Niche Relationships of Mountain Stream Bryophytes
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relatively homogeneous lead concentrations. However, it is also apparent from our results that rates of lead accumulation can be accurately measured by sampling thallus portions of different age.

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Niche Relationships of Mountain Stream Bryophytes

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Abstract. *Bryophyte community structure was studied in ten streams in the Adirondack Mountains of New York and adjacent areas over an elevation range of 625 m. Species composition, including frequency and cover and possible niche parameters including elevation, water temperature, pH, flow rate, incident light, substrate type and height above or depth below water level were measured. An ordination was done of the ten streams, and species diversity, niche breadth and niche overlap were calculated. Elevation and stream flow were important for niche separation between streams. Height and type of substrate including rock size were important niche parameters within streams. Characteristic height segregation was seen within streams for many species including several co-occurring members of the Brachytheciaceae and two morphological forms of* Hygrophypnum ochraceum. *The communities included 28 mosses, seven hepatics and one aquatic lichen.*

It is advantageous to be able to test interactions within a group of bryophytes in a habitat dominated by bryophytes. Many habitats fill this requirement, but few have been studied in terms of community structure. Forest floor communities (Slack 1977; Lee & LaRoi 1979a, 1979b) and bogs and fens (e.g., Slack et al. 1980; Vitt & Slack 1984) have been analyzed. Although both forest floors and mires are often dominated by bryophytes in the ground layer, these habitats are complicated by the large number of non-bryophyte plant species also present. Mountain streams, the subject of the present study, are often virtually free of higher plants. This absence of multilayer plant association facilitates the study of bryophyte species interactions.

Early studies of North American stream ecosystems emphasized the importance of allochthonous detritus as the major energy source. Naimer, in the 1982 meetings of the North American Benthological Society, was the first to report that bryophytes are important biological contributors to these systems since they constitute a major part of the primary productivity in lower order streams. Bryophytes are also important as a substrate for insects

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(Babcock 1949; Minkley 1963; Glime & Clemons 1972) and for algae (Douglas 1958) as well as a food source for insect larvae (Jones 1949). They thus contribute significantly, if indirectly, as food sources for fish. Certainly in mountain streams the bryophytes are the dominant organisms and their community structure is important to the dynamics of the stream ecosystem.

In North America there have been no studies defining community structure or niche relationships of stream bryophytes. Existing studies report patterns of presence of bryophytes in streams (Glime 1968, 1970); discuss tolerance limits and responses of individual species (e.g., Conboy & Glime 1971; Glime 1971; Glime & Acton 1979; Glime 1982) or are species lists and descriptive ecology. An early British study by Tutin (1949) provides a starting point for selecting possible niche parameters. She studied vertical zonation in a mountain stream in the English Lake District and concluded that water supply, air humidity, aeration, light intensity and altitude may all be important in determining species composition of stream bryophyte communities. Since height above the water correlates with humidity (Craw 1976), height is an important parameter which can be measured.

Niche breadth and niche overlap measures have been used to describe many animal and higher plant communities, but these useful methods of analysis have less often been applied to bryophytes (Slack 1982, 1984). Watson (1980) first applied niche breadth and overlap equations to one family of bryophytes, the Polytrichaceae, on Mt. Washington, New Hampshire. She elucidated niche or ecotope relationships between and within the *Polytrichum* and *Polytrichastrum* species in relation to environmental factors. Lee and LaRoi (1979) measured niche breadths and overlap for bryophytes in the Canadian Rockies over elevation and moisture gradients. Vitt and Slack (1984) recently measured niche breadths and overlap for 13 *Sphagnum* species in relation to eight microhabitat parameters in the Redlake Peatland in northern Minnesota. Four of these parameters were found to be important in niche diversification in *Sphagnum*.

In the present study we have examined niche breadth, niche overlap, community similarity and species diversity. Niche parameters investigated include altitude, pH of water, water movement, substrate, and height above the water.

Description of the Study Area

Ten streams were chosen, eight in the Adirondack Mountains, New York, and two for comparison south of the Adirondacks in Schenectady County, New York. The presence of bryophytes was the major criterion for inclusion in the study. Water movement was another criterion; very sluggish streams with almost no water movement were not included. Such streams sometimes do contain vascular plants. Within the Adirondack area a range of elevation (from 255 m to 825 m) was also a criterion for the choice of streams. The ten streams contained only bryophytes and one aquatic lichen, but no vascular plants. Most of the streams are small and lack names on area maps. Stream locations and characteristics are as follows:

Stream 1—Essex Co., District 4, North Elba (44°13′N, 73°52′W), 0.8 km above Cascade Mountain trailhead at Rt. 73, 0.6 km from road, elevation 825 m. A 1 m wide slow-moving stream; substrate granite rocks, fist to wheelbarrow size; canopy of *Acer saccharum, Fagus grandifolia, Betula alleghaniensis*; understory of *Viburnum cassinoides, Acer spicatum*. pH 6.8.

Stream 2—Essex Co., District 4, North Elba (44°13′N, 73°52′W), just above Cascade Mountain trailhead, elevation 670 m. A 1 m wide slow-moving stream; granite rocks fist to bucket size; canopy of *Betula papyrifera*; understory of *Acer spicatum*. pH 6.5.

Stream 3—Essex Co., District 4, North Elba (44°17′N, 74°56′W), Riverside Road, 0.8 km south of junction with Rt. 86, east side of road, elevation 524 m. A 4 m wide stream with rapid falls and moderate pools (17 cm/sec surface flow); granite boulders cement mixer size; canopy of *Abies balsamea, Betula alleghaniensis, Acer spicatum, Sorbus americanus*. pH 6.4.

Stream 4—Essex Co., District 4, Keene (44°12′N, 73°49′W), the "Garden" at base of Johns Brook trail, stream just south of parking lot, elevation 425 m. A 1 m wide slow, intermittent stream; small granite and schist rocks egg to fist size; sparse canopy of *Betula papyrifera, B. alleghaniensis, Tsuga canadensis*. pH 6.8.

Stream 5—Essex Co., District 4, Keene (44°9′N, 73°52′W), stream just below (east of) Johns Brook Lodge, elevation 685 m. A 4 m wide stream with moderate flow (25 cm/sec surface flow); granite boulders of wheelbarrow and cement mixer size; cover of *Betula alleghaniensis, Abies balsamea, Picea rubens*; understory of *Acer spicatum, Acer pensylvanicum, Acer saccharum*. pH 6.2.

Stream 6—Essex Co., District 4, Keene (44°10′N, 73°52′W), stream above junction with trail up Big Slide Mountain, east of Johns Brook Lodge, elevation 745 m. A 4 m wide stream with rapid flow (50 cm/sec surface flow), granite bedrock with few boulders, wheelbarrow to cement mixer size; cover of *Betula alleghaniensis, Betula papyrifera, Picea rubens, Abies balsamea, Acer saccharum*. pH 6.1.

Stream 7—Essex Co., District 4, Keene (44°9.5′N, 73°52′W), stream along trail to Johns Brook Lodge about 0.8 km northeast of lodge, elevation 685 m. A 1 m wide stream with slow flow; granite bucket to cement mixer size boulders; cover of *Betula alleghaniensis, Fagus grandifolia, Acer saccharum*. pH 6.3.

Stream 8—Essex Co., District 11, Schroon (43°50′N, 73°45′W), northeast corner of Schroon Lake, elevation 255 m. A 1 m wide stream with intermittent dry bed and small pools; granite bedrock and some cement mixer size boulders; cover of *Tsuga canadensis, Acer saccharum, Betula papyrifera, B. alleghaniensis*. pH 6.05.

Stream 9—Schenectady Co., District 18, Glenville (42°53′N, 74°1′W), Washout Creek, elevation 200 m. A 4 m wide stream with slow flow (8 cm/sec surface flow); Schenectady Sandstone and Shale bedrock; cover of *Acer saccharum, Fraxinus americana, Carya ovata, Carpinus caroliniana, Tilia americana*; understory of *Hamamelis virginiana*. pH 6.5–7.4.

Stream 10—Schenectady Co., District 17, Glenville (42°55′N, 74°5′W) Wolf Hollow Creek, elevation 200

m. A 4 m wide stream with slow flow (4 cm/sec surface flow); Schenectady Sandstone and Shale with numerous angular rocks; cover of *Acer saccharum* and *Fraxinus americana*. pH 7.3.

The district numbers refer to botanical districts of New York State, based on latitude and longitude. See, for example, Ketchledge's Revised Checklist of Mosses of New York State (1981) which uses these districts.

Methods

The ten streams chosen provided a variety of stream types within a limited geographic area. The latitudinal range was 1°22′ and the elevation range was 625 m (570 m within the Adirondack Mountain area).

All sampling was done from 13 to 20 July 1982. Since water levels are very variable seasonally, it was important to get comparable data for all streams. No rain occurred during the sampling period, so that height above water was comparable. Stream flow was too slight to use a flow meter, so a sample vial was dropped into the water and timed for 1–2 m to determine relative surface velocity. pH was determined in the field and/or in the laboratory within 24 hours with a Fisher Accumet Model 325 pH meter. Temperatures were measured at three locations in each stream, and light was measured in lux with a photographic meter at the surface.

In each stream, 10 random 0.5 × 1.0 m quadrats were chosen by drawing numbers from 0.5 to 3.0, with 0.5 intervals, and using these as the distance from the beginning of one quadrat to the beginning of the next. Horikawa and Kotake (1960) determined that 0.5 × 0.5 m stream quadrats were adequate based on the species-area curve, but we chose the 1 m length in order to sample both edge and mid-stream. If no mosses were present, a new number was selected. In each quadrat, species, percent cover, depth below or height above water surface, and substrate types including rock sizes were recorded. Substrates were divided into nine categories for niche analysis: egg size, fist size, bucket size, wheelbarrow size, cement mixer size, house size, bedrock, wood, soil. Stream depth was divided into 10 categories relative to the water surface: −10 cm and less, −10 cm to surface, surface to 10 cm, 10 to 20 cm, 20 to 30 cm, 30 to 40 cm, 40 to 50 cm, 50 to 60 cm, 60 to 70 cm, 70 cm and above.

Niche breadth was calculated according to the formula of Levins (1968):

$$\text{Niche breadth NB} = \frac{1}{\sum_{1}^{n} P_{ij}^2}$$

where

n = number of habitat states
P_{ij} = the abundance of species j in habitat state i/total abundance of species j in all habitat states.

The number of quadrats of occurrences (frequencies) in each habitat state was used as the measure of abundance. Ten habitat states were used for depth; nine were used for substrate.

Niche overlap is based on Pianka (1973), as modified from Levins (1968):

$$\text{overlap} = O_{jk} = \frac{\sum_{i}^{n} P_{ij}P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij}^2 \sum_{i}^{n} P_{ik}^2}}$$

where

n = number of samples (or streams)
P_{ij}, P_{ik} = proportion of the ith habitat state utilized by the jth and kth species respectively.

The range of values for both niche breadth and niche overlap is 0–1.0.

Both streams and species were ordinated using detrended correspondence analysis (DECORANA, Hill 1979, Hill & Gauch 1980). See Gauch (1982) and Slack (1984) for recent discussions of this and other ordination methods. Three ordinations were computed, based on frequency, cover, and prominence value (PV = $CF^{0.5}$, Horton et al. 1979). Cover represents mean percent cover for each stream and frequency is the absolute frequency. Species diversity indices were calculated by the Brillouin formula:

$$\bar{H} = \frac{k}{N}\left(\ln N! - \sum_{i=1}^{m} \ln n_i!\right)$$

where

n_i = mean cover in the stream
N = total cover
m = number of species
k = constant to convert to base 2

and by Shannon's formula (Shannon & Weaver, 1963)

$$H' = -\sum p_i \ln p_i$$

where p_i is the is the proportion of mean cover in the stream represented by the ith species. See Slack (1971, 1977, 1984) and Glime et al. (1981) for discussion of diversity indices in relation to bryophytes.

Results and Discussion

Several of the environmental factors measured in this study did not show sufficient within-stream variation to assess niche segregation of the bryophyte species within one stream. Surface flow, which was from 0 to 50 cm/sec, could not be measured for less than half a meter, so that it was not a reliable measure of flow over any given moss population. Many species occurred in both slow and faster moving streams, but some between-stream segregation of species was seen. This factor is discussed further below. Temperature within streams never varied more than 2°C; niche separation based on temperature was not possible within the streams. The temperature differential among streams (14–23°C) reflected both elevation and daily air temperature differences. Therefore elevation was a more reliable parameter for niche separation between streams than temperature. Light differed little among streams on comparable sampling dates, averaging about 1500 lux. Most streams had a patchy light distribution due to a mixed canopy of primarily birch, maple, and hemlock.

For the Adirondack streams pH varied from 6.05 to 6.8. Considering the recent acidification of Adirondack lakes, these stream pH readings seem relatively high. There is no calcareous rock substrate in any of the areas studied except Wolf Hollow

TABLE 1. Species of bryophytes found in Adirondack and neighboring streams with cover and frequency (cover, freq.) and Brillouin species diversity for each stream.

Species	Streams 1	2	3	4	5	6	7	8	9	10	Mean % cover
Anomodon attenuatus (Hedw.) Hüb.			5.0, 1	1.0, 1						3.0, 2	9.0
Atrichum undulatum (Hedw.) P. Beauv.	1.0, 1								1.0, 1		2.0
Brachythecium curtum (Lindb.) Limpr.		1.0, 2		1.0, 1							2.0
Brachythecium plumosum (Hedw.) B.S.G.	18.6, 7		1.0, 3	1.0, 1	1.0, 4		6.6, 9	4.0, 7	12.5, 2		44.7
Brachythecium rivulare B.S.G.	8.9, 8	3.0, 2	19.5, 10	1.0, 1			1.0, 2	27.5, 4		1.0, 6	61.9
Bryhnia novae-angliae (Sull. & Lesq.) Grout	1.0, 4							4.6, 7			5.6
Campylium chrysophyllum (Brid.) J. Lange								1.0, 3	1.0, 1		2.0
Eurhynchium riparioides (Hedw.) Rich.	9.6, 8	6.0, 7	4.6, 5	1.7, 6			13.1, 10	8.2, 9	21.2, 6		70.0
Fissidens bryoides Hedw.		1.0, 1		1.0, 1				1.0, 3	3.0, 2	1.0, 4	7.0
Fissidens taxifolius Hedw.			1.0, 3							1.0, 1	2.0
Fontinalis antipyretica Hedw.		1.0, 3		10.0, 1							11.0
Fontinalis dalecarlica Schimp.									24.0, 10		24.0
Fontinalis novae-angliae Sull.								14.1, 9			14.1
Grimmia alpicola Hedw. var. *rivularis* (Brid.) Wahlenb.	5.0, 1		1.0, 8				1.0, 1		3.4, 5		10.4
Grimmia apocarpa Hedw. var. *stricta* (Turn.) Hook. & Tayl.	1.0, 1										1.0
Hygroamblystegium tenax (Hedw.) Jenn.			10.6, 10	2.1, 8			1.0, 1	5.1, 7	5.3, 3	11.0, 10	35.1
Hygrohypnum eugyrium (B.S.G.) Loeske		3.0, 2			1.0, 1	9.0, 4	5.0, 1				18.0
Hygrohypnum molle (Hedw.) Loeske	5.3, 3	2.3, 3		1.0, 1	1.0, 3	5.0, 1	7.8, 6				22.4
Hygrohypnum ochraceum (Turn.) Loeske					28.0, 10	13.0, 8		1.5, 2	10.0, 1		52.5
Hygrohypnum subeugyrium (Ren. & Card.) Broth.								1.0, 2			1.0
Hypnum pallescens (Hedw.) P. Beauv.	1.0, 2								6.8, 10		7.8
Mnium thomsonii Schimp.	1.0, 1		5.0, 1								6.0
Plagiomnium ciliare (C. Mull.) Kop.	1.0, 5							1.0, 4	1.0, 1		3.0
Plagiomnium cuspidatum (Hedw.) Kop.										1.0, 3	1.0
Rhizomnium punctatum (Hedw.) Kop.	2.9, 9			1.0, 4	2.2, 5	1.0, 1	1.7, 6	1.0, 4	1.0, 1	1.0, 5	11.8
Rhacomitrium aciculare (Hedw.) Brid.					3.6, 8	1.0, 4	2.1, 8	1.0, 3	2.3, 3		10.0
Thamnobryum alleghaniense (C. Mull.) Nieuwl.								12.5, 2			12.5
Thuidium delicatulum (Hedw.) B.S.G.	10.3, 3			1.0, 3				1.0, 1			12.3
Chiloscyphus polyanthos (L.) Cords var. *rivularis* (Schrad.) Nees		1.0, 1						1.0, 8	1.8, 5		3.8
Cololejeunea biddlecomiae (Aust.) Evans								3.0, 2			3.0
Lophocolea heterophylla (Schrad.) Dum.				1.0, 3							1.0
Metzgeria conjugata Lindb.								3.0, 2			3.0
Plagiochila porelloides (Torrey) Lindenb.			1.0, 1		1.0, 1		1.0, 1	4.8, 9	5.0, 1		12.8
Scapania undulata (L.) Dum.					1.0, 7	1.0, 3		2.1, 7	2.6, 5		6.7
Trichocolea tomentella (Ehrh.) Dum.								1.0, 3			1.0
Dermatocarpon fluviatile (G. Web.) Th. Fr.									4.4, 5		4.4
Species diversity ($\bar{H}$)	2.67	2.04	2.14	2.20	1.29	1.92	2.32	3.14	3.07	1.52	
Species diversity (H′)	2.10	1.86	1.71	2.01	1.09	1.36	1.38	2.44	2.36	1.38	

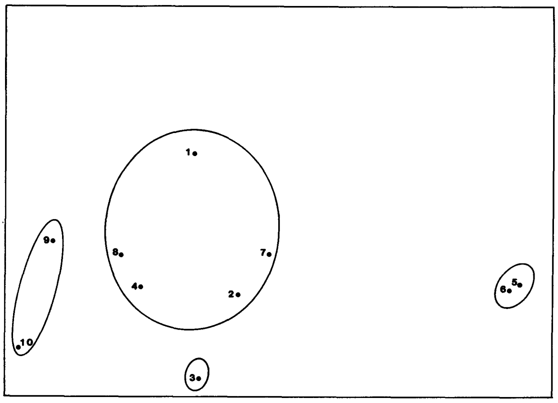

FIGURE 1. Ordination of streams based on prominence values (P = CF²) of bryophytes using detrended correspondence analysis (Hill 1979). Enclosures indicate authors' views of groupings (see text).

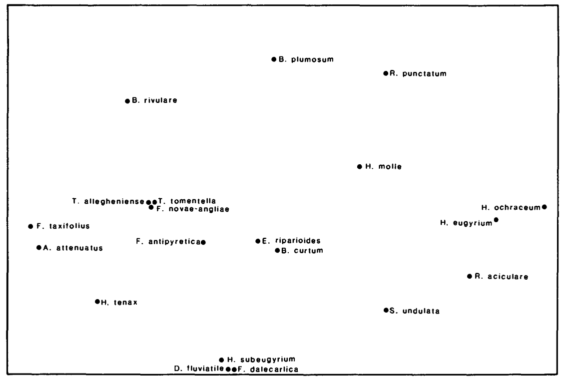

FIGURE 2. Ordination of species based on prominence values (P = CF²) of bryophytes using detrended correspondence analysis (Hill 1979).

(Stream 10). The stream there is in a fault zone where limestone rock of a much older age was uplifted; the stream bedrock itself is non-calcareous Schenectady Sandstone and Shale. Stream 9 is in the same formation. The pH range in this study is probably too small to determine the importance of this factor for stream bryophytes. Geissler (1976) found less difference in bryophytes of calcareous versus acid streams than in terrestrial systems. Jones (1949) found *Fontinalis antipyretica* in calcareous streams (pH 7.4–7.6) in Wales; it occurred at pH 6.5 in this study. On the other hand, aquatic and semiaquatic bryophytes found in lakes and mires have distinct pH preferences, for example among species of *Sphagnum* and *Drepanocladus* (see, e.g., Vitt & Slack 1975; Slack et al. 1980). *Hygrohypnum* is not found in the two streams with pH over 7.0; however, these are also the two streams with the lowest elevation and latitude, probably the more important factors here. Some species were found over the whole pH (and altitude and latitude) range. It is perhaps of interest that the stream with the lowest pH has the highest species richness and the highest Brillouin diversity as well as the highest cover of bryophytes.

Cover and frequency. Table 1 provides cover and frequency values for the 36 bryophyte species found in these streams. The most frequent moss among the streams was *Rhizomnium punctatum*, found in eight out of ten streams. Its cover however averaged only 1.2% whereas the greatest average cover for all streams was that of *Brachythecium rivulare* (6.2%). Some species had high cover values in one or more streams. The following species averaged over 20% cover in at least one stream: *Brachythecium rivulare, Eurhynchium riparioides, Fontinalis dalecarlica, Hygrohypnum ochraceum.* Many species had low cover values but high frequencies within streams; 13 species had frequencies of 0.8–1.0 (Table 1) in at least one stream. The latter is particularly true of the hepatic species, none of which had cover values of over 5%, but three of which, *Chiloscyphus polyanthus* var. *rivularis, Plagiochila porelloides,* and *Scapania undulata* had high frequencies (0.7–1.0) in one or several streams. An aquatic lichen, *Dermatocarpon fluviatile,* was found in the quadrats of one Adirondack stream where it had a cover value of 4.4% and a frequency of 0.5.

Species diversity. The Brillouin ($\bar{H}$) and Shannon (H′) diversity values are shown at the bottom of Table 1. They ranged from 1.29 to 3.14 for $\bar{H}$ and 1.09 to 2.44 for H′. The highest diversity occurred in the stream with the greatest cover, but there is no correlation over the diversity range. The stream with the lowest cover had intermediate diversity. The higher elevation mountain streams (#1, 2, 4–7) had a mean species diversity ($\bar{H}$) of 2.07, whereas the two lower elevation streams in the Adirondacks had diversities of 3.14 and 3.07. These two streams were quite different in flow rate and substrate characteristics. Similarity of species composition for these two streams based on presence or absence of species was 0.63; 12 species were found in both streams, but 14 were found in one stream but not the other. These two streams contained higher numbers of hepatic species than the other streams. Stream 8 had six hepatics (see Table 1), including all the hepatic species found in the study. Stream 3 contained *Dermatocarpon,* found also in one of the higher elevation mountain streams, but in the latter stream it was not in our quadrats. The two streams that were south of the mountain area, #9 and 10, had low diversities (2.14, 1.52); these streams lacked all *Fontinalis, Racomitrium,* and *Hygrohypnum* species, which are more common in the mountains. They also lacked all the hepatic species except *Plagiochila porelloides.*

TABLE 2. Niche breadth for each species based on all streams combined.

	Height	Substrate	$\sqrt{\text{Ht} \times \text{substrate}}$	$\bar{x}$
Anomodon attenuatus	0.50	0.30	0.39	(0.40)
Atrichum undulatum	0.28	0.11	0.18	(0.20)
Brachythecium curtum	0.23	0.20	0.21	(0.22)
Brachythecium plumosum	0.59	0.40	0.49	(0.50)
Brachythecium rivulare	0.39	0.52	0.45	(0.46)
Bryhnia novae-angliae	0.36	0.26	0.31	(0.31)
Campylium chrysophyllum	0.23	0.30	0.26	(0.27)
Eurhynchium riparioides	0.26	0.55	0.38	(0.41)
Fissidens bryoides	0.36	0.33	0.34	(0.35)
Fissidens taxifolius	0.27	0.18	0.22	(0.23)
Fontinalis antipyretica	0.20	0.16	0.18	(0.18)
Fontinalis dalecarlica	0.28	0.43	0.35	(0.36)
Fontinalis novae-angliae	0.12	0.56	0.26	(0.34)
Grimmia alpicola var. *rivularis*	0.43	0.36	0.39	(0.40)
Grimmia apocarpa var. *gracilis*	0.20	0.11	0.15	(0.16)
Hygroamblystegium tenax	0.41	0.60	0.50	(0.51)
Hygrohypnum eugyrium	0.46	0.31	0.38	(0.39)
Hygrohypnum molle	0.45	0.25	0.34	(0.35)
Hygrohypnum ochraceum	0.50	0.45	0.47	(0.48)
Hygrohypnum subeugyrium	0.44	0.47	0.45	(0.46)
Hypnum pallescens	0.45	0.33	0.39	(0.39)
Mnium thomsonii	0.20	0.22	0.21	(0.21)
Plagiomnium ciliare	0.39	0.36	0.37	(0.38)
Plagiomnium cuspidatum	0.30	0.20	0.24	(0.25)
Rhizomnium punctatum	0.39	0.38	0.38	(0.39)
Rhacomitrium aciculare	0.50	0.41	0.45	(0.46)
Thamnobryum alleghaniense	0.27	0.22	0.24	(0.25)
Thuidium delicatulum	0.46	0.31	0.38	(0.39)
Chiloscyphus polyanthus	0.20	0.59	0.34	(0.40)
Cololejeunea biddlecomiae	0.20	0.30	0.24	(0.25)
Lophocolea heterophylla	0.10	0.11	0.10	(0.11)
Metzgeria conjugata	0.20	0.22	0.21	(0.21)
Plagiochila porelloides	0.31	0.43	0.37	(0.37)
Scapania undulata	0.22	0.41	0.30	(0.31)
Trichocolea tomentella	0.30	0.20	0.24	(0.25)
Dermatocarpon fluviatile	0.45	0.29	0.36	(0.37)
Mean	0.33 ± 0.04	0.33 ± 0.04		

Species diversities found in this study were similar to those found in other bryophyte community studies. Glime et al. (1981) found Brillouin mean diversities of 1.90 to 2.34 for bryophyte epiphytes on four deciduous tree species. Mean diversities of bryophytes ranging from 0.65 to 1.1 were reported in the same paper for four zones of an alkaline marsh. Species diversity of bryophytes in deciduous forest in three different areas of New York state varied from approximately 0.5 to 2.5, in spruce-fir forest from 1.5 to 2.6 for two areas, and from 0.6 to 2.1 in arctic-alpine on Whiteface Mt. (Slack 1977). These figures do not include epiphytes and were calculated using the Shannon species diversity index, using natural logs (ln) as was done also in the present study. For both deciduous and spruce-fir forest, the bryophyte values are higher than those for vascular ground flora in the same samples.

Species diversity data are also given in some mire studies (Vitt et al. 1975; Slack et al. 1980), but in these studies Simpson and Whittaker's indices are used so that comparisons with results from the Brillouin and Shannon indices are difficult to make. Species richness can, however, be compared in some of these studies. For the aquatic or semiaquatic studies of bryophytes, species richness (numbers of species) is higher in alkaline patterned mires in Alberta (Slack et al. 1980) as compared to alkaline marsh habitats in Michigan. Thirty-six species of bryophytes were found in the former as compared to 20 in the latter. In the present study, 35 bryophyte species were found in all, with 21 species in the stream with the highest Brillouin diversity. It is obvious that more data, and especially more comparable data, are needed to evaluate bryophyte species diversity even in aquatic habitats. The use of both the Shannon and Brillouin indices in addition to species richness data would facilitate such comparison with both older and future studies. Comparisons between bryophyte habitats and between bryo-

TABLE 3. Niche breadth and overlap for height for species shown in Fig. 3.

	Stream	Niche overlap Species 1	Niche overlap Species 2	Niche overlap Species 3	Breadth
1. *Brachythecium plumosum*	1				0.57
	3				0.18
	7				0.43
	8				0.30
2. *Brachythecium rivulare*	1	0.84			0.41
	3	0.07			0.56
	7	0.83			0.23
	8	0.84			0.25
3. *Eurhynchium riparioides*	1	0.37	0.56		0.27
	3	0.00	0.68		0.23
	7	0.66	0.60		0.30
	8	0.51	0.89		0.14
4. *Hygroamblystegium tenax*	1				
	3	0.18	0.95	0.47	0.55
	7	0.70	0.85	0.82	0.20
	8	0.35	0.78	0.98	0.10

phytes and other plant groups are both needed. Species richness data are interesting but not sufficient because of differences in area and number of habitats sampled in the various studies.

Ordination of streams and of bryophytes. DCA ordination, unlike some other ordination programs, can be used to ordinate both samples and species. We have used it here to ordinate both the streams and the species in them. Ordinations were carried out using frequency and cover each separately and using prominence values (incorporating both). The latter, which incorporate the most information, are shown here (Fig. 1, 2). In the stream ordination (Fig. 1), it can be seen that the two lower latitude, lower elevation streams, 9 and 10, separate out from the others. These two streams are both in shale and sandstone bedrock and are slow moving. Streams 5 and 6 are both fast flowing, high elevation streams in the Johns Brook–Big Slide Mt. area of the Adirondacks. Stream 3, a large stream with relatively fast flow and huge granite boulders appears to separate out from all the remaining Adirondack streams to some extent. The other 5 streams, though geographically separated within the Adirondack area, and differing in elevation, have sufficiently similar species composition to loosely form one group. They are all similar in being small (about 1 meter wide) streams with slow flow, dry areas, and lack of water later in the summer. Streams 1 and 8 were revisited two weeks after the completion of the study and contained no running water; bryophytes that had been submerged were completely exposed.

The computer-generated species ordination Fig. 2 explains in large part both the similarities and differences seen in the stream ordination. Nineteen of the 36 species in the study are shown on the ordination space, including all species of *Fontinalis, Hygrohypnum,* and *Brachythecium,* and all species with high cover and/or frequency values in the study. A few species characteristic of certain groups of streams are included also. Streams 5 and 6 are characterized by *Hygrohypnum ochraceum, H. eugyrium* and *Racomitrium aciculare,* in particular by large quantities of *H. ochraceum,* in two different forms at different depths (see below). This moss was however also found in two of the other Adirondack streams, though in smaller quantities. *H. subeugyrium,* however, was found only in Stream 3, as was *Fontinalis dalecarlica.* Several species including *Trichocolea tomentella, Thamnobryum alleghaniense* and *Fontinalis novae-angliae* were found only in Stream 8 on the east shore of Schroon Lake, but this high diversity stream contained many species in common with other Adirondack streams and therefore did not separate out on the ordination. *Fissidens taxifolius, Anomodon attenuatus,* and *Hygroamblystegium tenax* were characteristic of Streams 9 and 10, south of the Adirondacks. The latter species was characteristic of Adirondack streams as well, though in lesser quantity. Most other species are found in the central part of the ordination and are not restricted to particular streams. It is of interest that all species of *Brachythecium, Fontinalis,* and all species of *Hygrohypnum* except *H. ochraceum* and *H. eugyrium* separate out on the ordination—that is, between streams. Within-stream species segregation will be considered below.

From the ordination and discussion above, the

TABLE 4. Niche breadth and overlap for height for species shown in Fig. 4.

		Niche overlap				
		Species				
	Stream	1	2	3	4	Breadth
1. *Hygrohypnum eugyrium*	5					0.30
	6					0.36
	7					0.30
	8					
	9					
2. *Hygrohypnum molle*	5	0.00				0.20
	6	0.94				0.40
	8	0.70				0.39
	8					
	9					0.30
3. *Hygrohypnum ochraceum*	5	0.11	0.64			0.54
	6	0.94	0.86			0.39
	7					
	8					
	9					
4. *Hygrohypnum subeugyrium*	5					
	6					
	7					
	8					0.10
	9		0.81			0.39
5. *Rhizomnium punctatum*	5		0.00	0.38		0.43
	6	0.40	1.00	0.57		0.10
	7	0.00	0.81			0.27
	8	0.71			0.55	0.19
	9		0.67		0.96	0.30

following parameters appear to be of some importance in species segregation among streams and should be investigated further: latitude and elevation, size of stream, rate of flow, type of substrate. pH differences were not important in this study, at least within the Adirondacks, but might prove important over a wider range in further studies. Nothing definitive can be said about species associations found in this study; they must be tested for more streams and over a wider geographical range, since most of the species have a wide range, at least in Eastern North America.

Niche separation. Niche breadth (Table 2) and overlap (Tables 3, 4) provide additional meaningful information on species interactions in these streams. Two parameters were used, the only two that could be shown to vary within a stream: height above the water and substrate including rock size. A combined value for niche breadth was also determined (Table 2) by calculating the geometric mean, the square root of the product of the niche breadth for each parameter (Pianka 1973). Although for some species, height on the rock is a function of the rock size, the correlation of height niche breadth and substrate niche breadth is low (Pearson Product Moment = 0.261, $p > 0.1$, df = 35), indicating that the two parameters we are measuring are not closely correlated. The arithmetic mean ($\bar{x}$) has also been used in previous studies (e.g., Watson 1981). These have also been calculated (Table 2). It can be seen that the two values are almost identical except in the two cases where the niche breadth for one parameter is low and the other high. The use of the geometric mean seems preferable in that it gives lower values in such cases. The overall niche breadth of a species that is restricted in one parameter is likely to be small relative to other species not so restricted, even though the breadth for another parameter is high.

A large range in niche breadths for height was found, from 0.10 for *Lophocolea heterophylla* and 0.12 for *Fontinalis novae-angliae* to 0.50 for *Anomodon attenuatus* and 0.59 for *Brachythecium plumosum.* Niche breadth for substrate is lowest for *Atrichum undulatum, Grimmia alpicola* var. *rivularis* (both 0.11) and highest for *Hygroamblystegium tenax* (0.60) and *Chiloscyphus polyanthus* (0.59). The latter species is unusual in that it is able to establish itself on very small rocks. The mean for each parameter was 0.33 ± 0.04. *Lophocolea* had the narrowest combined niche breadth (0.10) and *Hygroamblystegium* the widest (0.50) for height and substrate.

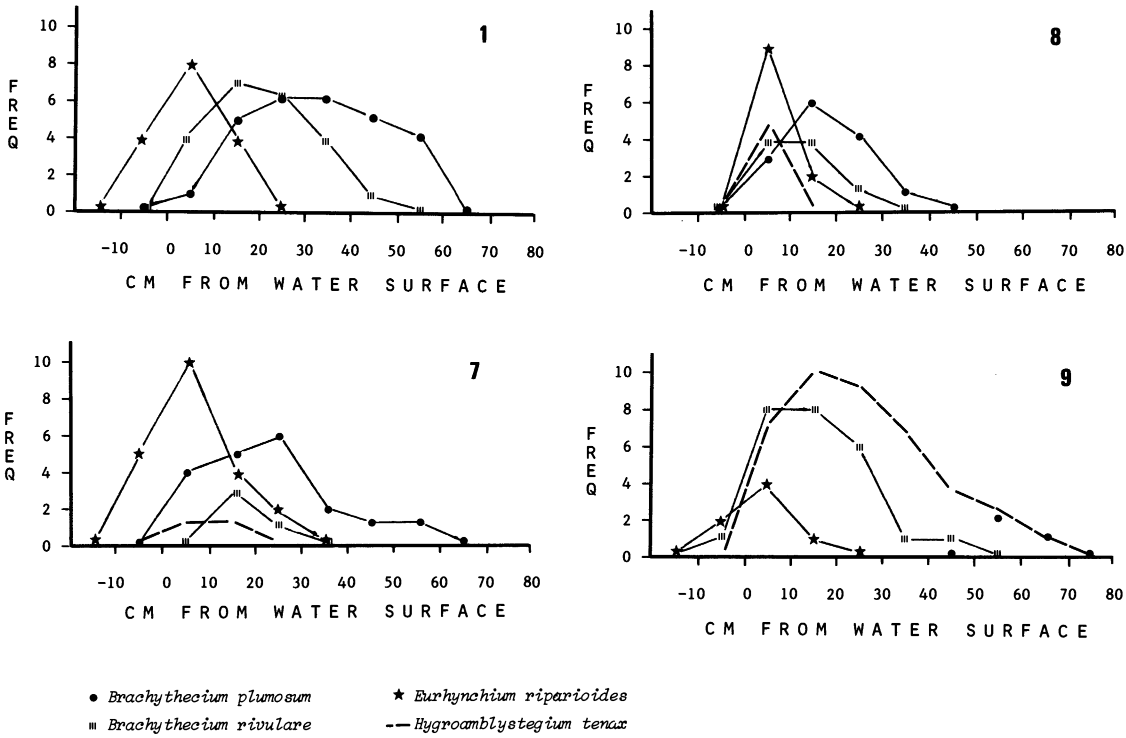

FIGURE 3. Height distribution in cm of four species, shown by frequency of quadrats in which the species was represented at that height. Stream number appears in the upper right. (*Eurhynchium riparioides* = star, *Brachythecium rivulare* = vertical bars, *B. plumosum* = black circle, *Hygroamblystegium tenax* = dashed line.)

These niche breadths can be compared with those found by Vitt and Slack (1984) for 13 *Sphagnum* species in northern Minnesota mires. These varied from 0.12 to 0.56 for pH, 0.20 to 0.48 for height above water, and 0.13 to 0.50 for amount of shading, for example. These figures are very similar in range to ours for stream bryophytes. In Watson's (1980) study of Polytrichaceae, niche breadths for mixed stands ranged from 0.24 to 0.61 for substrate, 0.18 to 0.63 for texture and 0.18 to 0.57 for pH, again within the same range. Each of these studies included a smaller number of closely related species and a larger number of samples than in the present study, although the geographical range and number of sites is larger in the stream study than in Watson's. If one looks only at the closely related species in the present study, niche breadths are as follows: *Fontinalis* (3 species): 0.12 to 0.28 for height, 0.16 to 0.56 for substrate; *Hygrohypnum* (4 species): 0.44 to 0.50 for height, 0.25 to 0.47 for substrate; *Brachythecium* (3 species): 0.23 to 0.59 for height, 0.20 to 0.52 for substrate; Mniaceae (4 species): 0.20 to 0.39 for height, 0.22 to 0.38 for substrate.

Thus considerable differences are seen in niche breadth even within genera. It should be noted that there is niche differentiation within the largely non-aquatic mosses *Brachythecium* and Mniaceae, shown indirectly by these data: Ketchledge's Revised Checklist (1981) of the mosses of New York includes 13 species of *Brachythecium* and 15 species of *Mnium* s.l. for districts 3 and 4 in the Adirondacks, of which only 3 *Brachythecium* and 4 *Mnium* s.l. species occurred in our streams.

The narrow niche breadth measurements for some species, e.g., *Atrichum undulatum, Grimmia apocarpa, Lophocolea heterophylla,* and *Fontinalis* species for height, although represented in few samples, may realistically reflect a narrow niche. The first three species are common terrestrial bryophytes producing abundant capsules, but within the stream ecosystem their niche, including reproductive aspects, is much more restricted. For *Fontinalis* the restriction seems to be much more a problem of establishment, combined with a requirement for water during most of the year. Differentiation is seen in *Fontinalis* in relation to the substrate parameter. *Fontinalis antipyretica* in this study was restricted to small (fist to bucket size) rocks with a niche breadth of 0.16, whereas the other two *Fontinalis* species have broad niches (0.43, 0.56). There is no evidence of height segregation in *Fontinalis* from these data.

Four species of *Hygrohypnum* were found in this

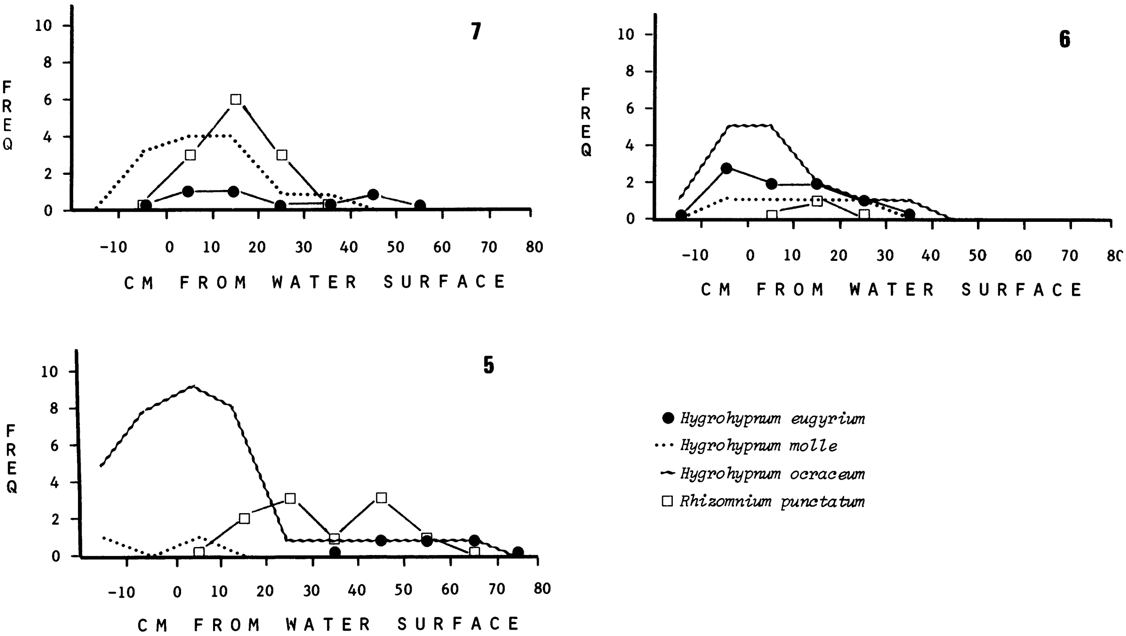

FIGURE 4. Height distribution in cm of four species, shown by frequency of quadrats in which the species was represented at that height. Stream number appears in the upper right. (*Hygrohypnum eugyrium* = black circle, *Hygrohypnum molle* = dotted line, *Hygrohypnum ochraceum* = waved line, *Rhizomnium punctatum* = open box.)

study; it is the most intriguing genus of those found in these streams, worthy of further investigation. Whereas *Fontinalis* species all occurred in different streams providing no relative height data, four streams contained at least two species of *Hygrohypnum,* and two streams contained three species. Moreover, *H. ochraceum* occurred in two distinct forms, straight and falcate-leaved, at different water levels. These forms have long been observed, for example in Grout (1903), "We have varietal forms in which the leaves are not at all falcate or secund . . . but I consider them mainly habitat forms." This cannot be proven without culture experiments, but the habitat segregation of the two forms of *H. ochraceum* is greater (from our data in this study) than that among the four species (see Fig. 4, 5) of *Hygrohypnum* present.

According to Jamieson's (1976) monograph of *Hygrohypnum,* the leaves of *H. ochraceum* vary from straight to falcate uncinate. In his discussion of previously named infraspecific taxa, he concluded that "leaf falcation is a highly variable feature and cannot effectively be used to delimit a taxon." He did not, however, discuss the variation in leaf falcation in relation to variation in water depth or other ecological factors. A striking correlation of leaf shape and water depth was seen in this study.

Height segregation was also obvious for the two more commonly found *Brachythecium* species, *B. rivulare* and *B. plumosum,* and among most of the species growing in any one stream. This segregation is illustrated graphically in Fig. 3, 4, and 5. Figure 3 shows three species of Brachytheciaeae, *Brachythecium rivulare, B. plumosum,* and *Eurhynchium riparioides,* and *Hygroamblystegium tenax* in four different streams. It can be seen from the Stream 1 diagram that although there is overlap among all three species found in that stream, there are definite height preferences. Only *Eurhynchium* is found submerged (during the summer low water), only *B. plumosum* at the greatest height. The order of the species in terms of height preference, *Eurhynchium, B. rivulare, B. plumosum* is evident, and is consistent for all four streams shown. In the three streams in which *Hygroamblystegium tenax* also occurred, it appears to order itself between *Eurhynchium* and *B. rivulare* in the two Adirondack streams in which it has a narrow niche breadth for height. In the lower latitude streams (9 and 10), however, it is a very abundant species with a wide niche, occurring even below the water, most abundantly in the middle range, but also as high as *B. plumosum* (see Fig. 3).

Streams 5, 6, and 7, all in the mountains, contain three species of *Hygrohypnum, H. ochraceum, H. molle,* and *H. eugyrium* (Fig. 4). All three species are in Streams 5 and 6, wide, fast-moving streams, but *H. ochraceum* is absent, perhaps significantly, from Stream 7 which is smaller and slow moving. All these species have large niche breadths, *H. ochraceum,* including its two forms, the largest. This

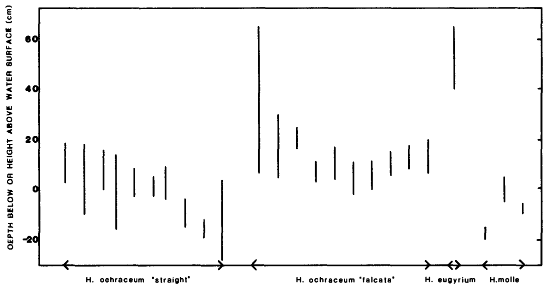

FIGURE 5. Height distribution in cm for *Hygrohypnum* species relative to July water level. Each mark represents a sample (quadrat) in which a given species occurred at that height.

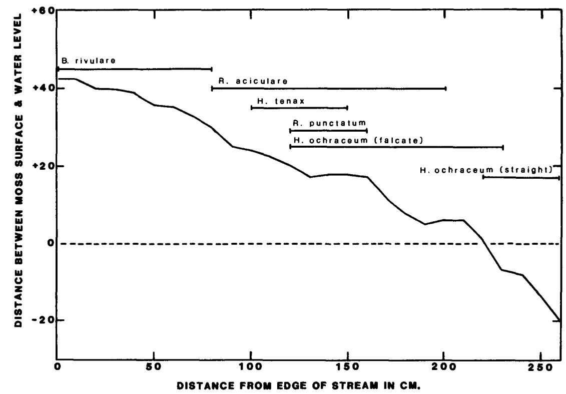

FIGURE 6. Cross-sectional profile of Stream 6 to show vertical zonation of mosses.

is also the only species of *Hygrohypnum* that occurred in abundance in this study. *Rhizomnium punctatum* is included on the figure since it occurred in all three streams. In the stream ecosystem, this species is often submerged, as were the *Hygrohypnum* species, but all four species also occur well above the water line. There is considerable niche overlap among them for height (see Table 4) and substrate. If there is within-stream segregation of *Hygrohypnum* species other than the two forms of *Hygrohypnum ochraceum* (Fig. 5), the relevant parameters have not yet been investigated. Figure 6 illustrates the vertical zonation of all major moss species in one of these streams (#6); going from rocks 40 cm above water level at the edge of the stream to 20 cm below the water level in the center of the stream. The segregation of the two very different-looking forms of *H. ochraceum* should be noted. *Racomitrium aciculare* and *Brachythecium rivulare* also have their own, higher zones (*B. rivulare* above the 100 cm mark used in the quadrats).

Some evidence of segregation of species according to substrate, especially rock size, was found. *Scapania undulata* was regularly found to colonize small egg-sized rocks under water. Establishment on such small and often unstable rocks was nearly restricted to this species. *Eurhynchium riparioides* and *Hygroamblystegium tenax* were often found on medium- or bucket-sized rocks, whereas *Brachythecium plumosum* and *B. rivulare* were more frequent on large boulders, as was *Racomitrium aciculare. Hygrohypnum ochraceum* also occurred most frequently on large boulders in spite of often being aquatic or nearly so; stability of large rocks, not their ability to raise the species above the water level, was probably the important factor here. Many species, however, had broad overall niches for substrate or rock size, including *E. riparioides* and *B. rivulare,* of those discussed above.

Thus a certain amount of niche differentiation among bryophyte species is found within streams on the basis both of height and to a lesser extent of substrate. In addition, between-stream segregation according to elevation, size, and rate of flow is suggested by these data. Other as yet unmeasured parameters may also be important. It is important to remember that different parameters may be important in different aspects of the life cycle of an aquatic or semiaquatic moss or hepatic. The stream environment is constantly changing, not only seasonally, but frequently even within a short period due to a heavy rainfall or prolonged drought. Very few of the over 600 bryophyte species occurring in the region of New York State in which these studies were conducted can establish themselves and/or survive under stream conditions; only 35 bryophytes were found in these streams. The single lichen species indicates the much greater difficulty of adaptation to these conditions by the hundreds of available lichen species.

In this unstable environment, bryophytes must initially establish themselves, must withstand currents and abrasion, must survive repeated desiccation and flooding, and must spread or at least maintain their populations by vegetative or sexual reproduction. For many species the latter is extremely difficult in this environment. Under such conditions, one would not expect to find the more complete niche separation found in *Sphagnum* species growing in mires, nor in Polytrichaceae growing in at least relatively more stable mountain habitats. It is likely that many aquatic bryophytes are to some extent opportunistic species as has been postulated from different data for other bryophytes (e.g., Slack 1982). The niche parameters studied here should be corroborated in other regions where the same species are found, and additional niche parameters should be sought. It is, however, very likely that stochastic factors are as important as true competition leading to competitive exclusion. It may well be that three species of *Hygrohypnum* can indeed live indefinitely in the same stream without either competitive exclusion or true niche segregation discoverable by bryophyte ecologists.

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