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Diversity and distribution of stream bryophytes: does pH matter?

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Abstract: Bryophytes can strongly influence biodiversity and ecosystem function in low-order streams. Mosses and liverworts have substantial biodiversity and biomass in streams, yet few investigators have examined which factors influence bryophyte species distributions, and fewer have examined assemblages across a wide pH gradient. We examined bryophyte assemblages across a pH gradient in 26 southeastern New York (USA) streams. We recorded bryophyte species richness, diversity, and abundance, in conjunction with pH, width, depth, canopy cover, substratum size, temperature, dissolved O_2, turbidity, conductivity, current velocity, dissolved organic C, dissolved Ca, Mg, Fe, NH_4^+, NO_3^-, soluble reactive P (SRP), and abundance of other autotrophs. pH ranged from ~4 to 7 and corresponded to the type of underlying bedrock. Nearly all streams had low or undetectable concentrations of SRP. Several species, e.g., *Hygrohypnum eugyrium* and *Codriophorus aduncoides*, were apparent pH generalists, whereas others were pH specialists. For example, *Hygrohypnum ochraceum* occurred only in neutral pH, whereas *Andreaea rothii* was restricted to low-pH sites. Vector fitting on a nonmetric multidimensional scaling ordination identified stream pH and amount of bedrock as key factors affecting species distributions. Latitude, longitude, altitude, canopy cover, and aqueous Ca, Mg, SRP, and turbidity also were correlated with species distributions, but many factors were colinear. Nearly all sites had low SRP, and species distributions were strongly related to pH, so we assayed several species and populations for phosphomonoesterase (PMEase) activity under different pH conditions. Species and populations from low-pH streams tended to have stronger PMEase activity at lower pH than those from higher pH streams, suggesting that species and populations may be adapted to specific pH conditions. Differential PMEase activity may be one mechanism by which aquatic bryophytes persist in low-pH environments.

Key words: aquatic bryophytes, pH, headwaters, streams, phosphatase activity, diversity

Bryophytes (mosses, liverworts, and hornworts) are a vital component of many headwater streams, where they often form the dominant plant communities (Vitt et al. 1986). Few other habitats are dominated by bryophytes. Even mire communities, where bryophytes form most of the ground layer, include many vascular plant species that make up a significant portion of the community biomass (Slack and Glime 1985). In headwater streams, bryophytes are often the most productive group of autotrophs and account for a significant portion of in-stream primary production (Stream Bryophyte Group 1999). Aquatic bryophytes can have substantial effects on ecosystem function, including hydraulic, nutrient, and trophic dynamics (Stream Bryophyte Group 1999). Thus, understanding of variables driving their abundance and composition is vital to the conservation of these systems (Cattaneo and Fortin 2000).

Stream bryophytes also form part of the base of stream food webs, directly as a food source for macroinvertebrates and indirectly by providing habitat for periphyton and other organisms (Glime and Clemons 1972, Suren 1991, Torres-Ruiz et al. 2007). They increase habitat heterogeneity and habitability, and serve as shelter and oviposition sites for stream-dwelling organisms. Large generalist consumers, such as Canada Geese and crayfish, avoid consuming bryophytes that contain acetylenic fatty acids and other compounds. Thus, stream bryophytes provide enemy-free space for macroinvertebrates and algae (Parker et al. 2007). Other long-chain fatty acids produced by bryophytes have been measured in several different types of macroinvertebrate larvae (Torres-Ruiz et al 2007). Bryophytes alter or reduce microhabitat water velocity, thereby allowing accumulation of periphyton and detritus, which, in turn, are often colonized or consumed by macroinvertebrates (Suren 1991, Georgian and Thorp 1992). Invertebrates living on stream bryophytes usually have similar or higher species richness and density than on bare substrata (Suren

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1991), and certain invertebrate species are more common on bryophytes than in other habitats (Egglishaw 1969). For these reasons, bryophytes may provide a more diverse and stable ecological habitat than other substrata within headwater environments (Glime and Clemons 1972, Suren 1991, 1992).

The importance of bryophytes in streams and the paucity of studies on them led a group of aquatic ecologists (Stream Bryophyte Group 1999) to review the state of this research and to propose several focal areas for future study. One suggested area was a review of the factors influencing the distributions of stream bryophyte communities over a broad geographic range. Surprisingly few studies have been conducted in this area, and even fewer have addressed multiple factors affecting the distributions of stream bryophytes (e.g., Slack and Glime 1985, Glime and Vitt 1987). This knowledge gap is important because stream bryophytes are undoubtedly influenced by several factors (Stream Bryophyte Group 1999). One likely factor of importance is pH because its effect on some other bryophytes is well established. For example, in mire communities, certain *Sphagnum* species occur within narrow pH ranges (Slack 1990).

The influence of pH on stream bryophytes has been examined sporadically, and several investigators described preliminary evidence that pH may be an important determinant of stream bryophyte species abundance (Cattaneo and Fortin 2000), richness (Heino et al. 2005), diversity (Glime and Vitt 1987), and spatial distribution (Slack and Glime 1985, Virtanen et al. 2009). Unfortunately, most studies have been conducted across narrow pH gradients. We are aware of very few studies, all of which were conducted in Europe, in which species distribution was examined across strong pH gradients. In those studies, pH was a strong influence on species' distributions (Paavola et al. 2006, Virtanen et al. 2009). In a study of a small, low-nutrient upland stream in Wales (UK), Ormerod et al. (1987) observed that strong pH gradients could profoundly affect the bryophyte flora and, in turn, macroinvertebrate assemblages.

Few data are available on nutrient uptake or availability in bryophytes, a situation that prompted the Stream Bryophyte Group (1999) to suggest this area as an important focus for future research. In headwaters where bryophytes often thrive (Crum and Anderson 1981), stream water is often poor in available P, particularly soluble inorganic P (Christmas and Whitton 1998a). In low-pH headwater streams, soluble P tends to be sorbed onto sediments by Al and Fe complexes (Tate et al. 1995, Gross 2000). Meyer (1979) demonstrated that sorption of added P by stream sediments in a headwater stream (Bear Brook, New Hampshire, USA) peaked at about pH 4.8 and declined between pH 5 and 6 (not tested at greater pH). Bryophyte abundance, and possibly species richness, appears to be strongly influenced by low concentrations of inorganic P. Bryophyte cover increased 10×, the dominant species changed (*Schistidium agassizii* to *Hygrohypnum* sp.), and a new species (*Fontinalis neomexicana*) was recruited during a long-term (16-y) study of the effects of inorganic P fertilization on the Kuparuk River in Alaska (Bowden et al. 1994, Slavik et al. 2004).

One mechanism by which aquatic bryophytes may obtain sufficient P for growth and reproduction across a pH gradient is via phosphatase activity. In particular, production of phosphomonoesterase (PMEase) allows stream bryophytes to use organic P when inorganic P supplies are in quantities that limit bryophyte growth and reproduction (= physiologically limiting; Christmas and Whitton 1998a), as often appears to be the case (e.g., Bowden et al. 1994). Along stream gradients in the UK from headwaters to lowland sites, aquatic mosses had significantly greater PMEase activity in upland reaches than in sites further downstream (Christmas and Whitton 1998a, b). These researchers also reported that higher-altitude sites had significantly lower pH, lower P, and lower tissue-P content (Christmas and Whitton 1998a, b). The mechanism or links between altitude, pH, and P availability were not clear, but the patterns were significant. These data indicated that low-pH streams were more physiologically limiting for bryophytes in terms of inorganic P near the headwaters than downstream. Stream reaches also can vary in the species of bryophytes present, and PMEase activity has rarely been compared among species or populations in streams with different pH levels (Turner et al. 2001).

The northeastern USA is especially rich in aquatic bryophytes and is an excellent area in which to examine the influence of pH on their distributions. Waters draining the Shawangunk Mountains of New York State and nearby forested areas have a wide range of pH because of the unique mix of bedrock (Chowdhury and Giles 2007). Some of these geologies also may be sensitive to human-caused changes in pH, a trend that the bryophyte flora may help to identify (Thiebaut et al. 1998). In addition, the Shawangunk waterways drain into the Catskill Aqueduct, which is part of the delivery system for New York City drinking water. In-depth knowledge of the waterways in this area is critical for maintaining high-quality drinking water for New York City.

The broad objective of our study was to examine the influence of pH on bryophyte distributions and how these conditions may affect nutrient acquisition. We also compared other ecological variables to bryophyte species distributions, species richness, diversity, and abundance. We tested 2 hypotheses: 1) some species will exhibit narrow pH optima, whereas others will occur across broad pH ranges, and 2) bryophyte species and populations from lower-pH streams will have lower pH optima for PMEase than species and populations from more neutral streams.

METHODS

Study sites

We sampled 26 streams in southeastern New York State: 15 from Minnewaska State Park, Mohonk Preserve, and adjacent areas, and 11 from Harriman State Park and adjacent areas. Minnewaska State Park (~8500 ha) and Mohonk Preserve (~2800 ha) are in Ulster County and contain a large portion of the Shawangunk Mountain Ridge, which is composed of highly resistant Shawangunk conglomerates, surrounded by Martinsburg shale (Fisher et al. 1970, Chowdhury and Giles 2007). Surficial geology of Harriman State Park (~18,600 ha; Rockland and Orange Counties) is predominantly metamorphic (mainly gneiss), with some granite (Fisher et al. 1970). We selected streams to represent a wide pH range within a small geographic area. Streams sampled had ≥1 aquatic bryophyte species present and measurable flow.

Species distributions

In each stream, we sampled a 20-m reach in spring and summer. We recorded the abundance of all submerged bryophytes in spring on a semiquantitative scale (Holmes and Whitton 1977). We collected voucher specimens (Tessler #1-221) in March 2012 and deposited them at the Louis Calder Center (Fordham University). Nomenclature followed Flora of North America Editorial Committee (2004–2007+) for mosses and Ley and Crowe (1999) for liverworts. All bryophytes sampled were predominantly aquatic in habit, sensu Vitt and Glime (1984), and we sampled under stable baseflow conditions. We also recorded abundances of broad categories of autotrophs (vascular plant, macroalgae, and aquatic lichen) when present. We calculated species richness, diversity (Simpson and Shannon), and total abundance for species recorded in ≥3 streams (Begon et al. 1990). We used a species accumulation curve to assess sampling sufficiency (*accumresult* [exact method] and *accumplot* functions; BiodiversityR package; Kindt and Coe 2005) in R (version 2.15.1; R Project for Statistical Computing, Vienna, Austria). The curves suggested that 15 streams represented adequate sampling intensity, and we sampled 26.

We collected water samples and measured ecological variables concurrently during 1 wk in March 2012 and 1 wk in June 2012. At every reach, we recorded stream width (±0.1 m) and depth (±1 cm), estimated % forest canopy cover with a canopy densiometer (Forest Densiometers, Bartlesville, Oklahoma; Strickler 1959), and visually estimated the size of rock substrata with a modified Wentworth scale (Cummins 1962).

We measured temperature, pH, dissolved O_2 (DO), turbidity, and specific conductivity of the water in situ with a Hydrolab Quanta (Hach Industries, Loveland, Colorado) and current velocity with a Flo-Mate flow meter (Marsh–McBirney, Frederick, Maryland). We collected water samples in acid-washed 8-mL sampling tubes, syringe-filtered them (0.2-μm pore size), preserved them with H_2SO_4 or HCl to a pH < 2.0, stored them cold (≤4.0°C), and analyzed them for dissolved NO_3^-, NH_4^+, soluble reactive P (SRP; Astoria 2 analyzer; Astoria, Clackamas, Oregon), dissolved organic C (DOC; TOC-L TOC analyzer; Shimadzu, Columbia, Maryland), and Fe, Ca, and Mg (1100B atomic absorption spectrophotometer; Perkin–Elmer, Waltham, Massachusetts). We analyzed NH_4^+ with the phenol-hypochlorite method. We analyzed NO_3^- as NO_2^- with the sulfanilamide-NNED method, after reduction to NO_2^- with a Cd–Cu column (APHA 1985). We removed inorganic C and measured the remaining C as DOC (Potter and Wimsatt 2009).

To elucidate patterns in species distributions in our 26 streams, we used nonmetric multidimensional scaling (NMDS) of species (*metaMDS* function in the *vegan* community ecology package (version 2.0-4; Oksanen et al. 2012) in R. We tested all 30 ecological vectors (including species richness, diversity, and abundance) individually for significant correlations with the NMDS ordination for both March and June samplings with the *envfit* function of *vegan* with 1000 permutations, and fitted significant variables to the NMDS ordination. Linearity of these species composition–environmental variable relationships was reviewed using the *ordisurf* function of *vegan* with a maximum likelihood (ML) model. We also tested the relationships among all significant variables with Spearman correlation analysis. We used an a priori $p = 0.01$ as a cutoff for statistical significance to minimize α inflation and potential problems with Bonferroni corrections (after Cisneros et al. 2011).

Phosphomonoesterase activity and pH

We used a subsample of 10 sites from the Shawangunk region to examine the general relationship between aqueous pH and P, bryophyte-P content, and PMEase activity. We measured streamwater pH and inorganic P at each site (as above) and bryophyte P tissue concentration (n = 31) (Solorzano and Sharp 1980). We assayed PMEase activities in specific bryophyte species and populations to test whether habitat pH could influence PMEase activity under a range of pH conditions. We sampled bryophytes and water from low-pH Peters Kill (pH 4.35) and near-neutral Palmaghatt Kill (pH 6.50). *Fontinalis* cf. *dalecarlica* was sampled from both sites, *Hygrohypnum ochraceum* from Palmaghatt Kill, and *Scapania undulata* from Peters Kill. We washed all specimens 10× in deionized water to remove loosely attached algae (microscopic observations were used to exclude any with substantial algal growth) and used apical 2-cm tips to ensure that PMEase activity was measured in areas of active growth (Turner et al. 2001). We placed ½ of the tips in water from Peters Kill (low pH) and ½ in water from Palmaghatt Kill (neutral) for 24 h to equilibrate any recent PMEase activity. We conducted assays with *para*-nitrophenyl phosphate (*p*NPP) as a substrate following the methods of Turner

et al. (2001). We used 4 experimental pH levels (4.0, 5.0, 6.0, and 7.0; the range tested by Turner et al. 2001), in a 2 (sites) × 4 (pH) factorial design, with 5 replicates/species.

We used Spearman correlations to test correlations between pH and stream inorganic P or bryophyte tissue P. We used 2-way analysis of variance to test for effects of species/population, pH, or their interaction on PMEase activity (separate experiments run in Peters Kill and Palmaghatt Kill water). We set an a priori $p = 0.05$ as a cutoff for statistical significance, and we $\sqrt{(x)}$-transformed data prior to these analyses to improve normality.

RESULTS

Species distributions

In total, 33 species (25 mosses and 8 liverworts) were collected. Of these, 15 were recorded from ≥3 streams. Some species occurred in broad or restricted pH ranges (Fig. 1). For instance, *Andreaea rothii* was restricted to low-pH sites, *H. ochraceum* was restricted to more neutral sites, and *Codriophorus aduncoides* occurred in low and neutral pH streams.

To test the importance of pH to bryophyte species distributions, we constructed and analyzed an NMDS ordination that was constrained to 2 dimensions (stress = 11.470; Fig. 2A, B). The *envfit* analyses indicated that pH was the strongest or 2nd strongest variable driving species distributions, depending on season. pH was the most significant variable in spring ($r^2 = 0.605$, $p < 0.001$; Table 1, Fig. 2A) and was 2nd strongest in summer ($r^2 = 0.485$, $p < 0.001$) when bedrock was the most significant variable ($r^2 = 0.545$, $p < 0.001$; Table 1, Fig. 2B). However, these variables were significantly correlated in summer ($r_s = -0.575$, $p = 0.002$; Table 2).

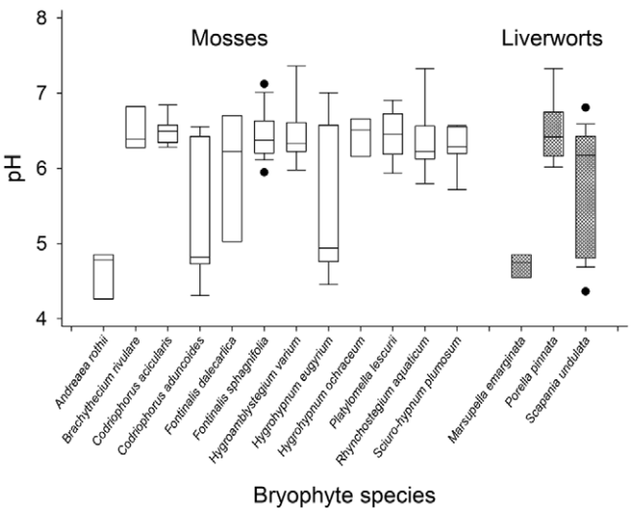

Figure 1. Box-and-whisker plots showing pH of streams (26 streams sampled during 2 seasons) in which each bryophyte species was found (spring samples). Lines in boxes are medians, box ends are the upper and lower quartiles, whiskers are 5th and 95th percentiles, and the outer points are extreme values.

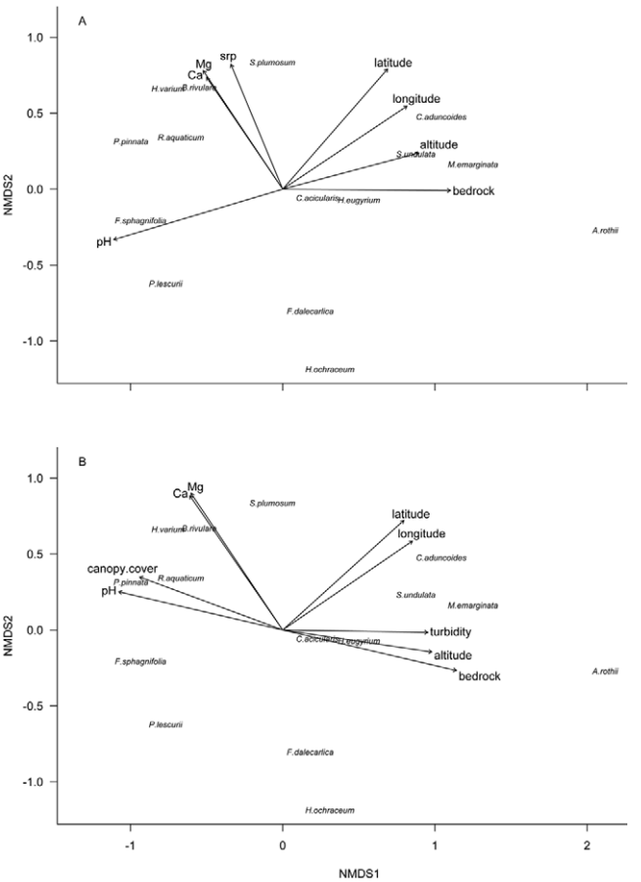

Figure 2. Nonmetric multidimensional scaling (NMDS) ordinations of bryophyte species from 26 streams, with significant ($p \leq 0.01$) spring (A) and summer (B) environmental vectors fitted using *envfit*. Arrows indicate the direction of the (increasing) environmental gradient, and their lengths are proportional to their correlations with the ordination. Full species names are listed in Fig. 1. SRP = soluble reactive P.

Aside from pH and bedrock, these analyses identified latitude, longitude, altitude, and dissolved Ca and Mg as important factors in both seasons. Species distributions were significantly correlated with SRP concentration in spring, and % canopy cover and turbidity in summer (Table 1, Fig. 2A, B). Latitude, longitude, and SRP in the spring, and turbidity in the summer all had linear relationships with the NMDS axes, whereas the other significant variables showed nonlinear relationships.

Ten environmental variables were identified as affecting species distributions, but several were significantly correlated with each other (Table 2). For instance, pH was significantly correlated with latitude ($r_s = -0.736$, $p < 0.001$) and altitude ($r_s = -0.680$, $p < 0.001$) in spring, and

Table 1. The range of environmental variables and the findings from correlations between the environmental variables and the nonmetric multidimensional scaling ordination for spring and summer using *envfit* analysis. Significant findings ($p \leq 0.01$) are displayed in bold.

			Envfit: spring		*Envfit*: summer	
Environmental variables	Range: spring	Range: summer	p	r^2	p	r^2
pH	4.24–7.14	4.77–7.51	**<0.001**	0.605	**<0.001**	0.485
Bedrock (%)	0–75	1–75	**<0.001**	0.548	**<0.001**	0.545
Latitude	41.148–41.767	41.148–41.768	**<0.001**	0.497	**0.002**	0.458
Longitude	74.066–74.329	74.066–74.330	**0.004**	0.436	**0.003**	0.423
Mg (mg/L)	0.06–2.80	0.04–3.27	**0.005**	0.399	**0.002**	0.465
Altitude (m)	149–541	150–541	**0.006**	0.386	**0.003**	0.389
Ca (mg/L)	0.1–6.5	0.1–7.7	**0.003**	0.357	**0.002**	0.457
Soluble reactive P (µg/L)	5.5–10.4	0.5–20.7	**0.008**	0.357	0.959	0.004
Dissolved organic C (mg/L)	1.7–6.8	1.8–8.5	0.017	0.315	0.164	0.168
Flow (cm/s)	0.03–0.91	0.05–1.51	0.018	0.304	0.033	0.258
Canopy cover (%)	16–100	4–100	0.026	0.291	**0.008**	0.398
Conductivity (µS/cm)	21–96	0–41	0.043	0.240	0.196	0.148
Macroalgae abundance	0–5	1–5	0.063	0.224	0.077	0.216
Turbidity (NTU)	12.6–54.0	6.0–58.0	0.085	0.203	**0.010**	0.360
Temperature (°C)	4.0–13.2	12.8–20.4	0.086	0.196	0.187	0.152
Boulders (%)	0–90	1–90	0.203	0.132	0.198	0.145
Shannon diversity	0.562–2.221	0.562–2.222	0.301	0.108	0.440	0.080
Species richness	2–11	3–11	0.317	0.104	0.503	0.064
Lichen abundance	0–3	0–3	0.325	0.101	0.251	0.127
Simpson diversity	0.375–0.875	0.375–0.876	0.345	0.097	0.463	0.078
Dissolved O_2 (mg/L)	9.10–12.91	5.72–10.15	0.345	0.094	0.030	0.288
Fe (mg/L)	0.06–0.20	0.01–0.53	0.372	0.083	0.710	0.039
Dissolved O_2 (%)	76–100	60–98	0.453	0.075	0.097	0.208
Abundance	4–16	5–16	0.573	0.052	0.313	0.113
NO_3^- (µg/L)	0.003–0.156	0.003–0.203	0.646	0.040	0.086	0.212
NH_4^+ (µg/L)	22.0–65. 2	1.2–97.4	0.681	0.037	0.320	0.111
Depth (cm)	7–40	7–56	0.775	0.024	0.041	0.262
Riffles and runs (% area)	50–98	70–98	0.813	0.023	0.602	0.050
Vascular plant abundance	0–3	0–3	0.840	0.016	0.692	0.035
Width (cm)	1.1–5.6	1.0–6.7	0.894	0.011	0.498	0.067

bedrock (r_s = 0.575, p = 0.002) and % canopy cover (r_s = 0.536, p = 0.005) in summer. Species richness, diversity, and abundance were correlated, but only abundance was correlated with any other variable (longitude, r_s = –0.547, p = 0.004).

PMEase activity and pH

Concentrations of inorganic P in stream water were positively correlated with pH during the summer sampling period (r_s = 0.915, p < 0.001; Fig. 3A). Bryophyte tissue P concentrations were significantly, but weakly, correlated with streamwater pH (r_s = 0.374, p = 0.038; Fig. 3B).

PMEase activity experiments using source water from 2 streams adjusted to 4 pH levels, indicated 2 broad patterns in bryophyte responses to pH, depending on population and species. Several bryophytes showed decreased activity with greater pH, whereas others had peaks in activity with moderate acidity (Fig. 4A, B). The pH effect was most pronounced in *Fontinalis* cf. *dalecarlica* collected from the lower pH site (Peters Kill), whereas PMEase activity in *F.* cf. *dalecarlica* from neutral Palmaghatt Kill was largely indifferent to pH over the experimental range of 4 to 7 or peaked at moderate pH. Activity levels of *F.* cf. *dalecarlica* also differed by population, with greater PMEase in Peters Kill plants than in those from Palmaghatt Kill.

PMEase activity in *Scapania undulata* (from Peters Kill) also varied inversely with pH in Peters Kill source

Table 2. Spearman correlations between environmental variables identified as significant in *envfit* and measures of species richness, diversity, and abundance for spring (top right) and summer (bottom left, and in italics). Significant findings ($p \leq 0.01$) are displayed in bold.

Variable	Lat	Long	Alt	Ca	Mg	SRP	Bedr	Can	pH	Turb	S	D	H′	Abun
Latitude (Lat)		0.481	0.327	−0.139	−0.145	0.189	0.228	0.019	**−0.736**	−0.119	0.045	0.002	−0.002	−0.370
Longitude (Long)	*0.481*		0.123	−0.396	−0.398	−0.204	0.319	−0.082	−0.394	−0.218	0.002	−0.050	−0.073	**−0.547**
Altitude (Alt)	*0.327*	*0.123*		**−0.501**	−0.397	0.019	0.438	0.005	**−0.680**	−0.302	0.217	0.178	0.180	0.180
Ca	*−0.254*	***−0.579***	*−0.442*		**0.899**	**0.506**	**−0.666**	0.070	0.450	0.108	−0.129	−0.110	−0.120	−0.038
Mg	*−0.191*	***−0.552***	*−0.369*	***0.960***		**0.585**	**−0.605**	0.005	0.419	0.195	−0.049	−0.048	−0.061	0.040
Soluble reactive P (SRP)	*−0.222*	*−0.455*	*−0.104*	***0.573***	***0.593***		−0.320	0.243	−0.025	0.195	0.021	0.012	−0.013	0.075
Bedrock (Bedr)	*0.228*	*0.319*	*0.438*	***−0.661***	***−0.643***	*−0.496*		−0.056	−0.447	−0.283	0.154	0.147	0.132	0.007
Canopy cover (Can)	*0.250*	*−0.090*	*−0.035*	*0.337*	*0.311*	*0.022*	*−0.087*		0.200	0.234	−0.106	−0.109	−0.126	0.077
pH	*0.023*	*−0.266*	*−0.421*	*0.488*	*0.440*	*0.414*	***−0.575***	***0.536***		0.441	−0.159	−0.138	−0.132	0.131
Turbidity (Turb)	*0.215*	***0.568***	*0.397*	*−0.395*	*−0.326*	*−0.170*	*0.233*	*−0.085*	*−0.410*		−0.011	−0.004	0.022	0.229
Species richness (S)	*0.045*	*0.002*	*0.217*	*−0.076*	*−0.040*	*−0.160*	*0.154*	*0.088*	*−0.139*	*0.158*		**0.970**	**0.973**	**0.588**
Simpson diversity (D)	*0.002*	*−0.050*	*0.178*	*−0.054*	*−0.022*	*−0.182*	*0.147*	*0.092*	*−0.101*	*0.082*	***0.970***		**0.997**	**0.630**
Shannon diversity (H′)	*−0.002*	*−0.073*	*0.180*	*−0.067*	*−0.033*	*−0.182*	*0.132*	*0.071*	*−0.100*	*0.053*	***0.973***	***0.997***		**0.639**
Abundance (Abun)	*−0.370*	***−0.547***	*0.180*	*0.147*	*0.154*	*0.056*	*0.007*	*0.095*	*−0.143*	*−0.090*	***0.588***	***0.630***	***0.639***	

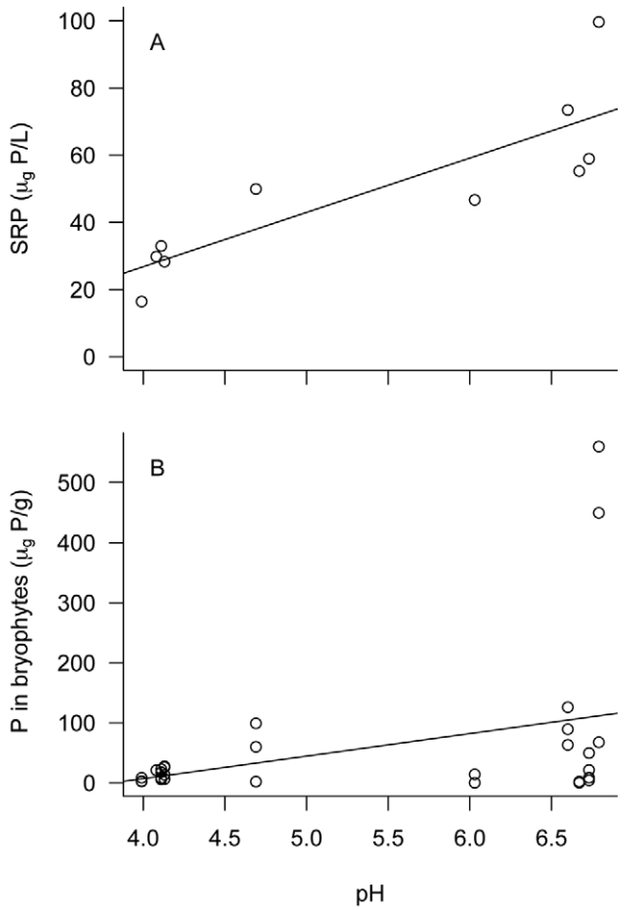

Figure 3. The relationship between aqueous pH and soluble reactive P (SRP) in stream water (A) and P content in bryophyte tissues (B) in 10 streams.

water, whereas PMEase activity peaked at an intermediate pH in Palmaghatt Kill source water. In contrast, *H. ochraceum* from Palmaghatt Kill had maximum PMEase activity at an experimental pH of 5, regardless of the source stream water (Fig. 4A, B). Two-way ANOVA for the experiment using Palmaghatt Kill water revealed significant populations/species (F = 84.655, p < 0.001) and pH (F = 34.379, p < 0.001) effects on PMEase activity, and a significant interaction of these factors (F = 6.839, p < 0.001). A similar test for experiments using Peters Kill water also yielded significant populations/species (F = 46.690, p < 0.001) and pH (F = 38.309, p < 0.001) effects on PMEase activity, but a nonsignificant interaction of these factors (F = 2.523, p = 0.064).

DISCUSSION

Few investigators have evaluated aquatic bryophyte distributions in relation to a wide pH range. We are aware of only 3 such studies, all conducted in Europe (Ormerod et al. 1987, Paavola et al. 2006, Virtanen et al. 2009), and none examined the influence of pH on distributions and its potential link to nutrient acquisition. Our study suggests that pH strongly influenced species distributions. These results are corroborated by the European studies, in which pH was one of the strongest influences on bryophyte species distributions. Several species in our study streams had relatively narrow pH optima, occurring in low (e.g., *A. rothii*, *M. emarginata*) or neutral (e.g., *H. ochraceum*, *Codriophorus acicularis*) pH waters. Others, such as *H. eugyrium*, had comparatively broad pH tolerances. *Andreaea rothii*, although usually reported as growing in seepy acidic environments, is not generally reported as being truly aquatic (e.g., Allen 2005). The populations we

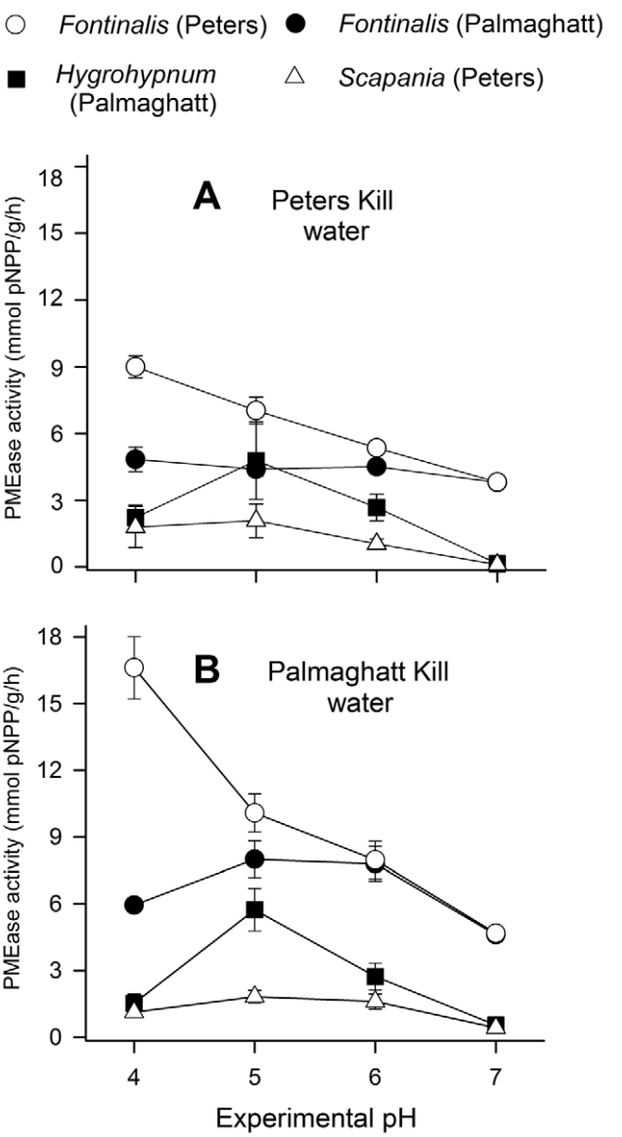

Figure 4. The relationship between pH and phosphomonoesterase (PMEase) activity for several bryophyte species and populations collected from a low-pH stream (Peters Kill) (A) and a neutral stream (Palmaghatt Kill) (B).

examined were always submersed. The influence of pH could not be assessed directly in the field portion of our study because pH was correlated with several other significant variables (e.g., altitude, bedrock, and % canopy cover).

The distribution of individual species did vary with pH, but we did not observe a general trend with species richness, diversity, or abundance, in contrast to some past studies. Some investigators have observed greater species richness and diversity at sites with low pH (Suren and Ormerod 1998, Heino et al. 2005), whereas in a study in the Canadian Rockies, alkaline sites had greater diversity (Glime and Vitt 1987). Bryophyte abundance also was negatively correlated with pH in some locations (Cattaneo and Fortin 2000). However, Paavola (2003) suggested that pH was less important than habitat heterogeneity and size of substrata for bryophyte species abundance and richness.

Canopy cover and turbidity, factors that have not been studied extensively for stream bryophyte distributions, also were significantly related to species distributions in our streams. Canopy cover was suggested as a significant predictor of variation in cover of terrestrial pleurocarpous mosses (Pharo and Vitt 2000) and of species richness for epiphytic bryophytes (Steffan-Dewenter et al. 2007). Aquatic bryophytes also can be more susceptible to burial by sediment than other aquatic macrophytes (Jones et al. 2012), and experimental increases of fine sediments in New Zealand decreased bryophyte abundance (Matthaei et al. 2006).

The Shawangunk ridge is largely composed of conglomerate bedrock that causes streams to have low pH, but the shale that the ridge sits on buffers water (Chowdhury and Giles 2007). Percent bedrock in the stream bed was the most significant factor in summer, but it was significantly correlated with pH, a finding that seems logical given our knowledge of this bedrock's influence on water pH. We also demonstrated that Mg and Ca were positively correlated, and Mg, Ca, and bedrock were significant factors in the vector-fitting analyses. Tahvanainen (2004) found a strong unimodal growth response to Ca in *Scorpidium revolvens*, which matches the Ca concentrations of fens in this species' natural distribution in Sweden. However, in the same study, Tahvanainen (2004) found no correlation between Mg and plant growth, despite the absence of *S. revolvens* from high-Mg fens.

SRP, but not NH_4^+ or NO_3^-, was identified as a significant factor influencing species distributions. Bryophytes have an important role in P cycling in headwater streams (Meyer 1979), and many species have the ability to acquire organic P when SRP is present in physiologically limiting concentrations (Christmas and Whitton 1998a, Turner et al. 2001).

In our study, pH and SRP were strongly linked with stream bryophyte distributions, so we assayed PMEase activity in selected species and populations. Studies conducted in Europe have shown that phosphatases, particularly PMEase, allow stream bryophytes to use organic P where inorganic P is largely unavailable, such as in low-pH streams, and that PMEase activity peaks at a pH < 7 (Tate et al. 1995, Christmas and Whitton 1998b, Gross 2000, Turner et al. 2001). Collectively, the results of these studies suggest that organic P may be an important resource for aquatic bryophytes in streams with below-neutral pH and physiologically limiting concentrations of inorganic P. Our findings corroborate those of these earlier works, in that we observed a significant positive correlation between inorganic P and pH in headwater streams (i.e., low levels of P at low pH), and bryophyte PMEase activity peaked at pH levels below neutral. Bryophytes also had greater P concentrations in their tissues in streams with higher pH. This correlation was significant but weaker than for stream inorganic P and was strongly influenced by 2 data points, a result that suggests that PMEase may compensate for physiologically limiting supplies of inorganic P. This idea is further supported by data from Ellwood et al. (2008), who found that phosphatase activity increased as tissue P decreased in *Fontinalis squamosa*.

PMEase activity in all species and populations measured appeared to peak at pH < 7, a result suggesting that organic P may become a necessary source of P at lower pH. However, different species and populations appear to be differentially adapted to dealing with inorganic P shortages because PMEase activity differed between species and populations. Those found in lower-pH streams tended to have peak PMEase activity at the lowest pH conditions tested, whereas those found in more neutral water tended to have peak PMEase activity at intermediate levels of pH. Within a single river system, Christmas and Whitton (1998a) observed that individuals of 2 bryophyte species had PMEase activity that increased with upstream distance, where inorganic P became increasingly scarce while pH decreased. Thus, phosphatase enzyme differences between species and populations may provide an explanation for why species' and populations' distributions in streams appear to be strongly linked to pH. In addition, pH may alter the availability of other required nutrients (Brady and Weil 2008), and species may have correspondingly different nutrient requirements.

Our data suggest that pH is an important factor affecting stream bryophyte distributions, and that its influence may be coupled with the ability of plants to acquire scarce supplies of P. Given that some species appear to have narrow or broad tolerances, further studies, such as reciprocal transplants coupled with laboratory experiments, are needed to identify the ways in which pH may more directly affect aquatic bryophyte activity, growth, and distribution.

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