the variation in species richness and composition (cf. Økland et al. 2003). It is likely that some of the variation could be attributed to variation among sites in species reproductive output in the surrounding landscape.

Nestedness

Although all habitat properties varied considerably among sites (Table 1) and were mostly uncorrelated (Table 2) the bryophyte flora displayed a significant pattern of nestedness, where the species found at species-poor sites were subsets of the communities at species-rich sites. The similarly significant nestedness when the sites were sorted according to species composition (PCA scores of the first ordination axis; Table 5) confirmed that the metacommunity was structured as nested subsets (cf. Leibold & Mikkelson 2002). Nestedness could be caused by a sorting of species according to their colonization ability or extinction probability (e.g. Bruun & Moen 2003). Another mechanism that is probably common, but less empirically investigated, is a nestedness of habitat properties (Worthen 1996), which seems to be a likely explanation in our case. Hylander et al. (2005b) proposed two different ways in which nestedness could be caused by differences in habitat properties among sites: nested habitats and nested habitat quality. For the overall pattern of nestedness in this study nested habitats seems a likely mechanism, where the species rich sites contain infrequent habitats (e.g. a *Populus tremula* tree, a deep crevice or substrates with relatively high pH) in addition to common habitat types (e.g. low-pH ground or tree bases). However, for some of the groups (notably boulder species and woody debris species) all species are favoured in the species-rich sites indicating a role for nested habitat quality.

In a situation with significant nestedness there may still be species mostly occurring in species-poor sites implying species turnover along the gradient in species richness (but see Kondrik-Brown & Brown 1993). It is important to identify these species for conservation purposes. Many species with low pH indicator values had eigenvectors pointing to the low-pH/species-poor end of the first ordination axis (Table 3, App. 1), but most of these had very low frequencies making it impossible to draw firm conclusions about their relationships to species-rich or species-poor sites. Many of the low-pH species with higher frequencies (thus allowing conclusions) are common in northern Sweden, for example on bogs and poor fens (e.g. the wet ground species *Sphagnum magellanicum* and the stream boulder species *Gymnocolea inflata*). However, a few species probably have their main occurrences in this region on acidic sand in streamside forests with low species numbers (e.g. *Nardia insecta*, *Mnium hornum*, and *Warnstorfia pseudostraminea*).

Woody debris species and pH

The correlations between the pH-index and both the species composition (PCA scores) and species-richness of woody debris species has not been demonstrated previously. One explanation for this relationship is that it is due to a non-causal positive relationship between pH-index and high population densities and reproductive output of woody debris species in the surrounding landscape, not accounted for in our study. However, a positive relationship between pH and both germination and establishment have been shown for a number of bryophyte species, including the woody debris species *Buxbaumia viridis* and several species growing mainly on exposed humus (Thomas et al. 1994; Wiklund & Rydin 2004; Dynesius, M. unpubl.), which indicates that there may be a casual relationship between pH and richness of epixylic bryophytes. Woody debris lying on the ground in streamside forests with relatively high water and soil pH should have higher surface pH and may therefore be more frequently colonized by more species.

Red-listed species

Most of the red-listed species were associated with logs, and surface area of soft logs also turned out to be the habitat factor with the strongest correlation with number of red-listed species. Total species richness correlated less with number of red-listed species indicating that it is not sufficient to preserve hotspots of species richness. However, a close correlation between number of red-listed species and any environmental variable is unlikely because of their low numbers. Dispersal limitation may also be important in determining the probability of occurrence of red-listed species at a specific site (cf. Edman et al. 2004).

Conclusions

A boreal streamside forest differs from an upland forest by its more moist conditions and by adding a unique structure, the stream channel. However, this is not enough to attain a considerably higher number of bryophyte species. Many boulders and, at least patches of, relatively high soil and/or water pH (sub-neutral to neutral as opposed to acidic) are also needed. For the species groups able to colonize substrate categories that are unique to, or much more frequent in, streamside forests (moist ground, stream channel margin and stream boulders) both species richness and composition were correlated with the pH-index. The species pools of these three groups appear to be large (Fig. 1a) together comprising 45% of all species found in our study (Table 3).

The nestedness of the bryophyte communities of streamside forests seems to be caused by a combination of nested habitats and nested habitat quality (*sensu* Hylander et al. 2005b). Species-rich sites containing rare microhabitats also include common substrates. Species-rich sites were also characterized by high habitat quality for all species in certain assemblages (e.g. high cover of boulders or woody debris). Although generally nested, the bryophyte communities of streamside forests varied considerably. The deviations from a perfectly nested pattern in the species by site matrix of the entire data set sorted by site richness and species frequency consisted of (1) differences in which habitat properties were important for the species richness and composition of different species groups (e.g. liverworts being mostly correlated to amount of boulders and mosses to pH-index); (2) species turnover along a compositional gradient of the sites (revealed by ordination and exemplified in Fig 2b) and (3) random absences and presences due to colonization/extinction dynamics (cf. Økland et al. 2003).

A significant nestedness indicates that conservation focus should be on the most species-rich sites but, as Fischer & Lindenmayer (2005) pointed out, many species could deviate from the main pattern. The high proportion of non-forest species in the most species-rich streamside forests (Fig. 1b) also indicates that these sites should not, by default, have a high priority. We argue that conservation of streamside forests should consider the different ways in which species on different substrates are assembled. For groups having little turnover along the gradient in species richness such as boulder and woody debris species conservation is relatively straight forward and should be focused on sites with high substrate availability (leading to high abundance, fertility or population stability). A more complicated approach is necessary for the groups showing turnover, but fortunately very few red-listed species or other species negatively affected by forestry are in these groups (Hylander et al. 2005a). The retention of buffer strips and care regarding hydrological alterations will probably be enough to conserve both species-poor and species-rich communities of these groups. We suggest that the preservation of streamside sites with large amounts of woody debris in various stages of decomposition would be an efficient approach to favour red-listed species, as their richness was correlated most strongly with this factor. In addition, restoration investments in streamside forests (e.g. addition of dead wood or forest buffer strip retention) would probably be highly cost efficient for bryophyte conservation, since mature streamside forests contain three times more red-listed bryophyte species than upland forests having approximately the same amount of decomposing wood (Dynesius 2001).

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