

Do small headwater streams have a riparian zone defined by plant communities?

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Abstract: Defining riparian zones is important because sustainable forestry programs typically include a requirement to protect riparian zones. To help determine whether small first-order headwater streams have a riparian zone, we surveyed vascular plant communities along 15 streams in a managed forest landscape in western Maine, USA. Along each stream we recorded all vascular plant species in 5 m × 50 m quadrats at different lateral distances from the stream bank: 0–5, 13–18, 25–30, and 40–45 m. Trees and shrubs showed no statistical differences among zones in either species richness or community composition. Species richness of herbaceous plants was greater in the 0–5 m zone adjacent to the stream bank than in other zones, and species composition of herbaceous plants was statistically different in the 0–5 m zone relative to more distant zones. Twenty-four herbaceous species (of 129) were determined to be indicators of the riparian plant community. Twenty-three of the 24 indicator species were more likely to occur near the stream, and 1 species was more likely to be found away from the stream (a negative riparian indicator). These results show that a narrow riparian zone exists on small headwater streams that is reflected by the herbaceous plant community.

Résumé : La définition des zones riveraines est importante parce que les programmes de foresterie durable exigent généralement la protection des zones riveraines. Afin d'aider à déterminer si une zone riveraine borde les petits cours d'eau de premier ordre situés en amont, nous avons inventorié les communautés de plantes vasculaires le long de 15 cours d'eau dans un paysage de forêt aménagée de l'ouest du Maine, aux États-Unis. Pour chaque cours d'eau, nous avons noté toutes les espèces de plantes vasculaires dans des parcelles de 5 m × 50 m établies à différentes distances de la rive des cours d'eau : 0–5, 13–18, 25–30 et 40–45 m. Il n'y avait aucune différence significative entre les zones en termes de richesse en espèces ou de composition des communautés dans le cas des arbres et des arbustes. La richesse en espèces herbacées était plus grande dans la zone de 0–5 m adjacente à la rive des cours d'eau comparative-ment aux autres zones et la composition en espèces herbacées de la zone 0–5 m était statistiquement différente de celle des zones plus distantes. Vingt-quatre espèces herbacées (sur 129) ont été identifiées comme étant indicatrices de la communauté végétale des milieux riverains. Vingt-trois de ces 24 espèces indicatrices se développaient principalement près des cours d'eau et 1 espèce se retrouvait généralement dans des milieux distants des cours d'eau (un indicateur riverain négatif). Ces résultats montrent qu'il existe une étroite zone riveraine le long des cours d'eau situés en amont et qu'elle se manifeste par la communauté des plantes herbacées.

[Traduit par la Rédaction]

Introduction

Foresters typically retain forested buffers along streams and other water bodies to protect aquatic systems from potential impacts of timber harvesting (Blinn and Kilgore 2001). One of the most debated questions in forest management has been "how wide should buffers be"; wider buffers represent greater forgone timber revenue for the landowner. Debates about buffer width are fueled by a lack of science and a lack of understanding that different riparian-zone values require different buffer widths (e.g., maintaining clean water requires less of a buffer than maintaining clean, cool

water). To help foresters determine the proper buffer width, much research has been focused on defining the riparian zone (Ilhardt et al. 2000).

One of the most widely used indicators of a riparian zone is the plant community. Riparian zones are known to contain high levels of plant biodiversity relative to upland forest (Gregory et al. 1991; Décamps and Tabacchi 1994; Naiman and Décamps 1997). This greater diversity may be attributed to geomorphology, hydrology, frequency and spatial extent of flooding, and lateral migration of streams (Gregory et al. 1991; Naiman et al. 1993, 2000). The geomorphic structure of each stream zone is reflected in patterns of the adjacent plant community, which explains why plants have been used to delineate the riparian zone (Reed 1988).

Much of the research on forestry and riparian zones has been conducted on larger, higher order streams (second order and above) (e.g., Spackman and Hughes 1995; Hughes and Cass 1997). Very little work has been done on small perennial streams or intermittent and ephemeral tributaries (Goebel et al. 2003; Becker and Pallardy 2003). Until recently, it had largely been assumed that such small streams have little or no riparian zone. However, Kahl (1996) sug-

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gested that smaller streams may need *wider* buffers than larger streams because small streams have small volumes of water and consequently greater sensitivity to environmental change. By contrast, Naiman et al. (1993) suggested that some first-order headwater streams may not have a discernible riparian zone based on vegetation. If small headwater streams have a riparian zone that warrants protection, such protection could be financially costly because first-order streams constitute 65%–75% of the total linear length of riparian systems in some watersheds (Leopold et al. 1964), and protecting such streams could potentially encumber a large amount of timber.

In Maine (USA), riparian-zone regulations for unorganized (unpopulated) townships require that shade be left over streams that drain less than 129.5 km² and more than 1.2 km² (classified as P-SL2 streams; Maine Land Use Regulation Commission 1999). Forest managers commonly exceed the regulation by leaving a ~23 m (75 ft) wide intact or partially cut buffer strip on each side of streams designated P-SL2. No buffer or shade is required along stream segments that drain less than 1.2 km², but public concern for the integrity of headwater streams has grown in recent years, and the policy debate continues.

The purpose of this study was to determine whether small headwater streams in a commercial forest landscape in Maine have a riparian zone that can be identified using plant communities. If we can detect a riparian zone based on plant communities, how far does the zone extend laterally from the stream, and which plant species are the best indicators of this extent? Such knowledge is fundamental to considering whether forested buffers might be needed along first-order headwater streams, and how wide they should be.

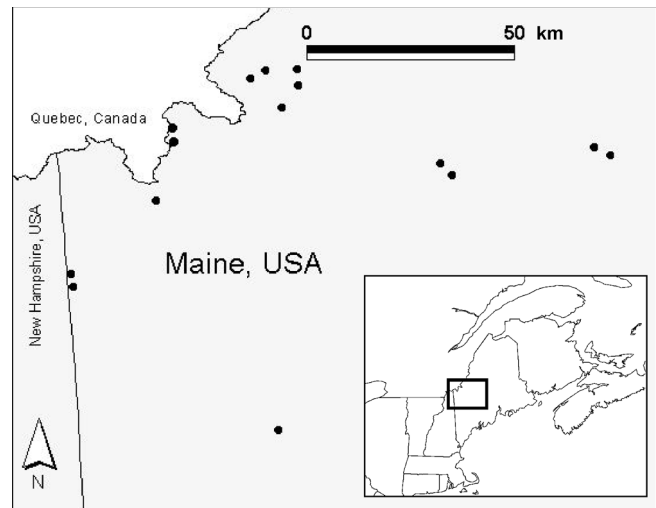
Methods

Study area

We selected 15 first-order headwater streams in the western mountainous region of Maine for study between June 2000 and May 2001 (Fig. 1). All streams were located within a 100 km radius of 45°00'00"N, 70°20'00"W. We determined stream order on the basis of topographic maps and ground truthing. Selected streams had had no adjacent logging for at least 20 years and had mature, closed-canopy (>85%) forest extending at least 200 m from both sides of each stream, for a 500 m length of stream. All streams were narrow (mean 3.0 m bankfull width (width of mineral soil – vegetation margins)) with a relatively high downstream gradient (mean 11.7%; Table 1). Lateral gradients were steeper than downstream gradients and averaged 17.4%, indicating a relatively deep topographic incision characteristic of streams in mountainous terrain. The wetted stream width was typically about one-half the bankfull width, but was highly variable from week to week depending on the timing of individual rainfall events (Table 1). Stream drainages were small, ranging from 30 to 195 ha (Table 1).

The study area was within the hemiboreal zone, a transition characterized by tree species common to the boreal zone and the temperate zone. All study streams were within Bailey et al.'s (1994) Adirondack – Northern Highlands ecoprovince. This ecoprovince is composed of subdued glaciated mountains and maturely dissected plateaus of moun-

Fig. 1. Locations of 15 study streams in western Maine.



tainous topography (Omernik 1987). The average annual temperature is 5.1 °C and average annual rainfall is 104.8 cm (National Oceanographic and Atmospheric Administration 2002).

Study streams were bordered by mature mixedwood (beech/birch/maple/spruce/fir) stands on lands owned or managed by Plum Creek Timber Company, International Paper, Seven Islands Land Company, and Mead–Westvaco. Dominant tree species in the understory included striped maple (*Acer pensylvanicum*), yellow birch (*Betula allegheniensis*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), mountain maple (*Acer spicatum*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*). Dominant shrubs included hobblebush (*Viburnum lantanoides*) and beaked hazelnut (*Corylus cornuta*). The most common herbaceous species were wild sarsaparilla (*Aralia nudicaulis*), bluebead (*Clintonia borealis*), Canada mayflower (*Maianthemum canadense*), common woodsorrel (*Oxalis montana*), whorled aster (*Oclemea acuminata*), twistedstalk (*Streptopus lanceolatus*), starflower (*Trientalis borealis*), and intermediate woodfern (*Dryopteris intermedia*).

Vegetation sampling

Vascular plants along each study stream were sampled from 24 July through 23 August 2001. Along each stream, four 5 m × 50 m quadrats (= 250 m²) were placed parallel to the stream at lateral distances from the stream bank (0–5, 13–18, 25–30, and 40–45 m; Fig. 2). The total area sampled on each stream was 1000 m². A 250 m² plot is much larger than is used in most herbaceous plant studies and should allow a thorough assessment of the full plant community (Small and McCarthy 2002). The plot immediately adjacent to the stream (0–5 m) was sampled within an irregularly shaped “rectangle” that precisely paralleled the stream channel (Fig. 2). The remaining plots were parallel to the stream orientation but had straight sides (Fig. 2). We chose parallel quadrats at four categorical distances from the stream rather than continuous perpendicular quadrats because parallel quadrats covered 150% more sampling area (for the selected distance categories) than the same sampling effort using perpendicular transects.

Table 1. Physical characteristics of the 15 study streams.

Stream No.	Elevation (m)	Watershed area (ha)	Aspect	Bankfull width (m) ^a	Canopy closure (%) ^{a,b}	Lateral gradient (%) ^{a,c}	Channel gradient (%) ^a	Flow (m ³ /min) ^d
1	681	30	NW	1.7	91	11	16	0.022
2	494	52	E	2.8	93	31	12	0.022
3	647	41	S	3.7	93	12	13	0.081
4	372	96	SE	3.9	92	4	12	0.003
5	425	80	NW	2.0	86	6	7	0.033
6	648	37	E	2.0	91	19	14	0.013
7	664	53	SW	2.9	88	14	14	0.085
8	389	67	E	2.3	91	19	10	0.102
9	487	185	W	3.7	85	24	12	0.138
10	623	58	W	2.1	93	21	14	0.082
11	483	44	E	2.1	93	23	11	0.040
12	660	140	N	4.6	78	16	5	0.101
13	721	82	SE	2.1	84	33	12	0.151
14	491	71	NW	4.6	94	6	14	0.038
15	608	195	NW	4.1	94	22	10	0.092

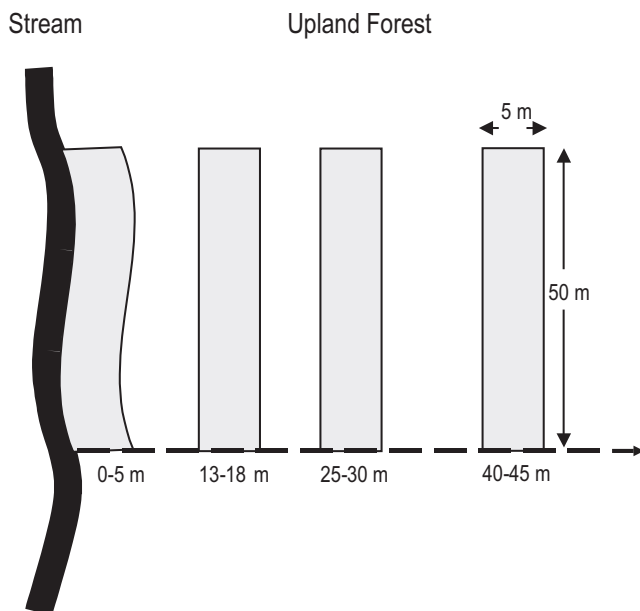
^aMean of three readings taken 20 m apart within the stream adjacent to the vegetation quadrats.

^bTaken with a spherical densiometer in the center of the stream channel.

^cTaken with a clinometer by sighting on a pole located 10 m from the stream center (using observer’s eye height) on the side of the vegetation quadrats.

^dMeasurements were taken on three occasions between 20 May and 25 June 2001.

Fig. 2. Schematic of four 5 m × 50 m (= 250 m²) sampling quadrats along each of 15 study streams. The total area sampled along each stream was 1000 m². The long edge of the plot immediately adjacent to the stream followed the sinuosity of the stream. In each sampling plot, all vascular plant species (trees, shrubs, and herbaceous plants) rooted within the 5 m × 50 m area were identified and assigned an abundance code.



Within each plot we recorded all tree, shrub, and herbaceous plant species. Each species encountered within a plot was assigned a code for species abundance within the plot (“1” for 1 individual, “2” for 2–10 individuals, “3” for 11–50 individuals, “4” for 51–100 individuals, and “5” for >100 individuals), but for multivariate analyses we used only presence/absence information. The 0 m side of the 0–5 m

quadrat began at the exposed mineral soil – vegetation barrier on the stream bank. The nomenclature of all plant taxa follows Haines and Vining (1998).

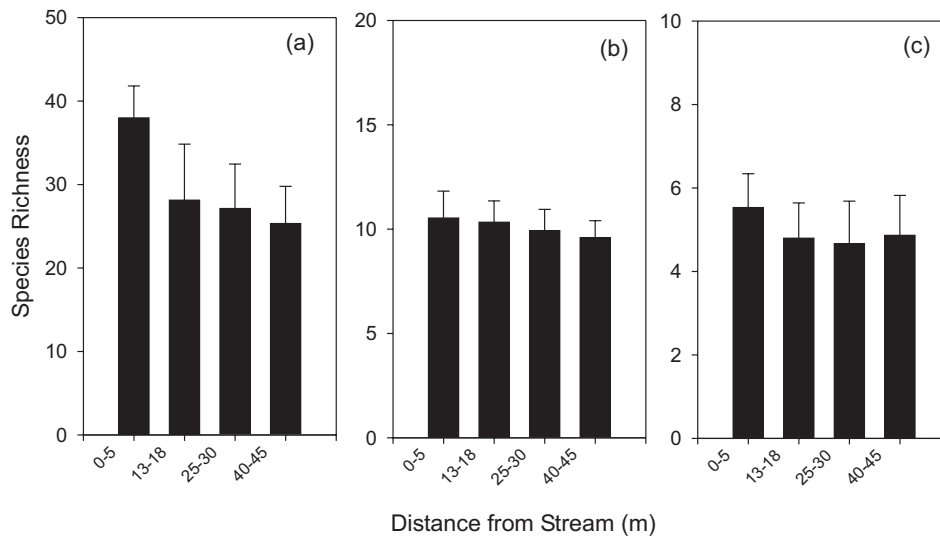
Data analysis

To understand vegetation patterns in relation to species–habitat associations, we assigned herbaceous species to one of six primary habitat categories: forest specialist, generalist, disturbance specialist, wetland–forest specialist, wetland generalist, and wetland disturbance species. We first assigned each species to the forest specialist, generalist, or disturbance specialist category on the basis of habitat associations described in Haines and Vining (1998). If the species was listed as a “facultative wetland” or “obligate wetland” species by Reed (1988), we added “wetland” to the designation. Using Haines and Vining (1998) we also categorized each species as common, occasional, uncommon, or rare.

Some plant specimens could only be identified to genus because they lacked the necessary reproductive structures for identification, or because the specimen was too immature to distinguish from congeners. For analyses, specimens that could not be identified below genus were dealt with according to the following rules: (1) if there were more total occurrences of individuals that could be identified to species in a given genus than of individuals that could be identified only to genus, then the latter were eliminated from the analysis (e.g., *Osmorhiza berteroi* and *Osmorhiza claytonii* were kept, while *Osmorhiza* spp. was dropped) and (2) if there were more total occurrences of individuals that could be identified only to genus than of individuals that could be identified to species of that genus, then the latter were lumped with the “genus spp.” occurrences (e.g., *Prenanthes altissima* was combined with *Prenanthes* spp.).

The result of this procedure was that 12 specimens identified only to genus were excluded from analysis, and 4 speci-

Fig. 3. Mean species richness for herbaceous plants (a), shrubs (b), and trees (c) for each of the four sampling zones adjacent to the study streams. Error bars represent 95% confidence intervals of the mean.



mens identified to species were combined with others in the same genus. The total herbaceous and shrub “species” count changed from 161 to 146 taxonomic units by applying these rules. We felt that this procedure represented a responsible approach to retaining as much taxonomic information as possible for analysis.

To compare species richness among zones we used standard ANOVA (SAS Institute Inc. 1989). We analyzed richness of trees, shrubs, and herbaceous plants separately. We also used ANOVA to compare the proportions of herbaceous plants among the four stream distance zones in different habitat association categories and the proportion of herbaceous plants by commonness categories. For these analyses we arcsine-transformed all proportions prior to analysis in order to improve the normality of small or large proportions (Zar 1999).

We examined plant-community changes with distance from the stream both graphically and statistically. To graphically examine changes we conducted a community ordination of tree species, shrub species, and herbaceous species using nonmetric multidimensional scaling (McCune and Medford 1999; PC-ORD Version 4, Gleneden Beach, Oreg.), which is an ordination technique well-suited to data that are non-normal or binary (e.g., presence/absence) (Clarke 1993). We statistically tested for differences in tree, shrub, and herbaceous species composition among zones using the multiresponse permutations procedure in PC-ORD (McCune and Medford 1999); this is a non-parametric test based on the Euclidean distances among groups (in our case, distance zones) (Mielke 1984; Mielke and Berry 2001) and has the advantage of not being dependent on distributional assumptions, which are seldom met with ecological community data (McCune and Grace 2002). We used canonical correspondence analysis (ter Braak 1994; Økland 1999) to explore and test for relationships between the herbaceous plant community structure (main matrix) and stream physical variables (secondary matrix) listed in Table 1. However, our sample (15 streams) was small for using this statistical approach. We used indicator species analysis (PC-ORD Version 4) to

identify species that showed strong occurrence gradients among the four zones (Dufrêne and Legendre 1997; McCune and Medford 1999). Indicator-species analysis uses a Monte Carlo method to randomly reassign sampling units (quadrats in this study) to different groups (zones in this study) to calculate the highest possible indicator value for a species (range = 0–1, where 1 is a perfect indicator species — a species that occurs in only one group (i.e., zone)). We used 1000 Monte Carlo runs for this analysis.

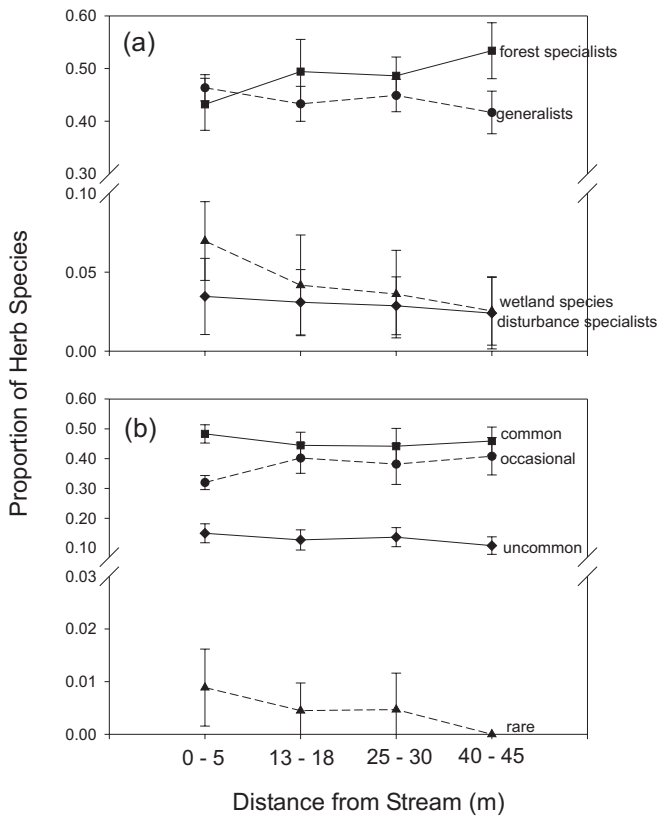
Results

We detected 129 herbaceous species, 17 shrub species, and 28 tree species. Mean species richness per 5 m × 50 m plot for herbaceous plants was greater within the 0–5 m zone adjacent to the stream than in the other three zones more distant from the stream ($P = 0.002$; Fig. 3). There were no differences in herbaceous species richness among the three zones most distant from the stream ($P = 0.73$). There were no differences in species richness among the four zones for either shrubs ($P = 0.48$) or trees ($P = 0.54$).

The proportion of forest-specialist herbaceous species increased significantly with distance from the stream ($P = 0.03$), and the proportion of wetland herbaceous species decreased with distance from the stream ($P = 0.04$) (Fig. 4a). The proportions of generalist herbaceous species ($P = 0.17$) and disturbance-specialist herbaceous species ($P = 0.82$) remained about the same with distance from the stream. There were no differences among the zones in the proportion of herbaceous species that were a priori classified as common ($P = 0.07$), uncommon ($P = 0.19$), occasional ($P = 0.52$), or rare ($P = 0.12$) (Fig. 4b).

Herbaceous communities varied statistically among the four zones (multiresponse permutation procedure, $P = 0.02$; Fig. 5), but neither shrub ($P = 0.80$) nor tree ($P = 1.00$) communities varied. When nonmetric multidimensional scaling was used to ordinate plots based on species composition, it was clear that herbaceous communities associated with the 0–5 m zone were different from those in the three more dis-

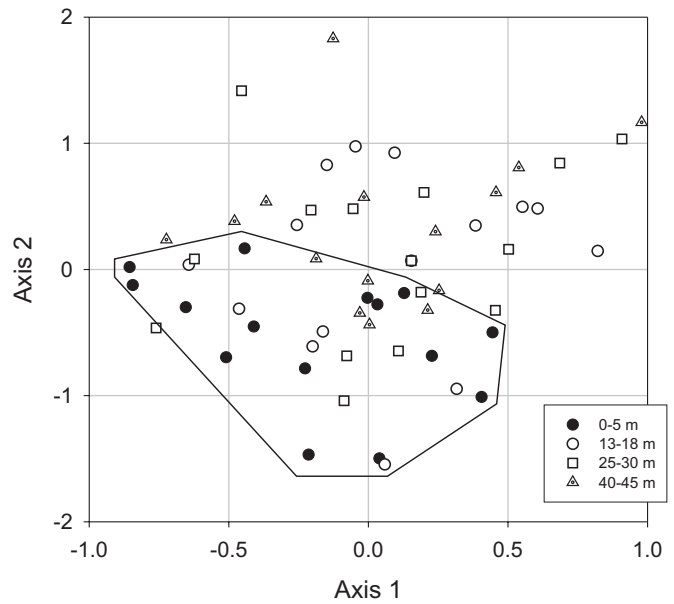
Fig. 4. (a) Proportions of herbaceous species that were forest specialists, disturbance specialists, wetland specialists, and generalists at different distances from the stream bank. (b) Proportions of herbaceous species at different distances from the stream bank that were common, occasional, uncommon, or rare.



tant zones (Fig. 5). Rerunning the multiresponse permutation procedure with only data on herbaceous communities from the three outer zones revealed no significant differences among zones ($P = 1.00$), suggesting that the differences among all four zones were driven by plant differences in the 0–5 m zone. Using only the data on herbaceous communities from the 0–5 m zone, we found no significant relationship between the herbaceous community and any of the stream physical parameters listed in Table 1 (canonical correspondence analysis, $P = 0.25$), but our sample for this analytical method was small (15 streams).

Because of the statistical differences among zones for herbaceous species, we employed indicator-species analysis to explore which species best distinguished the four zones. Twenty-four of the 129 species were shown to be good indicators of a lateral gradient (Table 2). Of these 24 species, 23 were more common in the 0–5 m zone adjacent to the stream than in the more distant zones. Of these 23 species, 10 were forest specialists, 10 were generalists, and 3 were disturbance specialists. Only one species (*Lycopodium dendroideum*) was identified both as a good indicator species and as being more common in the outer zones; this species was completely absent from the 0–5 m zone. Indicator-species analysis does not involve any a priori expectation that species would be more associated with any one of the four zones, therefore it is indicative of a stream–upland gradient that so many of the indicator species were most com-

Fig. 5. Nonmetric multidimensional scaling ordination of 60 plots sampled for herbaceous species in different sampling zones (0–5, 13–18, 25–30, or 40–45 m). The polygon surrounds plots in the 0–5 m zone.



mon in the 0–5 m streamside zone. This shows that it was the presence of species in the 0–5 m zone that was primarily driving the lateral herbaceous-community gradient rather than the absence of upland species near the stream.

Because a stream–upland herbaceous-community gradient was apparent in the data, we examined which species appeared to be driving the gradient. The species most frequently found only in the 0–5 m zone (5 of 15 plots) was *Prunella vulgaris*, a disturbance specialist (Table 3). Of the 16 species that were only detected within 5 m of the stream (0–5 m plots), 6 were forest specialists, 5 were disturbance specialists, 4 were generalists, and 1 was a wetland generalist (Table 3). Because many of these species occurred in only one plot, no statistical conclusions could be drawn about association with the stream.

Sixty species never occurred in the zone farthest from the stream (Table 3). These species represented all six habitat categories (forest specialist, generalist, disturbance specialist, wetland disturbance specialist, wetland–forest specialist, wetland generalist). This list includes more disturbance- and wetland-associated species than the list of indicator species. Common disturbance specialists such as *P. vulgaris* and *Symphitrichum puniceum* were restricted to within 18 m of the streams. However, rare forest specialists such as *Pyrola minor* and *O. berteroi* also were restricted to within 18 m of the streams. *Equisetum sylvaticum* and *Ranunculus abortivus*, which are considered to occur in wetlands 67%–99% of the time in the northeast (Reed 1988), were likewise restricted. *Cardamine pensylvanica* is classified as an obligate wetland species (defined as having a 99% probability of occurring under natural conditions in wetlands) for the Northeast Region (Reed 1988). This species occurred in eight plots, but only once in the 40–45 m zone. Twenty-three of these 60 species were listed as uncommon or rare (not counting

Table 2. List of indicator species, indicator values, statistical significance, and percent frequency of occurrence in plots in different sample zones.

Scientific name	Common name	Habitat guild ^a	Indicator			Percent frequency of occurrence (% of 15 plots in each zone)			
			Mean	SD	P	0–5 m	13–18 m	25–30 m	40–45 m
<i>Phegopteris connectilis</i>	Long beech fern	F	25.7	2.93	0.000	100	67	73	73
<i>Circaea alpina</i>	Alpine enchanter's nightshade	G	19.4	4.42	0.001	80	33	40	27
<i>Gymnocarpium dryopteris</i>	Oak fern	F	19.7	4.32	0.002	87	33	33	33
<i>Prenanthes</i> spp.	White lettuce; rattlesnake root	F	25.6	3.15	0.002	100	67	80	60
<i>Prunella vulgaris</i>	Selfheal	D	8.7	4.38	0.002	33	0	0	0
<i>Streptopus amplexifolius</i>	Twistedstalk	F	18.2	4.53	0.003	80	27	27	27
<i>Solidago flexicaulis</i>	Zigzag goldenrod	G	14.6	4.73	0.006	60	20	20	7
<i>Brachyelytrum septentrionale</i>	Unnamed grass	F	13.1	4.73	0.007	53	13	7	13
<i>Carex leptonevia</i>	Two-edged sedge	G	21.3	4.27	0.007	87	40	40	47
<i>Viola selkirkii</i>	Great-spurred violet	F	9.7	4.57	0.012	33	0	0	13
<i>Oclemena acuminata</i>	Whorled aster	G	26.0	2.56	0.014	100	87	73	67
<i>Thalictrum pubescens</i>	Tall meadow-rue	D	16.5	4.69	0.018	60	33	20	20
<i>Galium triflorum</i>	Sweet-scented bedstraw	F	17.3	4.59	0.018	67	20	33	27
<i>Impatiens</i> spp.	Jewelweeds	G	14.1	4.73	0.025	53	13	20	13
<i>Aster macrophyllus</i>	Big-leaved aster	G	9.1	4.49	0.029	27	7	7	0
<i>Viola blanda</i>	Sweet white violet	F	14.1	4.7	0.038	47	20	13	20
<i>Epipactis helleborine</i>	Helleborine	G	11.5	4.62	0.041	40	7	13	7
<i>Tiarella cordifolia</i>	Foam flower	F	16.9	4.61	0.044	60	27	40	13
<i>Carex arctata</i>	Drooping wood sedge	G	20.9	4.3	0.047	73	53	47	33
<i>Lycopodium dendroideum</i>	Prickly tree clubmoss	F	11.4	4.61	0.051	0	13	33	20
<i>Carex intumescens</i>	Unnamed sedge	G	20.8	4.2	0.072	80	40	47	40
<i>Athyrium filix-femina</i>	Lady fern	F	26.1	2.66	0.073	93	80	67	87
<i>Cinna latifolia</i>	Drooping woodreed	D	22.6	3.94	0.080	87	60	60	33
<i>Mitella nuda</i>	Naked miterwort	G	16.8	4.6	0.096	53	27	40	20

Note: Species are listed in order of increasing indicator *P* value (i.e., decreasing strength as an indicator species).

^aF, forest specialist; G, generalist; D, disturbance specialist; W, wetland-forest specialist; WG, wetland generalist; WD, wetland disturbance specialist.

Lactuca spp. and *Mentha* spp.; both genera potentially contain occasional to very rare species) (Table 3).

Discussion

This study showed that there is a narrow but detectable riparian plant community associated with small first-order headwater streams in our study area. Our data showed that herbaceous plants, but not trees or shrubs, were responsible for the plant-community gradient between the stream and the adjacent upland. The plant-community gradient statistically disappeared somewhere between our 0–5 and 13–18 m sampling zones. Our sampling design did not permit finer determination of gradient boundaries.

There are few empirical data on plant-community gradients adjacent to small first-order and intermittent streams. Becker and Pallardy (2003) studied first- through fifth-order streams in Missouri (USA) and found that vegetation along lower (first and second) order streams was more associated with parent material and underlying bedrock than with fluvial landform. Gemborys and Hodgkins (1971) found a distinctive plant community along intermittent and first-order streams in forest bottomlands in Alabama; factors correlated with the vegetation pattern were water-table depth, soil surface gradient, and soil pH. A vegetation study of intermittent and ephemeral streams in Arizona (USA) showed that plant

composition was related to changes in slope and substrate (Zimmerman et al. 1999). Quinby et al. (2000) studied vegetation patterns from 1 to 30 m from the stream bank on first-through fourth-order streams in Ontario. They found strong plant gradients adjacent to the streams and an average riparian width of 16.5 m based on indicator species; unfortunately, they combined data from all stream orders in the analysis, so riparian width for first-order streams only was not reported (Quinby et al. 2000). Goebel et al. (2003) documented ground-flora gradients perpendicular to intermittent streams in old-growth hardwood forest in Ohio. They found that species were ordered along a complex environmental gradient from the stream edge, across the floodplain, and into the adjacent uplands. Distance from the stream edge was not as good a predictor of plant-community composition as landform (e.g., floodplain, terrace slope), so they did not report a single riparian width represented by the riparian plant community (Goebel et al. 2003). Spackman and Hughes (1995) studied gradients of birds, amphibians, small mammals, and plants perpendicular to third- and fourth-order streams in Vermont (USA). They concluded that 90% of the streamside plant species occurred in a 10–30 m wide zone above the high-water mark (not the stream bank). Spackman and Hughes (1995) noted, as did others, that fluvial landform, especially the high-water mark, was an important correlate of the plant-community gradient. In a

Table 3. Herbaceous and woody shrub species that never occurred in the outermost zone (40–45 m); many species were detected only in the zone closest to the stream (0–5 m).

Scientific name	Common name	Habitat type ^a	Frequency of occurrence ^b	Not detected beyond:
<i>Prunella vulgaris</i>	Selfheal	D	5	5 m
<i>Osmorhiza claytonii</i>	Bland sweet cicely	F	2	5 m
<i>Pyrola minor</i> ^c	Little shinleaf	F	2	5 m
<i>Scutellaria lateriflora</i>	Mad-dog skullcap	WG	2	5 m
<i>Symphiotrichum cordifolium</i>	Common blue heart-leaved aster	G	2	5 m
<i>Taxus canadensis</i>	American yew	F	2	5 m
<i>Carex novae-angliae</i> ^c	New England sedge	F	1	5 m
<i>Dryopteris carthusiana</i> ^c	Spinulose woodfern	F	1	5 m
<i>Equisetum scirpoides</i> ^c	Dwarf scouring-rush	F	1	5 m
<i>Fragaria virginiana</i>	Wild strawberry	D	1	5 m
<i>Galium asprellum</i>	Rough bedstraw	G	1	5 m
<i>Lycopus uniflorus</i>	Northern water-horehound	G	1	5 m
<i>Polypodium appalachianum</i>	Appalachian polypody	G	1	5 m
<i>Ranunculus acris</i>	Common buttercup	D	1	5 m
<i>Solidago canadensis</i>	Canada goldenrod	D	1	5 m
<i>Veronica officinalis</i>	Common speedwell	D	1	5 m
<i>Matteucia struthiopteris</i> var. <i>pensylvanica</i>	Ostrich fern	F	5	18 m
<i>Symphiotrichum puniceum</i>	Purple-stemmed aster	D	4	18 m
<i>Bromus ciliatus</i> ^c	Fringed brome grass	G	3	18 m
<i>Diervilla lonicera</i>	Bush-honeysuckle	G	3	18 m
<i>Onoclea sensibilis</i>	Sensitive fern	WD	3	18 m
<i>Solidago rugosa</i>	Rough-stemmed goldenrod	D	3	18 m
<i>Carex gynandra</i>	Nodding sedge	G	2	18 m
<i>Carex trisperma</i>	Three-seeded sedge	WG	2	18 m
<i>Doellingeria umbellata</i>	Flat-topped white aster	D	2	18 m
<i>Mentha</i> spp.	Mints	G	2	18 m
<i>Osmorhiza berteroi</i> ^c	Mountain sweet cicely	F	2	18 m
<i>Osmunda cinnamomea</i>	Cinnamon fern	WG	2	18 m
<i>Ranunculus abortivus</i> ^c	Small-flowered crowfoot	WG	2	18 m
<i>Botrychium virginianum</i>	Rattlesnake fern	F	1	18 m
<i>Coeloglossom viride</i> var. <i>virescens</i> ^c	Long-bracted green orchid	G	1	18 m
<i>Equisetum arvense</i>	Common horsetail	D	1	18 m
<i>Equisetum sylvaticum</i>	Woodland horsetail	WF	1	18 m
<i>Gaultheria hispidula</i>	Creeping snowberry	G	1	18 m
<i>Geum macrophyllum</i> ^c	Big-leaved avens	G	1	18 m
<i>Hieracium scabrum</i>	Rough hawkweed	D	1	18 m
<i>Impatiens pallida</i> ^c	Yellow jewelweed	G	1	18 m
<i>Tussilago farfara</i>	Coltsfoot	D	1	18 m
<i>Aster macrophyllus</i>	Big-leaved aster	G	6	25 m
<i>Carex debilis</i>	White-edged sedge	G	5	25 m
<i>Glyceria striata</i> ^c	Fowl mannagrass	WG	5	25 m
<i>Milium effusum</i> ^c	Spreading millet grass	G	5	25 m
<i>Chrysosplenium americanum</i>	Golden-saxifrage	WG	4	25 m
<i>Epilobium strictum</i> ^c	Northeastern willow-herb	WG	4	25 m
<i>Galium aparine</i> ^c	Spring cleavers	G	4	25 m
<i>Ribes triste</i> ^c	Swamp red currant	G	4	25 m
<i>Lactuca</i> spp.	Wild lettuces	D	3	25 m
<i>Polystichum braunii</i> ^c	Braun's holly fern	F	3	25 m
<i>Taraxacum officinale</i>	Common dandelion	D	3	25 m
<i>Viola sororia</i>	Dooryard violet	G	3	25 m
<i>Carex communis</i>	Fibrous-rooted sedge	G	2	25 m
<i>Corallorhiza maculata</i> ^c	Spotted coralroot	F	2	25 m
<i>Galeopsis bifida</i> ^c	Splitlip hempenettle	D	2	25 m
<i>Galium kamschaticum</i> ^c	Boreal bedstraw	G	2	25 m
<i>Platanthera orbiculata</i> ^c	Large round-leaved orchid	F	2	25 m

Table 3 (concluded).

Scientific name	Common name	Habitat type ^a	Frequency of occurrence ^b	Not detected beyond:
<i>Ranunculus recurvatus</i> ^c	Hooked crowfoot	D	2	25 m
<i>Schizachne purpurascens</i> ^c	Unnamed grass	G	2	25 m
<i>Nemopanthus mucronatus</i>	Mountain holly	G	1	25 m
<i>Rubus allegheniensis</i>	Common blackberry	D	1	25 m
<i>Stellaria calycantha</i> ^c	Chickweed	WF	1	25 m

^aF, forest specialist; G, generalist; D, disturbance specialist; W, wetland–forest specialist; WG, wetland generalist; WD, wetland disturbance specialist.

^bThe number of 5 m × 50 m plots in which the species occurred (of 60 plots in total).

^cSpecies designated uncommon or rare by Haines and Vining (1998). *Lactuca* and *Mentha* are genera that contain both rare and common species; specimens of these genera could not be identified to species.

follow-up study, Hughes and Cass (1997) reported that vegetation patterns along fourth-order streams in Vermont were defined mainly by the flooding regime and its lateral extent. In our study, the average lateral gradient from the stream edge to a perpendicular distance of 10 m was 17%. Thus, the geomorphology of our study streams did not permit much lateral flooding, except perhaps during the most extreme and infrequent events. Thus, we concur with other authors that geomorphology is likely a primary driver of riparian plant communities. Differences in stream geomorphology offer the most probable explanation for the narrower riparian zone we observed (based on plants) compared with the wider riparian zone observed for third- and fourth-order streams by Spackman and Hughes (1995). Despite this qualitative conclusion, we found no significant relationship between the stream physical parameters listed in Table 1 and the herbaceous communities in the 0–5 m zone. We suspect that we needed much finer, more detailed physical measurements, such as lateral gradient within 1 or 5 m of the stream (we used 10 m in this study), and (or) more replicates (streams) to reveal this presumed relationship.

We believe that geomorphology and plant physiognomy also best explain why trees and shrubs showed no (or little) community gradient in relation to distance from the stream. Trees and shrubs are physically larger than herbaceous plants and therefore integrate soil, moisture, and geomorphology characteristics over a larger spatial scale. The scale of the physical factors on our study streams that influenced the herbaceous community may have been too fine and too narrow to have physically affected larger tree and shrub species. This is not the case on higher order streams (Spackman and Hughes 1995), where physical factors such as flooding have a much wider scale of influence.

Higher herbaceous community richness near the stream is likely caused by two key factors: (1) annual disturbance resulting from peak spring flows, and (2) soil moisture from the stream itself and associated geomorphology (e.g., Hupp 1982; Hupp and Ostercamp 1985; Kalliola and Puhakka 1988; Pollock et al. 1998). In our study, both wetland species and to a lesser extent disturbance species tended to occur more commonly in the 0–5 m zone. This zone was narrow because all 15 study streams were relatively well entrenched (very little meander) because of the steep gradient of the terrain. Some sections of some streams had a discernible floodplain and terrace slope, but most sections were incised and straight. Based on the conclusions drawn from other studies of vegetation along streams, we suspect that

the relatively short break in plant-community gradient (between 5 and 13 m) that we observed was related to the lateral extent of annual or semi-annual flooding events, geomorphology, and hydrology (i.e., fluvial landforms).

Many plant species are adapted to disturbance, and areas that experience disturbance (e.g., frequent flooding and scouring) often have greater species richness than areas without disturbance (Huston 1979; Pollock et al. 1998). Pollock et al. (1998) found that species richness was nonlinearly related to spatial variation in flood frequency; sites with intermediate flood frequencies had higher richness. In vegetation studies of larger streams, forbs, graminoids and other ruderal (weedy) species often help delineate a riparian zone (e.g., Spackman and Hughes 1995; Goebel et al. 2003). Because riparian areas along higher order streams are more open to the sky as a result of greater stream width and more lateral disturbance, streambanks may have been the original habitat for weedy plants prior to human modification of eastern North American forests (Marks 1983). However, the small streams that we studied had as much canopy closure as upland forest (Wilkerson et al. 2006). This may help explain why the 23 species that emerged as riparian indicators in our study were represented by a combination of forest specialists, forest generalists, wetland specialists, and disturbance specialists.

Maintaining natural plant communities along headwater streams will depend on maintaining fluvial landforms, hydrological flow, and microclimate on at least a portion of the headwater stream length. Changes in stream flow can affect stream-channel morphology (Dominick and O'Neill 1998), and changes in peak flows can affect riparian plant communities (Pollock et al. 1998). Groundwater also plays a key role in both peak and nonpeak flows in small streams (Freeze and Cherry 1979). Forestry practices can affect these parameters (e.g., Troendle and King 1985; Hornbeck et al. 1993; Lewis et al. 2001) and can therefore be expected to affect riparian vegetation (Goslee et al. 1997).

Streamside retention zones, or forest buffers, are typically used to protect streams from the potential effects of timber harvesting (Blinn and Kilgore 2001). It appears that small headwater streams have a riparian zone in our region. Maintaining plant communities within a 0–5 m zone adjacent to small first-order streams with buffers will require a better understanding of microclimatic temperature gradients along forest edges (i.e., the buffer–harvest boundary). Microclimatic gradients associated with forest edges influence the composition and structure of plant communities

within buffers (Gehlhausen et al. 2000; Hylander et al. 2005). The width of forested buffers required to maintain riparian microclimate appears to vary greatly, from 20 to over 73 m, depending on forest type and local climate (Chen et al. 1995, 1999; Brosofske et al. 1997; Dong et al. 1998; Danehy and Kirpes 2000). In Maine, streamside (1–5 m) air temperatures in 23 m wide buffers (both sides) were within 1–2 °C of those in intact riparian forest during the hottest part of the day in summer (Hagan and Whitman 2000), but we do not know whether this temperature difference is enough to alter the streamside herbaceous community.

We have demonstrated that small headwater streams can have a distinct riparian zone based on plant communities. In a companion study of the same streams, a narrow (7–9 m) riparian zone was found, based on the amphibian community (Perkins and Hunter 2006). Taken together, these results represent an important first step in establishing that small headwater streams can have an ecologically identifiable riparian zone that may warrant protection with forested buffers. More work is needed to determine the width of forested buffers required to maintain these riparian communities.

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