Riparian bryophyte vegetation in the Cascade mountain range, Northwest U.S.A.: patterns at different spatial scales

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Abstract: Riparian forests are productive and species rich ecosystems where the vegetation is structured by sharp environmental gradients. The study describes community patterns of bryophytes in stream-side forests, relates these patterns to major environmental gradients, and compares within-site factors with site level variables. Samples were collected from 360 plots 2 × 4 m in size distributed among 42 sites in old-growth *Pseudotsuga*–*Tsuga* forests. The sites ranged from 420 to 1250 m asl and stream size from 1st to 5th order streams. There were significant changes in species richness and composition along several environmental gradients. Richness within sites varied among different geomorphic surfaces with the highest number of species on areas periodically flooded. Richness was also higher in plots with high abundance of woody debris. No site level factors influenced richness at the sample plot level, while the highest species number at the site level was for large streams. The main gradients in the species composition within sites were changes with increasing distance from the stream and amount of woody debris. Both elevation and stream size significantly influenced species composition. The complex set of factors that influenced species richness and composition implies that management of riparian vegetation must be based on both coarse scale considerations such as regional distribution of different stream types and fine scale factors such as spatial availability of different substrate types.

Key words: old-growth forest; CCA analysis; fluvial disturbance; bryophytes; elevation effects; coarse woody debris.

Résumé : Les forêts ripariennes sont productives et constituent des écosystèmes riches en espèces où la végétation est structurée par des gradients environnementaux marqués. L'étude décrit les patrons des communautés de bryophytes forestières côtoyant les ruisseaux, relie ces patrons aux gradients environnementaux majeurs, et compare les variables à l'intérieur du site avec celles au niveau des sites. L'auteur a récolté des échantillons à partir de 360 parcelles mesurant 2 × 4 m, distribuées sur 42 sites dans des forêts âgées de *Pseudotsuga* et de *Tsuga*. Les sites vont de 420 à 1250 m au dessus du niveau de la mer et la dimension des ruisseaux du premier au cinquième ordre. On observe des changements significatifs dans la richesse en espèces et dans la composition le long de plusieurs gradients environnementaux. La richesse à l'intérieur des vites varie selon différentes surfaces géomorphiques, les nombres les plus grands en espèces se retrouvant sur les surfaces périodiquement submergées. La richesse est également plus grande dans les parcelles où il y a des débris ligneux. Aucun facteur du site influence la richesse au niveau de la parcelle échantillon, alors que le plus grand nombre d'espèce a été observé au niveau du site pour les plus gros ruisseaux. Les principaux gradients influençant la composition en espèces sur un site sont les changements liés à la distance croissante à partir du ruisseau et la quantité de débris ligneux. L'altitude ainsi que la dimension du ruisseau influencent significativement la composition en espèces. L'ensemble complexe de facteurs qui influencent la richesse en espèces et la composition, impliquent que l'aménagement de la végétation riparienne doit être basée sur la considération de facteurs à grande échelle tels que la distribution régionale des différents types de ruisseau et à l'échelle fine, de facteurs tels que la disponibilité spatiale des différents types de substrats.

Mots clés : forêts âgées, analyse CCA, perturbation fluviale, bryophytes, effets de l'altitude, débris ligneux grossiers. [Traduit par la rédaction]

Introduction

Riparian forests occupy the transition zone between an aquatic and a terrestrial environment. These habitats are often highly productive, structurally diverse, and rich in species (Salo et al. 1986; Nilsson 1992), and their vegetation is influenced by many sharp environmental gradients (Nilsson and Wilson 1991; Naiman et al. 1992). In addition, riparian areas are highly dynamic owing to both fluvial disturbance (Sigafoos 1964; Hupp and Osterkamp 1985) and nonfluvial disturbances such as forest fires and windthrows (Gregory et al. 1991). A number of studies (e.g., Hupp and Osterkamp 1985; Vitt et al. 1986; Gregory et al. 1991; Nilsson et al. 1994) on vegetation patterns in riparian areas exist and these have clarified some of the species–environment relations. Surprisingly few such studies have dealt with nonvascular plants (see, however, Slack and Glime 1985; Vitt et al. 1986; Glime and Vitt 1987; Englund et al. 1997), and thus general

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statements concerning the structure and dynamics of riparian vegetation might be biased towards the vascular flora.

In the mountainous Pacific Northwest in the U.S.A., riparian areas occupy a significant portion of the landscape and play crucial roles in maintaining the biodiversity of the forested area of the region (FEMAT 1993). In this context, it is striking that hardly any quantitative data on the riparian bryophyte vegetation is available (except Jonsson 1996) and even general ecological studies on bryophytes are rare from the region (see, however, Pike et al. 1975; Lesica et al. 1991; McCune 1993; J. Peck, S.A. Acker, and W.A. McKee, in preparation). It is clear that bryophytes are an important component of many forest ecosystems (Cajander 1909; Cooper 1912; Longton 1984) and may constitute a substantial part of plant biodiversity. They influence nutrient dynamics (Reiley et al 1979; Bates 1992), contribute significantly to stand biomass and production (Pike et al. 1977; Van Cleve et al. 1983), and serve as food and habitat for both invertebrates and vertebrates (Pakarinen and Vitt 1974; Glime 1978; Gerson 1982). At the same time, bryophytes are excellent model organisms to study community organisation and disturbance processes in forest ecosystems (Jonsson 1993; Økland and Eilertsen 1993).

The riparian system can be viewed as a gradient in disturbance, from intense and frequent disturbance in the stream channel to stable conditions on the hill slope. It is highly likely that this disturbance gradient should influence both species richness and composition patterns (cf. Kimmerer and Allen 1982). Processes such as inundation and abrasion by water may impose restriction to the number and type of species able to grow in the stream channel (cf. Vitt and Glime 1984; Slack 1990). By contrast, competitive interactions may be more important on higher areas less influenced by flooding. At intermediate levels, physical disturbance and competition may balance each other and, thus, provide conditions for high species richness. In addition, flooding disturbance is the major factor shaping the geomorphology of the habitat and, as such, providing a diverse set of microhabitats within the riparian zone (Gregory et al. 1991).

As the general knowledge of riparian bryophyte communities is scarce, one of the aims of the study is to describe community patterns of riparian bryophytes and relate these to major environmental gradients. Specifically, I want to compare the importance of local site factors with between-site differences. Information on the relative importance of factors at different spatial scales is of basic ecological interest but also has strong forest management implications. One pertinent question is whether to emphasise maintenance of canopy cover and abundance of woody debris or to consider riparian areas from different elevations and of different stream sizes as important as well.

Study area

The study was performed at the H.J. Andrews Experimental Forest (AEF), which is located on the western slope of the Cascade Range in central Oregon, U.S.A. The forest is about 6400 ha in area and contains a significant portion of old-growth *Pseudotsuga menziesii* – *Tsuga heterophylla* stands with trees of more than 500 years in age and 75 m in height. The elevation range is 400–1600 m asl. The climate is mild maritime with wet winters and cool, dry summers. Annual precipitation usually exceeds 2500 mm and mainly occurs during the winter. Extensive snowpacks are common at higher elevations (> 1000 m asl), while lower elevations usually remain free of snow except for shorter periods. The mean annual temperature at 420 m is 8.5°C, ranging from a monthly average of 0.6°C in January to 17.8°C in July. At 1300 m, the values are approximately 2°C lower (Bierlmaier and McKee 1989).

The study was carried out in the entire Lookout Creek watershed (Fig. 1). Lookout Creek is a high gradient mountain stream fed by numerous tributaries of varying sizes, and at its confluence with Blue River (part of the McKenzie River system) it is a 5th order stream. Streamflow follows the precipitation and snowmelt patterns with highest flows during winter and spring. Large pieces of wood significantly shape the structure of the stream by creating pools and redirecting waterflow. In old-growth stands, generally more than 2×10^5 kg/ha of coarse woody debris occurs in the riparian areas (Swanson et al. 1982). The riparian zone as defined in this study includes the whole gradient from the actual stream channel up to the lower parts of the hillslope (cf. Fig. 2). Thus, the study includes the following geomorphic surfaces: stream channel (with constant water), active channel (dry during short periods of low flow), flood plain (flooded annually), transition slope (steep bank separating the flood plain from the stream terraces or the hillslope), stream terrace (flat level area with history of flooding), toeslope (lowest part of hillslope), and hillslope (areas above highest flood level). Stream channel, active channel, and floodplain are collectively called the valley floor.

The vascular vegetation[2] is species rich mainly owing to a high diversity of microsites and complex disturbance regimes. On average, twice as many species occur in old-growth riparian zones as in hillslope habitats (Gregory et al. 1991). The tree layer is dominated by large conifers: *Tsuga heterophylla*, *Pseudotsuga menziesii*, and *Thuja plicata*. On wider stream terraces, a significant component of deciduous trees such as *Alnus rubra* and *Acer macrophyllum* occurs. Dominant understory shrubs are *Acer circinatum*, *Vaccinium* spp., *Oplopanax horridum*, *Rhododendron macrophyllum*, *Gaultheria shallon*, and *Berberis nervosa*. The herb layer is dominated by *Polystichum minitum*, *Linnaea borealis*, and *Trientalis latifolia* on drier sites, while *Vancouveria hexandra*, *Achlys triphylla*, and *Oxalis oregana* are common in moister sites. Bryophytes as a group are common and the epiphytic, epixylic, and epilithic as well as the ground flora are well developed. For further details on vascular plant vegetation, consult Zobel et al. (1976).

Methods

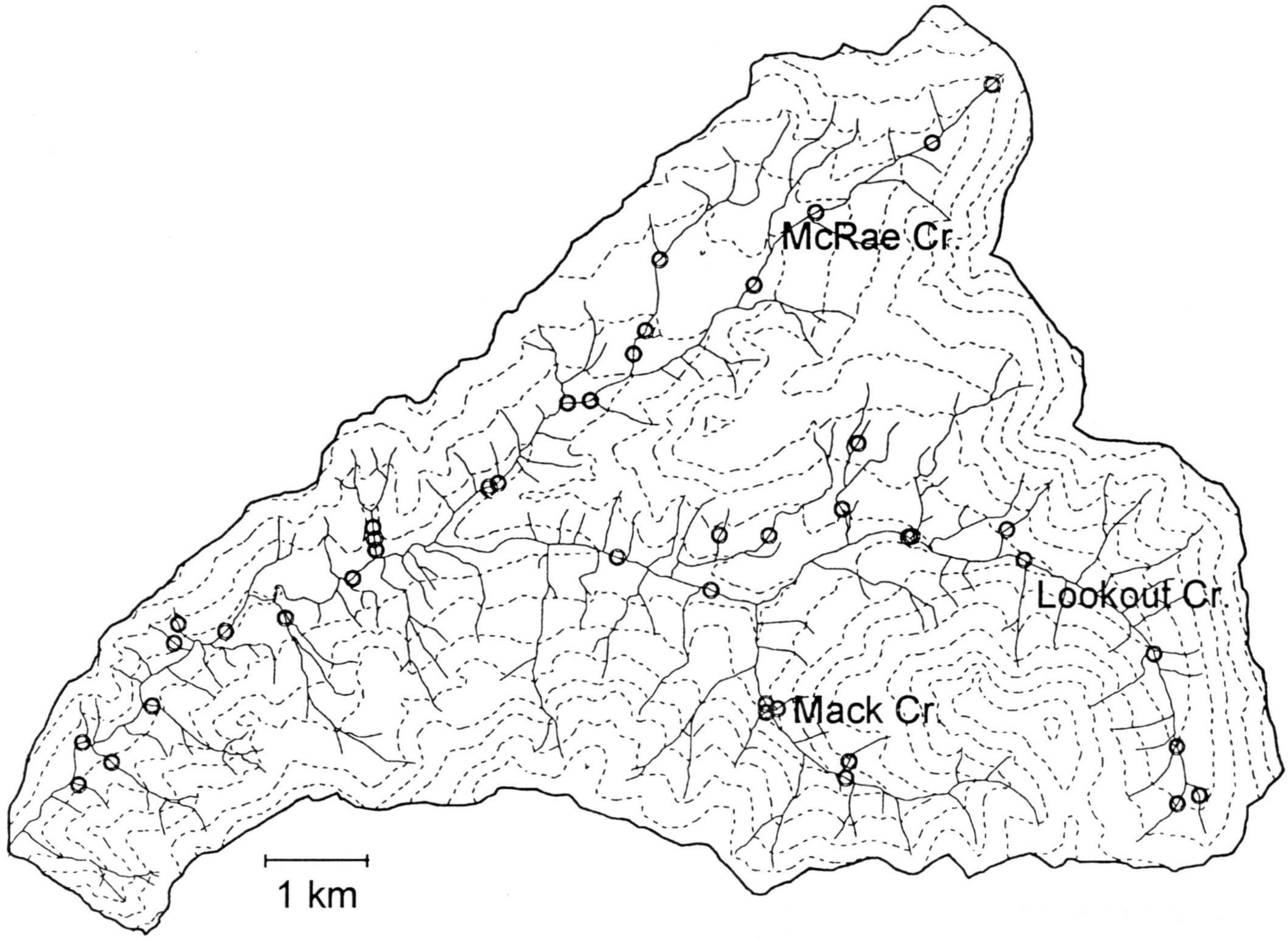
Sampling design

The sampling was performed during September and October 1994. The distribution of sample sites was stratified by elevation and stream order. Four elevation levels (<600 m, 600–800 m, 800–1000 m, and > 1000 m asl) and five stream orders (1st to 5th order) were used for the stratification. However, the sampling design was not a full factorial because 5th order streams occurred only at the lowest elevation, 4th order streams only below 800 m, and 3rd order streams only below 1000 m. Three sites were chosen from each of the 14 possible elevation – stream order strata, giving 42 sample sites (Fig. 1). Site locations were chosen subjectively from the forest map constrained to be located in old-growth stands and at least 100 m from the nearest road, young stand, or clear-cut. At each site, an initial position along the stream was determined at random.

At each site, a transect (hereafter referred to as the site) beginning in the centre of the stream channel was established. Five 2 × 4 m contiguous sample plots (hereafter referred to as plots) were

[2] Nomenclature follows Hitchcock and Cronquist (1973) for vascular plants and Appendix 1 for bryophytes.

Fig. 1. Location of sample sites (circles) within the H.J. Andrews Experimental Forest, Western Cascades, Central Oregon (lat. 44°15′N, long. 122°10′W). The relief of the area is indicated with 100-m contours.



located along the first 10 m. In 1st order streams the hillslope was always reached in 10 m. In all other streams, five additional plots were placed, on every 8th m up to 50 m giving a total of 10 sample points per transect. A total of 360 plots 8 m^2 in area were sampled.

Environmental variables

In each sample plot, a number of environmental variables was measured. Percent canopy cover of conifers and deciduous trees and ground cover of shrubs and herbs were guided by the use of a 'moose horn' (Robinson 1947) that projects the vegetation on a quadratic grid. The average of three different estimates within each plot was used. Percent ground cover of exposed soil, sand, gravel (including pebbles and cobbles), boulders, debris (litter and woody debris <10 cm in diameter), and coarse woody debris (>10 cm in diameter) were visually estimated. Transect slope, and hence height above stream channel, was measured by the use of a 2-m measuring stick. Each plot was assigned to one specific geomorphic surface (Stream channel, Active channel, Floodplain, Transition slope, Stream terrace, Toeslope, and Hillslope).

The sites (transects) were characterised by elevation, aspect, stream slope, and stream size. The aspect of the transect was assigned to be either predominantly northerly or southerly. Stream slope and size were calculated from existing GIS databases of the AEF. The general stream slope at the sample site was calculated as the difference in elevation between an upstream and a downstream intersection of known elevation. Stream size, i.e., basin area, was calculated as the total drainage area above the sample site.

Bryophyte recording

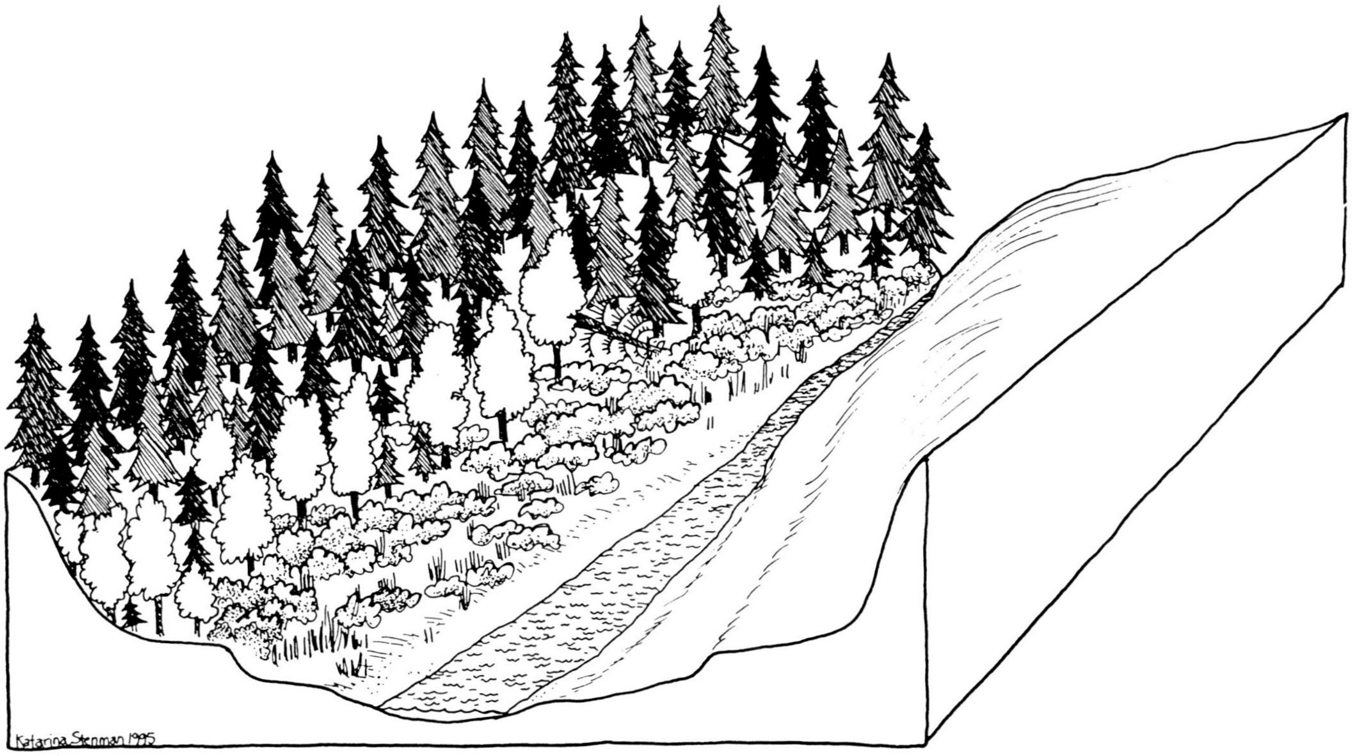
The percent cover of all bryophytes (i.e., mosses and liverworts), including epiphytic species up to about 2 m above the ground, was estimated. Species with less than 1% cover were recorded as 'traces', which was coded as 0.1% in the quantitative analyses. For species with more than 10% cover, the midpoint of 10%-intervals was used (i.e., 15, 25, . . .95) as abundance value. To guide cover estimates, a sheet representing 1% cover (26 × 31 cm) was used. A few taxa were not possible to effectively separate in the field and are lumped at genus level or by the oldest name in species pairs, thus all *Bryum* sp. except *Bryum pseudotriquetrum* are treated as *Bryum* sp., *Calypogeia muelleriana* and *Calypogeia fissa* as *Calypogeia fissa*, *Chiloscyphus cuspidatus* and *Chiloscyphus latifolius* as *Chiloscyphus latifolius*, and finally *Plagiothecium curvifolium* and *Plagiothecium laetum* as *Plagiothecium laetum*.

Voucher specimens have been deposited at the herbaria OSC and UME. Primary data are stored at the Forest Science Laboratory Database (study TV036) at the Department of Forest Science, Oregon State University, Corvallis, Oreg.

Analysis of species composition

To explore potential relationships between species composition and the measured environmental variables, canonical correspondence analysis (CCA) was applied. This method is at present probably the most widely used gradient analysis technique and it is able to deal with many of the shortcomings of other techniques (e.g., CA, DCA; see Palmer 1993). After extraction of the canonical axes, the

Fig. 2. Habitat sketch of riparian forests with the geomorphic surfaces recognised in the study. The sketch also visualises changes in habitat features (cf. Tables 1 and 2) and loss of geomorphic surfaces with decreasing stream size.



significance of the fit between environmental variables and species composition was tested by an unrestricted Monte Carlo permutation test (ter Braak 1990). Forward selection of variables was performed and a total of 99 permutations was applied, giving a significance level of 1%. The influence of rare species was downweighted and species cover values log-transformed (using $y = \ln(10x + 1)$) prior to analysis. When analysing plots, sites were chosen as covariables to control for block effects. As elevation and stream size were correlated owing to the sampling design (larger streams absent at high elevations), the relative effects of elevation and stream size were partitioned by three separate runs of the CCA analysis. In these runs, the variables were used as covariables in the three possible combinations: elevation and stream size individually and jointly (see Borcard et al. 1992; Økland and Eilertsen 1994). The analysis was made using the program CANOCO, version 3.1 (ter Braak 1988, 1990).

Statistical procedures

As plots within sites were placed along a transect and not randomly, a subset of plots was chosen for the analysis of species richness patterns. The degree of spatial dependence among plots was tested by correlating the number of species in adjacent plots. The plots 1, 3, and 5 (separated by 2 m), and 6–10 (separated by 8 m) in each transect were thus chosen for the analysis ($N = 276$), as the number of species between adjacent plots showed only minor correlation ($R^2 < 5\%$). Although significant at the 5% level (owing to the large sample size), this correlation was presumed to be of negligible biological relevance. A significance level of $\alpha = 0.05$ and Pearsons product–moment correlation (Zar 1984) were used throughout the study.

Results

Riparian habitat conditions

Site level

Owing to the absence of larger streams at higher elevations, stream size and elevation are correlated. This complicates interpretation of the habitat structure data. However, a number of environmental variables changed over the stream size – elevation gradients (Table 1). Large streams at low elevation had higher canopy cover of deciduous trees and lower cover of conifers than small, high elevation streams. At higher elevations, the shrub cover tended to be higher than at low elevations. Larger streams had a less steep gradient and higher average cover of gravel than small streams (ranging from 7.6% cover in 1st order streams to 32.3% in 5th order ones).

The frequency of the different geomorphic surfaces varied among stream orders. In the smallest streams, the valley floor was narrow and developed stream terraces were more or less lacking, while the larger streams often had wide channels and well developed terraces (cf. Fig. 2).

Within sites

Several environmental factors changed with distance from the stream. Generally, increasing distance from the stream implied a loss of aquatic habitats and increasingly drier conditions. Imposed on this gradient were a number of structural changes. Cover of different vegetation layers changed from typically low vegetation cover near the stream to high cover of deciduous trees and herbs on stream terraces to higher dominance by conifers on the hillslope (Table 2). The apparently high cover of coniferous trees in the stream channel was associated with the narrow valley floor and lack of terraces in small streams implying nearly hillslope conditions close to the stream channel.

The abundance of different substrates also changed markedly with increasing distance from stream. Exposed sand, gravel, and boulders were most abundant on the valley floor

Table 1. Means (± SE) of site environmental variables by elevation classes and stream size.

	Basin area (ha)	Stream slope (%)	Conifers (%)	Deciduous trees (%)	Shrubs (%)	Herbs (%)
Elevation classes						
<600 (N = 15)	1590 (590)	9.1 (2.0)	47.3 (6.9)	37.6 (5.6)	15.1 (3.1)	25.6 (3.0)
600–800 (N = 12)	657 (230)	9.4 (2.3)	68.2 (4.5)	9.9 (3.8)	22.5 (6.1)	29.4 (3.9)
800–1000 (n = 9)	277 (91)	9.6 (1.1)	73.6 (6.0)	4.4 (6.5)	19.0 (3.5)	22.6 (4.0)
>1000 (N = 6)	119 (56)	9.2 (2.2)	62.1 (10.1)	17.5 (6.5)	37.1 (7.2)	28.1 (5.4)
Stream size						
1st order (N = 12)	23.2 (6.1)	16.9 (1.7)	68.7 (7.6)	10.1 (3.9)	23.6 (7.0)	28.7 (4.2)
2nd order (N = 12)	187 (32)	6.8 (1.0)	70.1 (3.3)	15.5 (4.4)	22.9 (4.0)	25.3 (3.1)
3rd order (N = 9)	468 (140)	9.1 (0.9)	62.6 (7.1)	15.9 (5.8)	17.0 (4.3)	25.0 (5.4)
4th order (N = 6)	1840 (320)	3.0 (0.4)	43.3 (6.5)	36.4 (8.3)	23.5 (5.5)	27.4 (3.3)
5th order (N = 5)	5710 (250)	2.0 (0.6)	25.1 (16)	52.5 (22)	12.7 (5.9)	23.8 (5.5)
Overall mean (SE)	831 (240)	9.3 (1.0)	61.0 (3.7)	19.7 (3.3)	21.2 (2.6)	26.4 (1.9)

Table 2. Percent cover (± SE) of vegetation layers and substrates on different geomorphic surfaces.

	Valley floor (N = 93)	Transition slope (N = 31)	Stream terrace (N = 55)	Hillslope (N = 181)
Vegetation layers				
Coniferous canopy	31.6 (3.9)	53.4 (6.0)	47.1 (5.3)	79.2 (1.9)
Deciduous canopy	28.3 (3.9)	22.7 (5.9)	43.6 (5.5)	10.6 (1.7)
Shrubs	15.8 (2.7)	25.9 (5.5)	23.7 (3.9)	21.6 (1.9)
Herbs	18.4 (2.6)	30.4 (4.2)	34.8 (3.6)	26.5 (1.9)
Bryophytes	32.4 (2.6)	51.6 (4.7)	41.0 (3.1)	45.4 (1.7)
Substrates				
Exposed soil	2.5 (1.1)	6.4 (2.8)	1.4 (1.6)	1.1 (0.3)
Sand	9.5 (1.2)	0.9 (0.5)	0.4 (0.4)	0.0 (—)
Gravel	45.4 (3.4)	6.7 (2.4)	0.5 (0.3)	0.1 (0.0)
Boulders	14.1 (2.1)	4.6 (2.4)	0.4 (0.3)	0.5 (0.2)
Debris	2.9 (0.7)	2.8 (0.9)	7.5 (1.9)	4.6 (0.7)
Coarse woody debris	9.3 (1.6)	6.6 (2.0)	17.2 (2.6)	9.7 (0.9)

Note: "Valley floor" includes the stream channel, active channel, and the flood plain, while "Hillslope" includes both hillslope plots and toeslope plots (cf. Fig. 2). Values are means grouped by stream order to compensate for different number of samples in different stream orders.

surfaces, whereas debris and coarse woody debris were most abundant on stream terraces. Exposed soil was most abundant in transition slopes (Table 2).

Species richness patterns

A total of 128 taxa (Appendix 1) was found in the 360 samples. The average number of species per plot was 16 (range 1–40) while, on average, 43 species (range 23–59) occurred at each site. All major bryophyte groups except peat mosses (*Sphagnum* spp.) were represented. The most common species was the forest floor pleurocarp *Eurhynchium oreganum*, which had a mean cover of 15.6% and occurred in 89% of all plots. The second most common species was the predominantly epiphytic *Isothecium stoloniferum* with a mean cover of 4.8% and a frequency of 87%. Other frequent species were *Hypnum circinale*, *Dicranum fuscescens*, and *Scapania bolanderi* all occurring in more than two thirds of the plots.

Site level

At the site level, both site factors and plot factors were related to species richness (Table 3). Small streams with steep profiles and sites with high cover of conifers showed lower species richness, while sites with abundant gravel and boulders had higher species richness. The lower number of samples in 1st order streams (5 compared with 10 in 2nd to 5th order streams) might have increased the apparent difference between small and large streams. However, examination of the species–area relationship showed that the average cumulative number of species increased only by 0.7 species between the fourth (mean 32.5 species) and the fifth sample plot (mean 33.2 species) in 1st order streams. Thus, additional samples in 1st order streams would not significantly change the overall pattern. There was no significant correlation between elevation and species richness based on pooled data for whole sites. However, for the valley floor, there was a significant increase in species richness with elevation (Table 4).

Within sites

At the sample plot level, species richness varied with the changes in habitat structure related to increasing distance from stream. Thus, species richness was positively correlated with the abundance of sand, boulders, and canopy cover of deciduous trees, while height above and distance

Table 3. Correlation coefficients between species richness and environmental variables at the site and plot level.

	Sites (N = 42)	Plots (N = 276)
Site level		
Elevation	−0.12	−0.01
Basin area	0.34*	−0.01
Aspect	0.12	−0.09
Stream slope	−0.51*	0.05
Plot level		
Canopy cover conifers	−0.33*	−0.27*
Canopy cover deciduous	0.14	0.22*
Shrub cover	0.07	0.01
Herb cover	0.02	0.04
Soil	−0.12	0.09
Sand	0.14	0.37*
Gravel	0.32*	0.11
Boulders	0.43*	0.16*
Debris	0.03	0.06
Coarse woody debris	0.07	0.32*
Distance from stream		−0.32*
Height above stream		−0.33*

Note: *, significant at $p < 0.05$. Averaged values of sample plot environmental variables are used in the correlation between species richness and environment at the site level.

Table 4. Correlation coefficients between species richness in plots grouped by geomorphic surfaces and site variables.

	Valley floor (N = 93)	Transition slope – toeslope (N = 94)	Hillslope (N = 173)
Elevation	0.26*	−0.07	−0.04
Basin area	−0.46*	−0.01	0.13
Aspect	−0.15	−0.11	−0.04
Stream slope	0.31*	−0.09	0.05

Note: *, significant at $p < 0.05$.

from stream as well as canopy cover of conifers were negatively correlated to species richness (Table 3). Species richness strongly varied between different geomorphic surfaces (Fig. 3), with the highest richness observed on floodplains. In addition to the variables related to distance from stream, richness was positively correlated with abundance of coarse woody debris (Table 3).

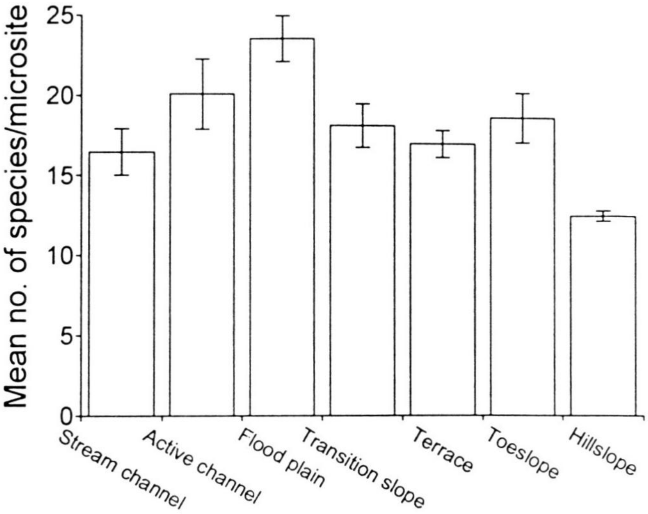
No site level factors were significantly correlated with species richness at the plot level (Table 3). Although the mean number of species per plot was significantly correlated with the total number of species at the site (R = 0.44, p < 0.05, N = 42), only 19% of the variation in species richness on the plot level could be explained by the total site richness.

Species composition

Site level

Five of the measured environmental variables were chosen by the forward selection procedure in the CCA analysis (Table 5), and together they explained 28.3% of the variation (across all axes) in species composition at the site level (Table 6). The first ordination axis was strongly correlated with elevation, while the second axis mainly reflected the stream size gradient (Fig. 4a). Variance partitioning showed that elevation and stream size explained 19.9% of the variation combined, while their individual contributions were 12.9% for elevation and 8.4% for stream size. Thus, only 1.4% of the variation was attributed to overlap between elevation and stream size effects. This indicates that the relationship between these two major variables is primarily orthogonal. The correlation of boulders and canopy cover of conifer with the second axis mainly relates to their specific occurrence on the stream size gradient. The third axis is more complex and includes effects of herb cover, boulders, and canopy cover of conifers (Fig. 4b). Although they show a roughly orthogonal relationship with both stream size and elevation on the first axis, many other environmental variables are correlated with these, hampering evaluation of their individual importance. There was no apparent pattern in the occurrence of different types of species, as all species groups were widely distributed in the ordination space.

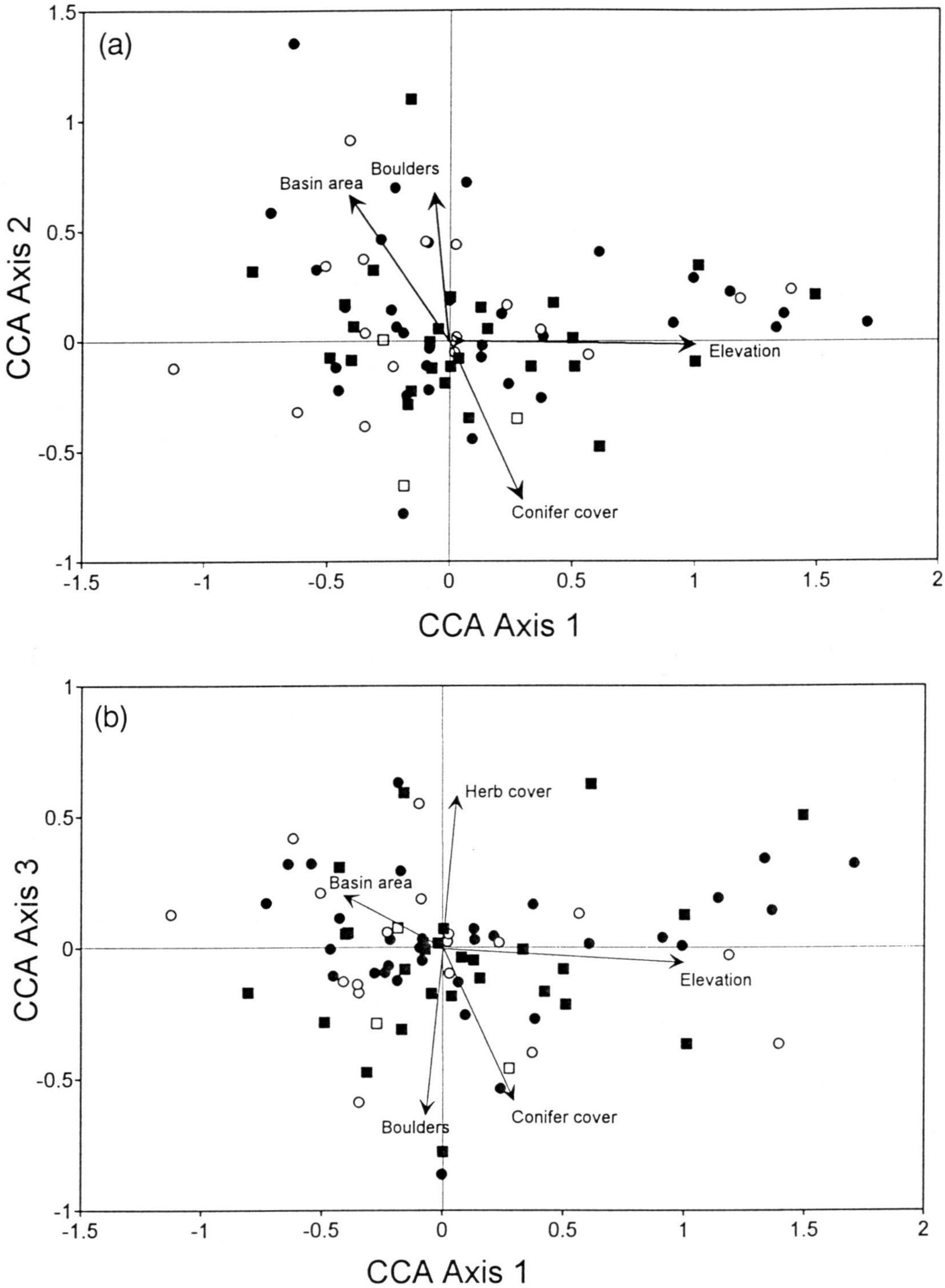
Fig. 3. Species richness (mean ± SE) in different geomorphic surfaces.



Within sites

Nine variables were chosen by the forward selection procedure in the CCA analysis (Table 7), and together they explained 13.6% of the total variation in species composition at the plot level (Table 6). The effect of sites as covariables in the analysis was large and explained 25.5% of the variation. Both the first and second axes in the ordination relate to variables associated with distance from stream. Thus, valley floor features such as gravel, boulders, stream channel, and sand were positively correlated with the first axis, while the geomorphic surfaces above the valley floor separated on the second axis. Of these, hillslope and height above the stream channel were positively correlated with the second axis, while terraces showed negative correlation with the second axis (Fig. 5a). The third axis clearly represented abundance of coarse woody debris (Fig. 5b). As at site level, species responses along the gradients appear largely individualistic and none of the species groups were confined to any particular region in the ordination space.

Fig. 4. Species ordination diagram from the Canonical Correspondence Analysis based on sites (stream transects, $N = 42$) for (*a*) the first and second ordination axes and (*b*) the first and third axes. Biplot vectors are included for significant environmental variables, where the length and direction correspond to the strength of the correlation with the ordination axes. ●, pleurocarpous moss; ○, acrocarpous moss; □, thallose hepatic; ■, leafy hepatic. Rare species are not plotted.



Species distributions along site gradients

The importance of the major gradients in the studied system (elevation, stream size, and distance from stream) is further emphasised by the distinctive occurrence of many species over these gradients (Fig. 6). A number of species could be characterised as either high or low elevation species. Thus, abundant species as *Rhytidiadelphus triquetrus*, *Porella navicularis*, and *Neckera douglasii* had their main occurrence at low elevation. In contrast, *Rhytidiopsis robusta*, *Heterocladium macounii*, and *Ptilidium californicum* were high elevation species.

Some species typical of higher geomorphic surfaces, such

Table 5. Correlation coefficients (inter-set correlations) between environmental variables selected by the forward selection procedure and the first three axes in the CCA analysis of site data (pooled data from plots, $N = 42$).

		Correlation coefficient		
Variable	Selected	Axis 1	Axis 2	Axis 3
Elevation	1st	0.923	−0.003	−0.162
Basin area	2nd	−0.378	0.557	0.116
Boulders	3rd	−0.068	0.512	0.058
Coniferous canopy cover	4th	0.263	−0.586	−0.357
Herb cover	5th	0.084	−0.078	0.621
Species−environment correlation		0.938	0.886	0.857

Table 6. Cumulative percentage variation explained by the first four axes in the CCA analysis of sites ($N = 42$) and plots ($N = 360$).

	Axis 1	Axis 2	Axis 3	Axis 4	Total
Sites	12.9	19.1	22.5	25.6	28.3
Plots	8.5	10.4	11.5	12.0	13.6

Note: At the plot level, sites were treated as covariables and explained additionally 25.5% of the variation at the plot level.

as *Ptilidium californicum* and *Pseudotaxiphyllum elegans*, had their major occurrence on hillslopes along small streams. Most of the aquatic species, however, were more abundant in medium to large streams than in small (e.g., *Hygrohypnum ochraceum*, *Scelorpodium obtusifolium*, *Chiloscyphus polyanthos*, *Racomitrium aciculare*). Exceptions from this pattern were *Fontinalis neomexicana* and *Fissidens ventricosus*, which mainly occurred in 1st order streams. Only a few species were strongly associated with hillslope conditions, of which *Trachybryum megaptilum* was the only abundant species.

Discussion

The present study demonstrates significant changes in riparian bryophyte species richness and composition along several environmental gradients. These gradients occur both within sites (e.g., distance from stream, occurrence of boulders, deciduous stems, and coarse woody debris) as well as between sites (elevation and stream size) on a landscape scale. Thus, the bryophyte vegetation varies among different types of streams and the total diversity of this plant group is not represented in a single or a few stream types. These results are in accordance with other studies of riparian bryophytes that have shown that site factors, such as elevation, stream flow, and bedrock, as well as within-site factors, such as height above water level and substrate types, are all important niche parameters for individual species and influence the overall community structure (Slack and Glime 1985; Vitt et al. 1986; Glime and Vitt 1987).

Within-site patterns

Distance from the stream is a complex gradient that is likely to be composed of a number of more or less interrelated gradients. Available substrate types, microclimate, disturbance patterns, vascular plant composition, and small-scale topography vary in many cases dramatically between different geomorphic surfaces (Gregory et al. 1991; Table 2). It is thus not surprising that changes in the bryophyte community along this gradient also are pronounced. The present study was not primarily designed to estimate the relative role of these different factors. However, the ecology of the bryophytes and the dynamics of riparian zones suggest some causal factors.

Disturbance

Disturbance plays a major role in structuring riparian vegetation (Vannote et al. 1980; Kimmerer and Allen 1982; Nilsson 1987). The disturbance regime in streams is complex and ranges from constant small-scale disturbance in the stream channel to destructive debris flows caused by large-scale but infrequent flooding events. Flowing water in the stream is a factor that can restrict the occurrence of species lacking adaptations to high flow (Vitt and Glime 1984). Small steep streams in the study area exhibit high water velocities and relatively large fluctuations in water level, whereas the larger streams at lower elevations have a more constant flow but lower velocity. Such differences represent important niche parameters among stream bryophytes (Slack and Glime 1985; Glime and Vitt 1987). In the present study, several rheophilous species (sensu Vitt and Glime 1984) were present but their affinity to stream size varied. Thus, species like *Fissidens ventricosus* and *Fontinalis neomexicana* occurred mainly in small streams, whereas *Hygrohypnum ochraceum* and *Chiloscyphus polyanthos* dominated in larger ones (cf. Fig. 6). To what extent their occurrences are related to flow patterns in different sized streams or to other environmental factors is open to further investigation.

The effects of flooding are most severe in the valley floor but extend up to the stream terraces and comprise effects of inundation, bank cutting, surface scarring, and deposition of both inorganic sediments and different sized organic matter (Gregory et al. 1991). Thus, despite the overall terrestrial conditions on terraces, dominant forest floor species, such as *Eurhynchium oreganum* and *Trachybryum megaptilum*, do not achieve the same high dominance as on more stable hillslopes. Instead, the ground vegetation is generally diverse on stream terraces and floodplains, and is constituted of both hillslope species and species like *Leucolepis acanthoneuron*, *Conocephalum conicum*, *Eurhynchium praelongum* var.

Table 7. Correlation coefficients (inter-set correlations) between environmental variables selected by the forward selection procedure and the first three axes in the CCA analysis of plot data (2 × 4 m plots, N = 360) with sites as covariables.

		Correlation coefficient		
Variable	Selected	Axis 1	Axis 2	Axis 3
Gravel	1st	0.773	0.129	0.045
Hillslope	2nd	−0.538	0.459	−0.035
Boulders	3rd	0.597	0.040	−0.014
Coarse woody debris	4th	−0.142	−0.061	0.517
Stream channel	5th	0.595	0.037	0.156
Height above stream	6th	−0.494	0.420	−0.056
Terrace	7th	−0.248	−0.245	−0.050
Sand	8th	0.450	−0.113	0.207
Shrub cover	9th	−0.156	−0.092	−0.147
Species−environment correlation		0.869	0.665	0.600

stokesii, and *Plagiomnium insigne*, which are rare or absent on the dry and stable hillslopes. These patterns could be viewed as an example of intermediate levels of disturbance coinciding with high diversity (Connell 1978; Kimmerer and Allen 1982). The central part of the stream is exposed by continuous and severe disturbance by the fast flowing turbulent water, while the upslope conditions is characterised by much higher stability. The peak in richness occurs on areas where flooding is less severe than in the stream channel but frequent enough to expose patches of bare soil (cf. Table 2) and thus reduce the dominance of competitively strong species. The bryophyte community seems, thus, to parallel the vascular plants which show highest diversity on floodplains (Gregory et al. 1991) and at intermediate stream velocity (Nilsson 1987).

Substrate affinity

Substrate affinity is pronounced among many bryophytes. Thus changes with distance from stream in abundance of substrates such as boulders, exposed soil, coarse woody debris, and deciduous trees contributed to the changes in bryophyte richness and composition on different geomorphic surfaces. The role of coarse woody debris is particularly noticeable by its correlation to the third axis in the ordination (cf. Fig. 5*b*) and the significant correlation with sample plot diversity (Table 3). A fairly large number of species were strictly epixylic (e.g., *Blepharostoma trichophylla*, *Jungermannia leiantha*, *Scapania umbrosa*, and *Buxbaumia piperi*) or had their major occurrence on wood (e.g., *Scapania bolanderi*, *Hypnum circinale*, and *Dicranum fuscescens*). Of all species, more than 40% of the hepatics and almost 20% of the mosses clearly preferred decaying wood. Although no specific data were collected, it was clear that the epixylic flora was best developed on medium to highly decayed logs relatively close to the streams. Thus, the results support the hypothesis that woody debris has a key role in maintaining biodiversity in forests (Harmon et al. 1986; Söderström 1988; Esseen et al. 1992; Samuelsson et al. 1994; Bader et al. 1995) and riparian ecosystems (Sedell et al. 1988; Naiman et al. 1992).

Several epiphytic species were frequent and contributed significantly to both abundance and species richness in the bryophyte community. The host specificity varied with some species ubiquitous (e.g., *Isothecium stoloniferum*, *Antitrichia curtipendula*) while some mainly occurred on deciduous trees (e.g., *Radula complanata*, *Orthotrichum speciosum*). This pattern probably contributed to the higher species richness on the stream terraces, where the deciduous tree layer was best developed.

Between-site patterns

Two major gradients, stream size and elevation, strongly influenced the between-site patterns. Both of these were correlated with other environmental variables and with each other. The separate importance of both gradients is, however, indicated by the fact that only stream size was correlated with species richness and by their orthogonal relationship in the ordination analysis.

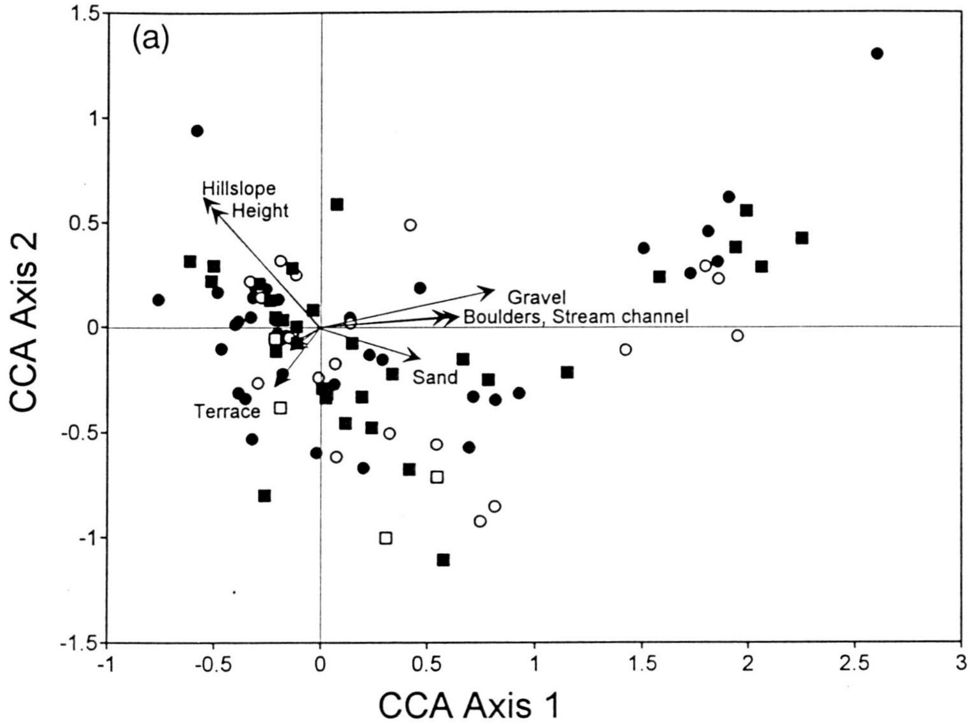
Stream size gradient

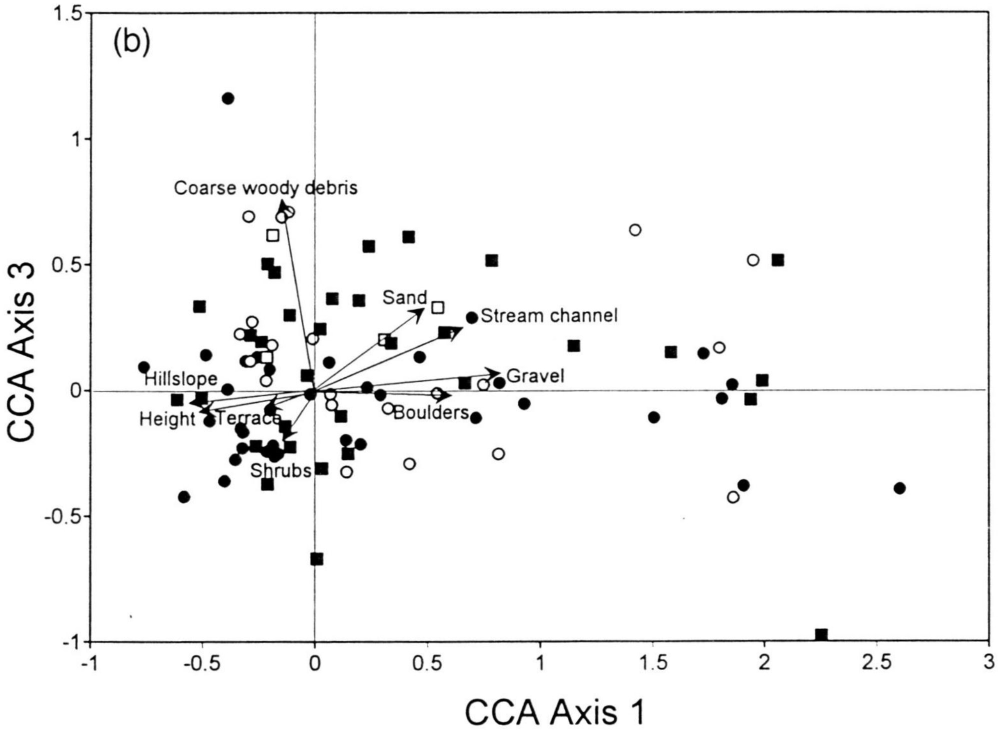
Stream size is presumed to be a major factor influencing vegetation composition along and among streams (Vannote et al. 1980; Naiman et al. 1987; Nilsson et al. 1991, 1994). It is, however, not necessarily size per se that causes this difference, but rather the specific structures and processes that occur in different sized streams (Osterkamp and Hupp 1984; Hupp and Osterkamp 1985). This seems to be in accordance with the results of the present study. The increase in species richness and changes in composition in the larger streams is associated with increased amount of substrates, such as boulders and deciduous trees, and the occurrence of well developed floodplains and stream terraces. In the smaller streams, typical hillslope conditions (i.e., high canopy cover of conifers, low abundance of boulders, gravel, and coarse woody debris) extended down to the stream channel. However, the largest sampled portion of Lookout Creek is only a 5th order stream and the patterns of species richness and composition of larger streams might be different. Especially the species−area relationships might change, as the number, width, and complexity of geomorphic surfaces increase in larger streams.

Elevation gradient

Contrasting data exist considering species richness and elevation from the AEF. J. Peck, S.A. Acker, and W.A.

Fig. 5. Species ordination diagram from the Canonical Correspondence Analysis based on sample plots (N = 360, 2 × 4 m plots in the 42 sites) for (*a*) the first and second ordination axes and (*b*) the first and third axes. Biplot vectors are included for significant environmental variables, where the length and direction correspond to the strength of the correlation with the ordination axes. Symbols as in Fig. 4. Rare species are not plotted.





McKee, in preparation, studied bryophytes on logs, tree bases and the forest floor of upland sites, and found decreasing richness with altitude. Considering vascular plant species, the most diverse upland communities occurred either at low elevation hot, dry sites or upper elevation moist sites, whereas sites at medium elevations showed lower species richness (Zobel et al. 1976). In the present case, there was no clear relationship between species richness and elevation either on the site level or generally within sites (cf. Table 3). Separate analysis of the geomorphic surfaces revealed that

Fig. 6. Distribution of individual species over the major environmental gradients, (*a*) elevation, (*b*) stream size, and (*c*) geomorphic surfaces representing increasing distance from stream. Species are ordered according to their position on the gradient by a weighted mean procedure.

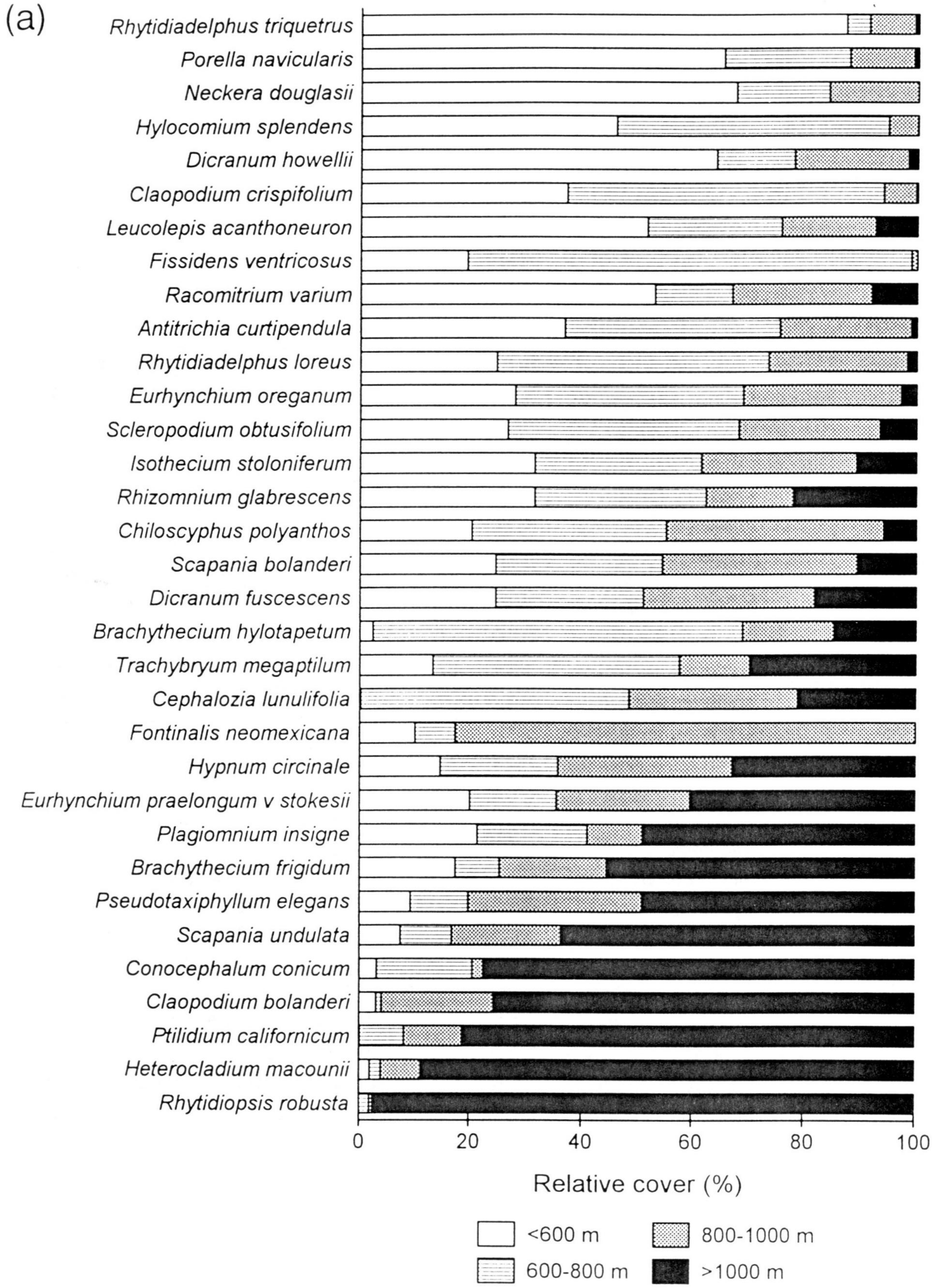


Fig. 6 (*continued*).

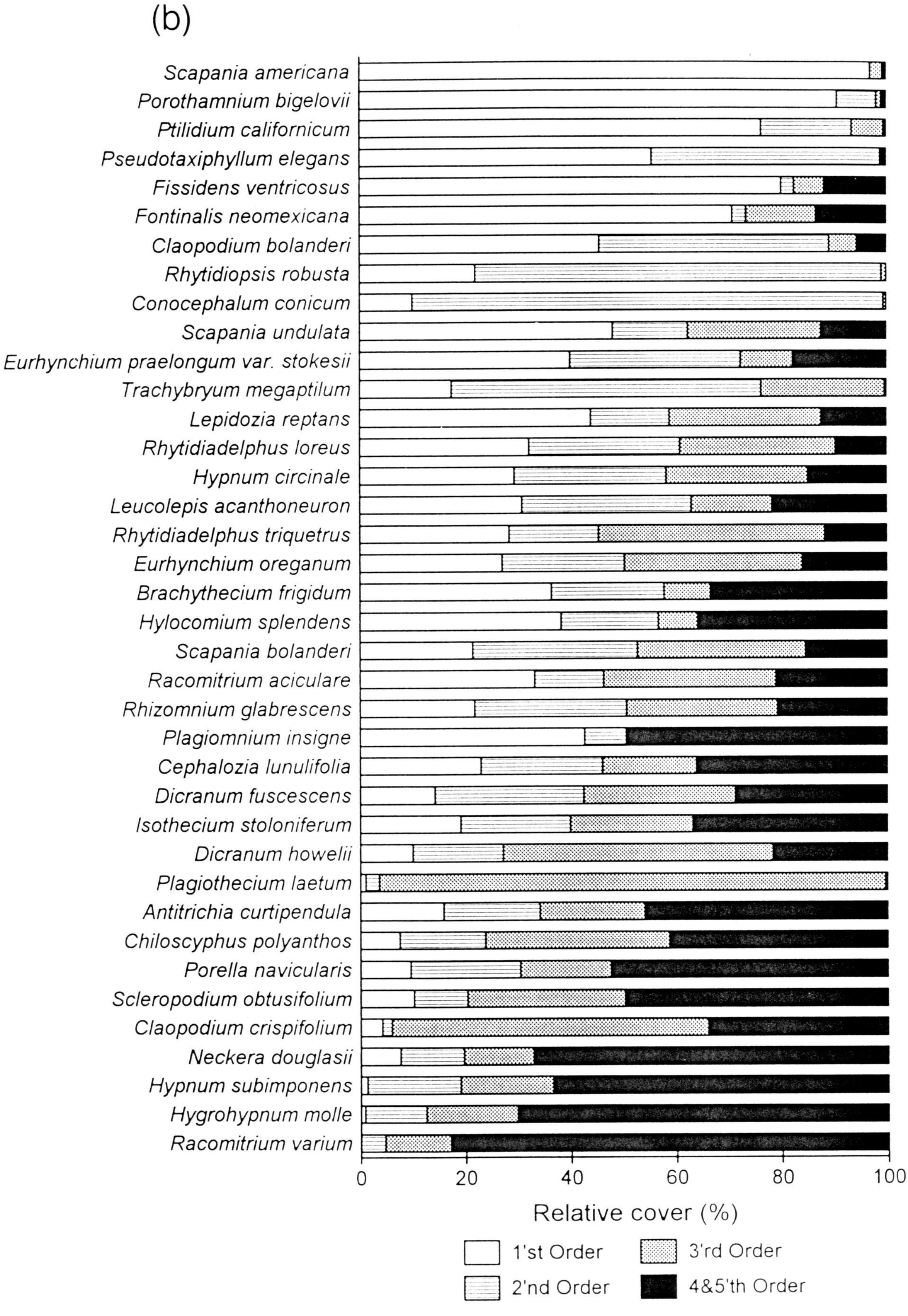
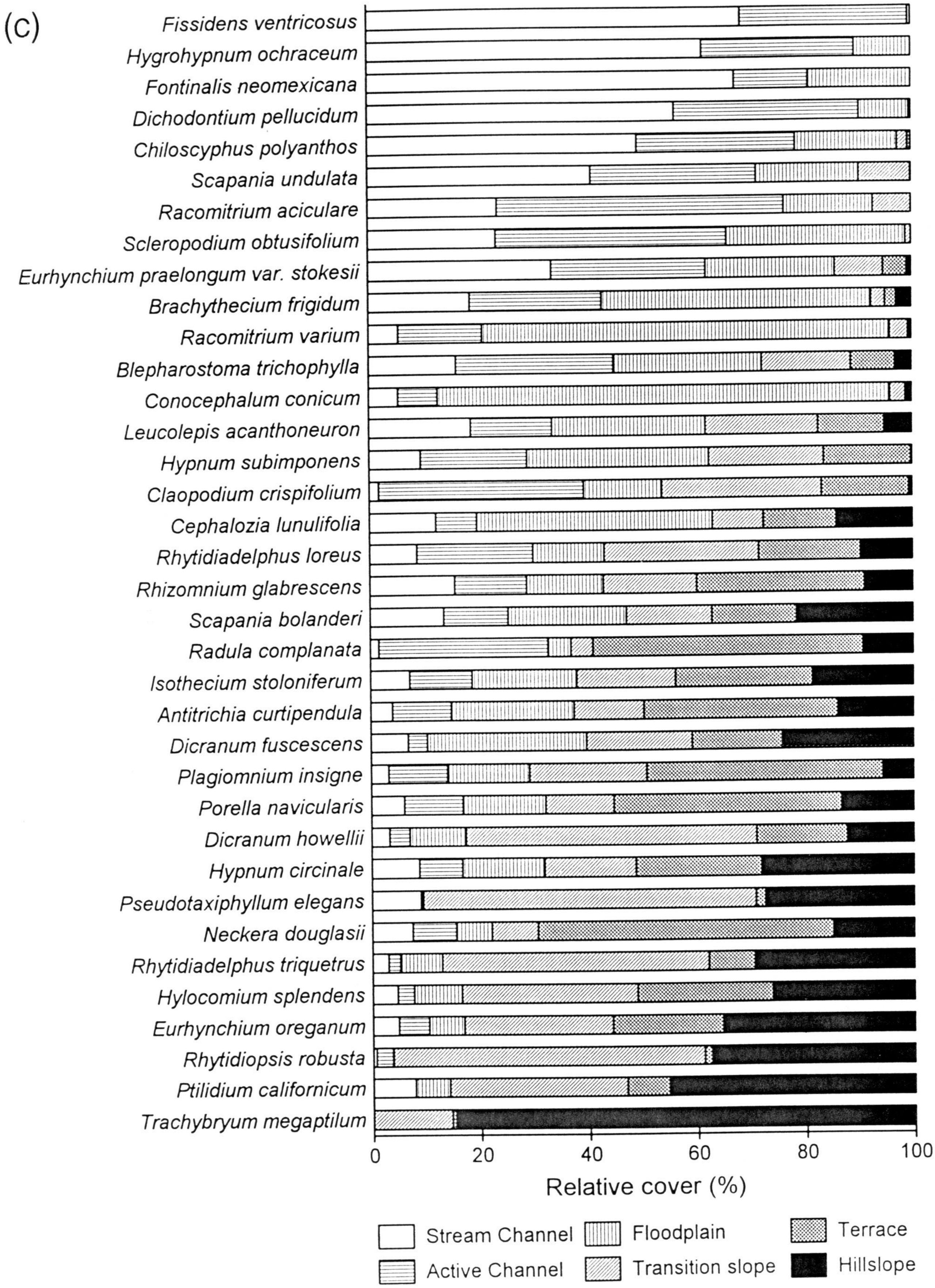


Fig. 6 (*concluded*).



there was a positive correlation between species richness and elevation for the valley floor (cf. Table 4). However, the cause of this pattern is most likely a sampling artefact owing to the condensed nature of the riparian zonation in small streams (over-represented at high elevations) with overlapping vegetation zones within single 2 × 4 m plots. This will cause an apparent increase in species richness in stream plots at higher elevations.

Elevation was the single most important variable associated with species composition at the site level (cf. Fig. 4*a*, 6*a*). This gradient is as complex as the stream size gradient. Several of the measured environmental variables showed correlation with elevation (i.e., canopy cover of deciduous and coniferous trees and shrubs, bryophyte and debris cover; cf. Table 1). In addition, snowpack depth and duration and growing season, as well as microclimate variation, change over the gradient (Zobel et al. 1976; Bierlmaier and McKee 1989). The lower abundance of deciduous trees at higher elevations contributed to the change in species composition. This is exemplified by *Porella navicularis*, which is a common epiphyte on deciduous trees at low elevations, and *Ptilidium californicum*, which is a common conifer epiphyte at higher altitudes.

However, the change in species composition was mostly connected with species replacing each other over the elevation gradient. This occurred among forest floor species (*Rhytidiadelphus triquetrus*, *Hylocomium splendens*, and *Eurhynchium oreganum* being replaced by *Rhytidiopsis robusta* at high elevation), species with affinity to floodplains (*Leucolepis acanthoneuron* being replaced by *Brachythecium frigidum* and *Conocephalum conicum*), and aquatic species (*Fissidens ventricosus* being replaced by *Scapania undulata*). The strong elevational separation of the cogeneric *Claopodium crispifolium* (low elevations) and *Claopodium bolanderi* (high elevations), both growing on boulders, decaying wood, and tree stems, is also notable. Whether these patterns occur because of different microclimatic demands or as a consequence of competition is of interest and merits further studies.

Scale issues

In an analysis of riparian vegetation in Colorado, Baker (1989) showed that different macro- and micro-scale variables operated in different regions. The conclusion drawn from these results suggests that simple general relationships might not be present to explain the community structure in riparian vegetation. Instead, patterns in one spatial scale or location may be caused by factors unimportant at other scales and sites. The present study supports this complexity of causal factors. The environmental variables correlated with species richness and composition differed between the plot and site level. In addition, the response variables, richness and composition, themselves were influenced by different environmental variables. Thus, the results indicate that management of riparian vegetation must be based on a hierarchical approach that spans from coarse scale considerations such as stream sizes and elevation to fine scale stand structures, such as abundance of coarse woody debris and tree species composition. This is necessary if the goals are to preserve both overall biodiversity as well as to protect rare bryophyte species.

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Appendix 1. Mean cover and frequency of bryophytes in riparian forests

	Frequency (%)		
	Plot $N = 360$	Sites $N = 42$	Cover (%)
Pleurocarpous mosses			
Eurhynchium oreganum (Sull.) Jaeg.	88.6	100.0	15.60
Isothecium stoloniferum Brid.	86.7	97.6	4.77
Hypnum circinale Hook.	76.9	69.0	2.00
Antitrichia curtipendula (Hedw.) Brid.	53.9	97.6	0.43
Rhytidiadelphus triquetrus (Hedw.) Warnst.	35.6	76.2	1.67
Neckera douglasii Hook.	34.2	100.0	0.24
Eurynchium praelongum var. *stokesii* (Turn.) Dix.	33.9	35.7	1.42
Hylocomium splendens (Hedw.) Schimp.	25.6	73.8	2.56
Rhytidiadelphus loreus (Hedw.) Warnst.	18.9	95.2	0.42
Brachythecium frigidum (C. Müll.) Besch.	17.8	61.9	0.37
Scleropodium obtusifolium (Jaeg.) Kindb.	17.2	73.8	0.71
Pseudotaxiphyllum elegans (Brid.) Iwats.	16.9	76.2	0.15
Hypnum subimponens Lesq.	16.9	50.0	0.14
Claopodium bolanderi Best	15.6	66.7	0.11
Rhytidiopsis robusta (Hook.) Broth.	14.4	52.4	1.10
Claopodium crispifolium (Hook.) Ren. & Card.	13.9	33.3	0.24
Hygrohypnum ochraceum (Turn. ex Wils.) Loeske	11.4	52.4	0.10
Homalothecium nuttallii (Wils.) Jaeg.	10.8	59.5	0.03
Claopodium whippleanum (Sull.) Ren. & Card.	9.4	33.3	0.04
Porothamnium bigelovii (Sull.) Fleisch.	8.6	19.0	0.07
Brachythecium hylotapetum B. Hig. & N. Hig.	7.8	42.9	0.08
Plagiothecium laetum Schimp.*	7.8	28.6	0.02
Lescuraea stenophylla (Ren. & Card.) Kindb.	7.5	47.6	0.02
Heterocladium macounii Best	6.4	38.1	0.05
Trachybryum megaptilum (Sull.) Schof.	5.8	14.3	0.11
Fontinalis neomexicana Sull. & Lesq.	4.7	2.4	0.07
Scleropodium tourettii (Brid.) L. Koch	4.7	16.7	0.01
Plagiothecium undulatum (Hedw.) Schimp.	2.8	40.5	0.03
Brachythecium velutinum (Hedw.) Schimp.	2.8	31.0	0.02
Heterocladium procurrens (Mitt.) Jaeg.	2.2	7.1	t
Homalothecium fulgescens (Mitt. Ex C. Müll) Lawt.	1.7	28.6	0.01
Brachythecium oedipodium (Mitt.) Jaeg.	1.7	9.5	0.01
Plagiothecium cavifolium (Brid.) Iwats.	1.1	4.8	0.02
Thamnobryum neckeroides (Hook.) Lawt.	1.1	4.8	0.01
Plagiothecium denticulatum (Hedw.) Schimp.	1.1	11.9	t
Isothecium cristatum (Hampe) Robins.	0.8	16.7	0.01
Metaneckera menziesii (Hook.) Steere	0.6	9.5	0.01
Brachythecium leibergii Grout	0.3	2.4	t
Heterocladium dimorphum (Brid.) Schimp.	0.3	2.4	t
Hygrohypnum dilatatum (Wils.) Loeske	0.3	2.4	t
Isopterygiopsis pulchella (Hedw.) Iwats.	0.3	2.4	t
Pterigyandrum filiforme Hedw.	0.3	2.4	t
Acrocarpous mosses			
Dicranum fuscescens Turn.	68.1	88.1	1.02
Rhizomnium glabrescens (Kindb.) T.Kop.	56.9	97.6	1.20
Dicranum howellii Ren. & Card.	36.7	97.6	0.95
Leucolepis acanthoneuron (Schwaegr.) Lindb.	35.6	71.4	1.46
Plagiomnium insigne (Mitt.) T.Kop.	26.7	78.6	0.83
Dicranum tauricum Sapeh.	25.0	38.1	0.05
Orthotrichum speciosum Nees	14.4	45.2	0.01
Racomitrium aciculare (Hedw.) Brid.	11.1	31.0	0.11
Dichodontium pellucidum (Hedw.) Schimp.	9.7	4.8	0.05

Appendix 1 (*continued*).

	Frequency (%) Plot N = 360	Frequency (%) Sites N = 42	Cover (%)
Racomitrium varium (Mitt.) Jaeg.	8.9	64.3	0.20
Mnium spinulosum Bruch & Schimp.	6.9	61.9	0.03
Aulacomium androgynum (Hedw.) Schwaegr.	6.9	21.4	0.01
Atrichum selwynii Aust.	5.6	28.6	0.02
Plagiomnium rostratum (Schrad.) T.Kop.	5.0	4.8	0.05
Fissidens ventricosus Lesq.	4.7	28.6	0.08
Tetraphis pellucida Hedw.	4.2	14.3	0.01
Bryoerythrophyllum recurvirostre (Hedw.) Chen	2.2	11.9	0.01
Roellia roelii (Broth.) Andr.	2.2	54.8	t
Fissidens bryoides Hedw.	2.2	35.7	t
Racomitrium heterostichum s.l. (Hedw.) Brid.	1.9	14.3	0.07
Polytrichum juniperinum Hedw.	1.9	21.4	0.02
Rhizomnium magnifolium (Horik.) T.Kop.	1.9	9.5	0.02
Bryum spp.	1.9	7.1	t
Orthotrichum rivulare Turn.	1.7	9.5	0.01
Scouleria aquatica Hook.	1.4	4.8	0.01
Hookeria lucens (Hedw.) Sm.	1.4	7.1	t
Racomitrium occidentale (Ren & Card.) Ren. & Card.	1.1	14.3	t
Racomitrium canescens s.l. (Hedw.) Brid	0.8	11.9	0.03
Buxbaumia piperi Best	0.8	9.5	t
Polytrichum lyalii (Mitt.) Kindb.	0.8	7.1	t
Schistidium rivulare (Brid.) Podp.	0.8	7.1	t
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	0.6	4.8	t
Dicranoweisia cirrata (Hedw.) Lindb.	0.6	4.8	t
Ditrichum montanum Leib.	0.6	2.4	t
Philonotis fontana (Hedw.) Brid.	0.6	4.8	t
Blindia acuta (Hedw.) Bruch & Schimp.	0.6	4.8	t
Mnium lycopodioides Schwaegr.	0.3	2.4	t
Orthotrichum affine Brid.	0.3	2.4	t
Orthotrichum lyellii Hook. & Tayl.	0.3	2.4	t
Pohlia cruda (Hedw.) Lindb.	0.3	2.4	t
Pohlia nutans (Hedw.) Lindb.	0.3	2.4	t
Leafy hepatics			
Scapania bolanderi Aust.	70.8	100.0	1.20
Cephalozia lunulifolia (Dum.) Dum.	58.3	95.2	0.41
Porella navicularis (Lehm. & Lindenb.) Pfieff.	55.0	81.0	0.28
Scapania umbrosa (Schrad.) Dum.	38.1	92.9	0.08
Blepharostoma trichophyllum (L.) Dum.	36.9	78.6	0.11
Chiloscyphus profundus (Nees) Engel & Schust.	35.0	64.3	0.04
Radula bolanderi Gott.	24.2	90.5	0.02
Ptilidium californicum (Aust.) Underw.	22.8	61.9	0.18
Radula complanata (L.) Dum.	18.6	92.9	0.07
Scapania undulata (L.) Dum.	18.3	59.5	0.26
Lepidozia reptans (L.) Dum.	18.3	54.8	0.11
Chiloscyphus polyanthos (L.) Corda	18.1	19.0	0.34
Calypogeia fissa (L.) Raddi[†]	13.1	90.5	0.01
Frullania nisquallensis Sull.	12.8	73.8	0.01
Geocalyx graveolens (Schrad.) Nees	9.7	38.1	0.02
Plagiochila porelloides (Nees) Lindenb.	9.4	45.2	0.05
Cephalozia bicuspidata (L.) Dum.	9.4	9.5	0.02
Scapania americana K. Muell.	4.7	14.3	0.04
Chiloscyphus latifolius (Nees) Engel. & Schust.[‡]	4.4	57.1	t
Jungermannia leiantha Grolle	4.2	47.6	t
Cephaloziella rubella (Nees) Warnst.	3.3	21.4	0.01

Appendix 1 (*concluded*).

	Frequency (%)		
	Plot N = 360	Sites N = 42	Cover (%)
Porella cordeana (Hueb.) Moore	3.3	19.0	t
Douinia ovata (Dicks.) Buch	2.8	21.4	0.01
Lophozia incisa (Schrad.) Dum.	2.8	11.9	t
Jungermannia exsertifolia ssp. *cordifolia* (Dum.) Vana	2.2	11.9	0.02
Frullania californica M.A. Howe	2.2	26.2	t
Lophozia longiflora (Nees) Schiffn.	2.2	14.3	t
Chiloscyphus pallescens (Hoffm.) Dum.	1.9	21.4	t
Calypogeia azurea Stotler & Crotz	1.4	16.7	t
Jungermannia pumila With.	1.4	2.4	t
Marsupella emarginata (Erhr.) Dum.	1.1	9.5	0.02
Blepharostoma arachnoideum M.A. Howe	1.1	9.5	t
Cephaloziella divaricata (Sm.) Schiffn.	1.1	7.1	t
Plagiochila asplenoides (L.) Dum.	0.3	9.5	t
Anastrophyllum sp.	0.3	2.4	t
Asterella sp.	0.3	2.4	t
Frullania bolanderi Aust.	0.3	2.4	t
Gymnocolea inflata (Huds.) Dum.	0.3	2.4	t
Jamesoniella autumnalis (DC.) Steph.	0.3	2.4	t
Thallous hepatics			
Riccardia latifrons (Lindb.) Lindb.	8.3	23.8	0.03
Riccardia multifida (L.) S. Gray	5.8	33.3	0.03
Conocephalum conicum (L.) Lindb.	4.7	38.1	0.12
Pellia neesiana (Gott.) Limpr.	1.7	11.9	0.01
Marchantia polymorpha L.	0.3	2.4	t
Riccardia palmata (Hedw.) Carruth.	0.3	2.4	t

Note: Species are in order by decreasing frequency within each group. A "t" denotes a mean cover of less than 0.01%.

*, includes *Plagiothecium curvifolium* Limpr.

†, includes *Calypogeia muelleriana* (Schiffn.) K. Müll.

‡, includes *Chiloscyphus cuspidatus* (Nees) Engel & Schust.