

Can structural and functional characteristics be used to identify riparian zone width in southern Appalachian headwater catchments?

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Abstract: We characterized structural and functional attributes along hillslope gradients in headwater catchments. We endeavored to identify parameters that described significant transitions along the hillslope. On each of four catchments, we installed eight 50 m transects perpendicular to the stream. Structural attributes included woody and herbaceous vegetation; woody debris and forest floor mass, nitrogen (N) and carbon (C); total soil C and N; litterfall amount and quality by species; and microclimatic conditions. Functional attributes included litter decomposition, soil microarthropods, soil CO₂ evolution, soil solution chemistry, and soil extractable N. Forest floor mass, N and C, and soil depth increased with distance from the stream and transitioned between 10 and 20 m. In contrast, litterfall N rate (kilograms of nitrogen per hectare per day), downed woody debris, soil A-horizon C and N, and soil solution NO₃ concentration all decreased with distance, and exhibited significant transitions. Certain overstory species were more abundant in the uplands than near the stream. Herbaceous diversity and richness were similar across the hillslope, but species distributions varied in response to hillslope moisture content. Taken together, these results suggest that at 10–20 m from the stream, transitions occur that separate riparian from upland conditions and may provide valuable insight into riparian zone definition.

Résumé : Nous avons caractérisés les attributs structuraux et fonctionnels le long de gradients de pente dans des bassins versants de tête. Nous avons tenté d'identifier les paramètres qui caractérisent les zones de transition importante le long des pentes. Dans chacun de quatre bassins versants, nous avons installé huit transects de 50 m perpendiculaires au cours d'eau. Les attributs structuraux incluaient la végétation ligneuse et herbacée, la teneur en N et C ainsi que la masse des débris ligneux et de la couverture morte, la quantité totale de C et N dans le sol, la quantité et la qualité de la chute de litière par espèce et les conditions microclimatiques. Les attributs fonctionnels incluaient la décomposition de la litière, les microarthropodes du sol, l'évolution du CO₂ dans le sol, les caractéristiques chimiques de la solution du sol et la quantité de N extractible dans le sol. La teneur en N et C ainsi que la masse de la couverture morte et la profondeur du sol augmentaient avec la distance depuis le cours d'eau et subissaient une transition à une distance de 10 à 20 m. Par contre, le taux de N (kg N·ha⁻¹·j⁻¹) dans la chute de litière, les débris ligneux au sol, la quantité de C et N dans l'horizon A du sol et la concentration de NO₃ dans la solution du sol diminuaient avec la distance et connaissaient d'importantes transitions. Certaines espèces de l'étage dominant étaient plus abondantes en terrain élevé qu'à proximité des cours d'eau. La diversité et la richesse des espèces herbacées étaient semblables le long de la pente mais leur distribution variait en fonction de la teneur en humidité le long de la pente. Globalement, ces résultats indiquent qu'à 10 à 20 m du cours d'eau, des zones de transition séparent les conditions riveraines des conditions en terrain élevé et peuvent donner un aperçu intéressant de la définition de la zone riveraine.

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Introduction

Forested riparian areas mediate a number of terrestrial–aquatic linkages (Karr and Schlosser 1978) through their influence on physical, chemical, and biological dimensions of streams. Riparian zones are three-dimensional areas of direct interaction between terrestrial and aquatic ecosystems

(Meehan et al. 1977; Gregory et al. 1991). This interaction occurs primarily in the form of energy and material exchanges or 'reciprocal subsidies' (sensu Nakano and Murakami 2001) and can represent strong connectivity between aquatic and terrestrial components of forest ecosystems. For example, continuous two-way nutrient exchanges occur through hyporheic connections (Findlay 1995); stream-to-forest subsidies occur

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through insect emergence; and forest-to-stream fluxes may include a variety of materials, including nutrients, woody debris, leaf litter, sediment, fine particulate organic carbon (C), and terrestrial arthropods (Haycock et al. 1997; Polis et al. 1997; Bragg and Kershner 1999; Lindenmayer and Franklin 2002; Sabo and Power 2002). These exchanges, particularly forest-to-stream subsidies, can have profound effects on the productivity of the receiving system (Wallace et al. 1999).

First-order streams are the dominant stream type (i.e., 50% of the total stream network length) in most forested watersheds (National Research Council 2002; Wipfli et al. 2007); yet, most of the scientific knowledge about riparian zone structure and function has been derived from studies of higher-order streams, where geomorphic and fluvial controls are much more important (Verry et al. 2004). In high-order stream systems, repeated flooding results in the development of distinct terracing and alluvial deposits that can be linked directly to subsurface hydrology, geomorphology, and floodplain development. These characters are sometimes useful for definition and delineation of the riparian zone in high-order systems (Verry et al. 2004). Although fluvial and geomorphic processes are at work in low-order streams, their usefulness for riparian zone delineation is limited.

Considerable interest and debate surround the use of structural and functional attributes of riparian ecosystems as metrics to assign appropriate riparian buffer widths to protect aquatic and terrestrial resources and habitats from upland disturbance (Castelle et al. 1994; Grubbs and Cummins 1996). While scientists and policy makers often contend that forest ecosystems should be managed, protected, or restored based on our understanding of structure and function and their interactions (Franklin 1999; National Research Council 2002), in many cases not enough is known about structural and functional characteristics of specific ecosystems (or their components) to make sound, science-based management decisions. Indeed, most riparian classification systems focus on a few simplistic attributes typically derived from high-order streams, such as topography, flora and fauna assemblages, and wildlife use or travel corridor requirements to delineate the extent of the riparian zone. Some studies have focused on the use of a single or few parameters as an indication of function in managed riparian zones (Palik et al. 1999). For example, indicator plants are assumed to be linked to soil conditions, such as extended periods of saturated and (or) anaerobic conditions (Tabacchi et al. 1998). This assumption fails in most southern Appalachian headwater catchments because anaerobic conditions rarely exist because of steep sideslopes and well-drained soils. Similarly, riparian zone use by wildlife (particularly amphibians) is often an important consideration in riparian-buffer management and delineation in many forest ecosystems (e.g., Vesely and McComb 2002; Gillies and St. Clair 2008). These perspectives are adequate singular assessments of riparian zone plant community composition, or usefulness as wildlife habitat, but do little to address the wide array of ecological processes associated with the riparian zone of headwater streams.

As a result of inadequate or incomplete knowledge of riparian zone width, land managers are often faced with the challenge of making decisions about appropriate riparian zone protection without a science-based understanding of

the structural and functional characteristics that define the riparian area. To address this lack of understanding, our study goals were (1) to characterize abiotic and biotic conditions and structural and functional attributes of forested riparian zones along first-order, perennial streams in southern Appalachian headwater catchments, and (2) to assess the usefulness of these structural and functional attributes to objectively determine riparian zone width. We hypothesized that even in these small headwater catchments, distinct differences in abiotic (e.g., soil moisture, light, temperature) and biotic (e.g., vegetation, forest floor and soils, nutrient and C cycling) variables could be used to delineate the transition zone between upland and riparian areas.

Methods

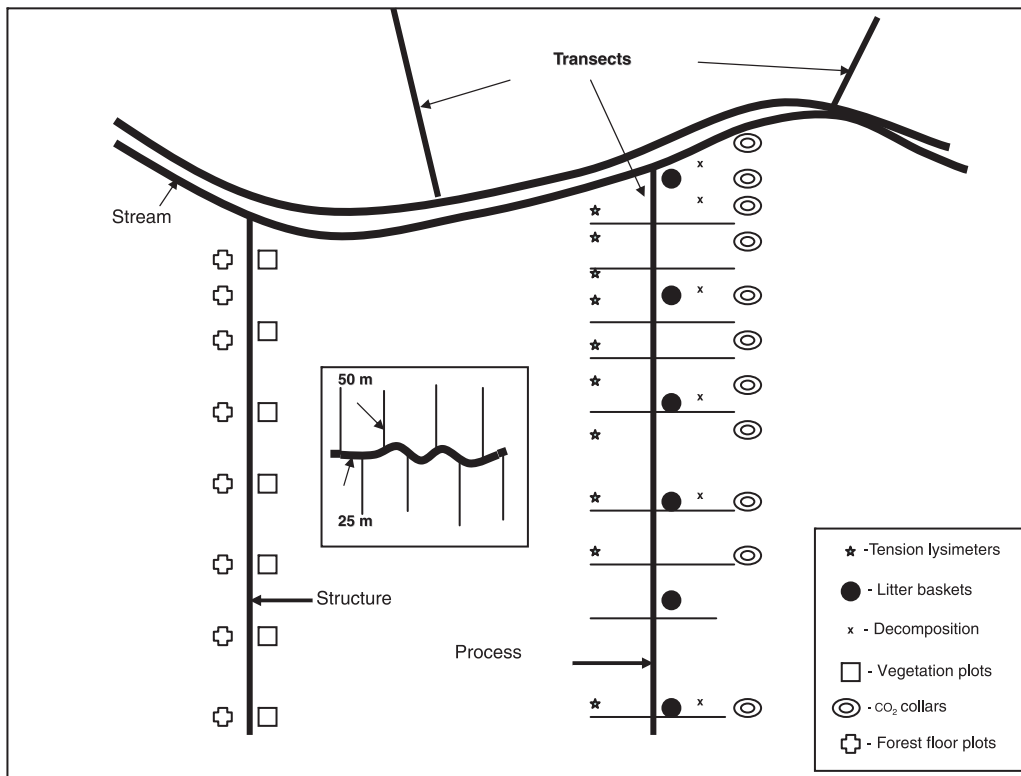
Study catchments

Study catchments were located on the Nantahala Ranger District of the Nantahala National Forest in the Blue Ridge Physiographic Province of western North Carolina (35°6'N, 83°6'W). This region of the southern Appalachians receives abundant rainfall (approx. 1800 mm·year⁻¹) distributed evenly throughout the year (Swift et al. 1988). Less than 5% of the total annual precipitation falls as snow or ice. The mean annual air temperature is 12.6 °C, ranging from 3.3 °C in January to 21.6 °C in July. Four headwater catchments containing first-order perennial streams, having similar vegetation, topography, and soils, were selected for the study. Among our study sites, elevations ranged from 850 to 950 m, were east facing, ranged in area from 6 to 10 ha, and had stream gradients ranging from -0.07% to -0.23%. Catchment sideslopes ranged from 25% to 75% among catchments, but sideslopes were generally consistent within catchments. Overstory on all sites consisted of mixed hardwoods (*Quercus* spp., *Acer* spp., *Carya* spp., *Liriodendron tulipifera*), with a lesser component of conifers (*Pinus strobus*, *Tsuga canadensis*) (see Appendix A, Table A1) for more detail). All sites had not been logged for more than 60 years. Sites have similar soils, which are generally loamy to coarse loamy and are derived from material weathered from high-grade metamorphosed rock or from colluvium. Sideslope soils are mapped in the Evard-Cowee complex (fine-loamy, mixed, mesic Typic Hapludults), which includes about 20% inclusion of the Trimont series (fine-loamy, mixed, mesic Humic Hapludults). These Ultisols are moderately well drained to well drained and are deep (solum layer thickness ~1 m, >1.5 m to bedrock). The saprolite layer beneath the solum may be up to 6 m deep (Thomas 1996). Cove or stream-side soils were formed in colluvium, 15% to 50% slope, and are mapped in the Cullasaja series. These soils are loamy-skeletal, mixed, mesic Typic Haplumbrepts and very deep, well-drained soils; solum thickness is <1.5 m; >1.8 m to bedrock (Thomas 1996).

Sampling approach

We used a transect-based approach to quantify structural and functional attributes from stream edge (defined as bank-full) to the upland. Within each catchment, a 200 m stream reach was selected for intensive study. Streamflow was not measured; however, streams within all study catchments were perennial first-order streams and flow occurred through-

Fig. 1. Schematic of field sampling design. Hypothetical birds-eye view of riparian area. Represented are the transects used for intensive process-level measurements and less intensive structural measurements. Some measured parameters are not included in the drawing and legend.



out the duration of the study. Eight 50 m transects, spaced 25 m apart, were established perpendicular to each stream reach (four on each side) (Fig. 1). These transects served as the focal point for all abiotic, structural, and functional measurements. The attributes measured were overstory and ground layer vegetation, microclimate, litterfall, forest floor characteristics, downed woody debris, soil and soil solution chemistry, soil CO₂ evolution, litter decomposition, and litter and soil microarthropods. Four transects were randomly assigned to either vegetation or C and nutrient cycling measurements. The number of transects sampled and the sample collection interval along the transects varied with the structural and functional attribute measured. For most functional attributes we expected a higher degree of variability nearer the stems, so we generally used a greater sampling intensity for these parameters within 20 m of the stream to increase the likelihood of detecting critical transition zones.

Measurements

Vegetation

Vegetation inventories were conducted during the growing season of 2004 and 2005 along four vegetation transects per study catchment. Transects were located on both sides of the stream. Vegetation was measured in layers: the overstory layer included all woody stems with a ≥ 2.5 cm diameter at

breast height (DBH, 1.37 m above ground), the midstory layer included all woody stems with a < 2.5 cm DBH and ≥ 0.5 m height, the ground flora layer (hereinafter referred to as the ground layer) included woody stems < 0.5 m height and all herbaceous species. For overstory and mid-story sampling, we located three $10 \text{ m} \times 10 \text{ m}$ plots along each transect beginning at streamside (lower slope) and at 20 m (midslope) and 40 m (upper slope) from the stream edge. The DBH of all overstory trees was measured to the nearest 0.1 cm and recorded by species. Estimates of above-ground woody and foliar biomass for deciduous species were based on species-specific allometric equations of Martin et al. (1998) and on that of Santee and Monk (1981) for *Tsuga canadensis*. In the midstory layer, all woody stems were counted and recorded by species. In addition, all tree seedlings < 0.5 m in height were counted in each $10 \text{ m} \times 10 \text{ m}$ plot. For ground layer sampling, we established ten 1.0 m^2 quadrats at 5 m intervals along the four vegetation transects. Ground layer richness (total number of species present), diversity (Shannon index), and percent cover (estimated visually and recorded by species) were estimated in each of the 1.0 m^2 quadrats. Percent cover was estimated using a scale that emphasizes intermediate accuracy: in 1% intervals from 1% to 5%, in 5% intervals from 5% to 20%, and in 10% intervals above 20%. The vegetation sampling design resulted in twelve $10 \text{ m} \times 10 \text{ m}$ plots for overstory

and midstory (three per transect) and forty 1.0 m² quadrats for the ground layer (10 per transect) in each catchment. All species nomenclature follows Gleason and Cronquist (1991).

Microclimate

Microclimate (light and soil moisture) was characterized monthly at each ground layer vegetation plot on each study catchment. Beginning in early spring and continuing through late fall, incident solar radiation (photosynthetically active radiation; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was measured at 1 m above the forest floor using a handheld portable light meter (AccuPAR LP-80; Decagon Devices, Pullman, Washington, USA) between the hours of 1130 and 1530. Measurements were only made during periods of full sun. The mean of two readings at each plot was recorded. Percent full sun was estimated using periodic open readings. Volumetric soil water content (v/v , %) within the top 20 cm of soil was measured with a handheld portable soil moisture meter (HydroSense, Campbell Scientific, Logan, Utah, USA).

Litterfall

Litterfall was collected along four transects using 0.2 m² collection baskets located at 0, 10, 20, 30, 40, and 50 m from the stream. The 0 m location along transects was defined as the stream edge at bankfull. Litter was collected approximately biweekly from early September until autumnal leaf fall was completed (December). Litter was dried at 65 °C for 48 h and sorted into eight categories: wood, oaks, maple, yellow poplar, evergreen shrubs, white pine, hemlock, and others. The wood category included any woody material regardless of size and source (e.g., twigs, branches, woody fruit). Sorted litter was then weighed to the nearest 0.01 g, ground to pass through a 2 mm mesh, and analyzed for [C] and [N] (PerkinElmer 2400 CHN). Estimates of litterfall or litterfall C and N input rates for each distance along the transects were expressed on a daily basis ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$) by dividing total mass, total C, and total N by the number of days within the entire collection period (September to December). This method standardized litterfall input rates over time by accounting for differences in litterfall collection intervals and served as an expression of the quality of litter inputs over time along the transects.

Forest floor

Forest floor mass was sampled on each catchment using a 30 cm × 30 cm sampling frame. Two adjacent paired samples were taken along each of four transects per catchment at 0, 1, 4, 7, 10, 20, 30, and 50 m from the stream. Material within the frame was separated into small wood (<7.5 cm diameter), litter (Oi), and humus plus fermentation (Oa + Oe). Samples were oven-dried at 65 °C to a constant mass and then weighed. The paired samples were composited by material type and then ground and analyzed for [C] and [N], as described above. C and N pools were estimated by the product of mass and concentration of each material type. Subsamples were muffled at 480 °C to determine ash-free mass; all forest floor data are presented on an ash-free mass basis.

Downed woody debris

Coarse wood (CW) volume was estimated using the line

transect method (Brown 1974) at 10 m intervals from streamside up to 50 m. At each 10 m interval, transects were established parallel to the stream and 100 m in length. The diameter of all woody material (≥ 2 cm) that intercepted the transects was measured and assigned a decay class of I–IV. Decay classes were defined as follows: I, fresh woody material with bark 100% intact; II, fresh woody material with bark 50% or more intact; III, intermediate stage of decomposition with <50% of bark intact; IV, advanced stage of decomposition with very little or no bark remaining and becoming incorporated into the forest floor. Estimates of total mass and pools of C and N were made using published [C] and [N] and specific masses of species derived from similar ecosystems in the southern Appalachians (see Vose et al. 1999).

Soil sample collection and chemical analyses

Soil profiles along each of the four nutrient cycling transects were described and sampled during the summer of 2004 and 2005 — two transects each year. Sample locations were established 1, 2, 4, 7, 10, 13, 16, 20, 30, and 50 m from the stream. At each sample location, we used a 2.54 cm soil probe to describe and collect soil samples from the entire soil profile by horizon using basic soil taxonomic characterization (USDA Natural Resources Conservation Service 1996), based on changes in color and texture. We established a minimum horizon depth of 5 cm; horizons greater than 20 cm thick were divided for sample collection, resulting in 80–100 samples per transect. Soil profiles were described and samples were collected until the C horizon (saprolite) was reached or to a maximum profile depth of 110 cm. Samples were placed in reclosable plastic bags and mixed thoroughly. Approximately 10 g of soil was added to 50 mL of 2 mol·L⁻¹ KCl in preweighed 125 mL Nalgene bottles for NO₃ and NH₄-N extraction within 1 h of collection. Bottles plus soil were weighed upon returning to the laboratory to determine actual soil mass and were placed in a refrigerator (4 °C); soil was allowed to settle out of the solution overnight. KCl only was pipetted into 15 mL centrifuge tubes for later analysis. Concentrations of NH₄ and NO₃-N were determined on an autoanalyzer by using alkaline phenol (USEPA 1983a) and cadmium reduction (USEPA 1983b) techniques, respectively. Soil [NO₃] and [NH₄] are reported on a fresh-mass basis. Total C and N were determined on air-dried, sieved (<2 mm), and ground soil samples by combustion (Elementar Flash EA 1112 series C and N Analyzer). Soil profile N and C contents were determined using average bulk density values from other soil experiments in the southern Appalachians (Knoepp et al. 2000; J.D. Knoepp, personal communication, 2008) as were [NO₃], [NH₄], total [C], and total [N]. Total nutrient content for estimated A and B soil horizons was calculated using samples collected from horizons morphologically defined as only A or B; we did not include mixed A or B horizons; the A-horizon depth was limited to 20 cm.

Soil solution sampling

We installed soil tension lysimeters on two of the nutrient cycling transects at distances of 1, 2, 4, 7, 10, 13, 16, 20, 30, and 50 m from the stream. At each location we installed two straight PVC, porous cup, tension lysimeters, one at 15 cm

depth, and the other at the bottom of the B horizon above the saprolite (maximum depth 100 cm). Depths were intended to sample plant available nutrients (15 cm; shallow lysimeters), and nutrient loss from the sites (B horizon; deep lysimeters). We applied 0.3 bar of tension to all lysimeters after weekly sample collection. Soil solution samples were composited into a monthly sample by freezing a subsample of weekly collections. We determined the concentrations of NO_3^- , SO_4^{2-} , and PO_4^{3-} using ion chromatography; of calcium, magnesium, and potassium using atomic absorption; and of $\text{NH}_4\text{-N}$ using an autoanalyzer alkaline phenol method (USEPA 1983a) on all soil solution samples.

Ion exchange resin sheets

Changes in soil nutrient availability along all four nutrient cycling transects were estimated with anion and cation exchange resin membrane sheets, using the methods of W. Jarrell (personal communication, 1996). Both cation and anion resin sheets were prepared for placement in the soil by repeated washing (three times for 10 min each) in $0.5 \text{ mol}\cdot\text{L}^{-1}$ NaHCO_3 solution to charge all exchange sites. Resin sheets were placed at all plots (1, 2, 4, 7, 10, 13, 16, 20, 30, and 50 m) along the four transects (40 cation and 40 anion sheets per catchment). Sheets were placed 5 cm below the surface of the mineral soil and left in place for 14 days. Sheets were removed from the soil; excess soil and organic matter were removed, placed in reclosable plastic bags, and returned to the laboratory where they were rinsed thoroughly with deionized water to remove any remaining debris. To extract adsorbed nutrients, each pair (anion plus cation sheets) was placed in a 10 cm diameter Petri dish with 25 mL of $0.5 \text{ mol}\cdot\text{L}^{-1}$ HCl and shaken gently for 20 h. Solutions were analyzed for $\text{NO}_3\text{-N}$, PO_4 , and $\text{NH}_4\text{-N}$ concentrations using an autoanalyzer (Perstorp) and for calcium, potassium, and magnesium concentrations using an atomic absorption spectrophotometer (PerkinElmer AAnalyst 300). All values are presented as micrograms per square centimetre of resin sheet surface area.

Soil CO_2 efflux

Soil CO_2 efflux ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was measured monthly along two nutrient cycling transects per catchment using a portable infrared gas analyzer (Licor 6400, LI-COR Biosciences Inc., Lincoln, Nebraska) at 0, 1, 2, 4, 7, 10, 13, 16, 20, 30, and 50 m from the stream. At each distance location, three measurements were taken within 1 m of each other along the slope contour. Measurements began in early spring (March) and continued approximately bimonthly through early winter (December). Concurrent with soil CO_2 efflux measurements, soil temperature ($^{\circ}\text{C}$) was measured with a 15 cm long probe and soil moisture was measured as described above.

Litter decomposition

Litter decomposition was estimated along two nutrient cycling transects on each catchment at 0, 4, 10, 20, 30, and 50 m from the stream. At each distance, one set of nine $10 \text{ cm} \times 10 \text{ cm}$ bags (1.5 mm mesh) containing 2.5 g (exact mass recorded) of air-dried *Acer rubrum* L. (red maple) senesced leaf material. Red maple was selected because of its rapid decomposition rate (Cromack and Monk 1975) and

widespread distribution within our study catchments. Ten bags were selected for initial ($t = 0$) nutrient and percent moisture determination. The remaining litterbags were placed in the Oi layer 1 m apart along the contour in February 2005. One bag from each set was collected every 4 weeks through November 2005 (244 days). Collected litterbags were oven-dried, ground, weighed (described above), analyzed for total [C] and [N] (PerkinElmer 2400 CHN), and ashed to correct for mineral soil (described above). Rates of loss of mass, N, and C ($-k$) were determined using an exponential decay model (Olson 1963; Petersen and Cummins 1974).

Litter and soil microarthropods

For each litterbag collection, microarthropods were extracted immediately from the litterbags using a modified Tullgren funnel apparatus (Mallow and Crossley 1984). Owing to equipment limitations, microarthropod extraction was conducted on three sites. Litterbags were left on the funnels for 3–4 days; the extracted microarthropods were preserved in 70% ethanol.

To obtain soil microarthropod counts, soil core samples were collected from five $1 \text{ m} \times 2 \text{ m}$ plots at distances of 1, 4, 10, 16, and 50 m from the stream along three of the eight transects at all four catchments (60 plots). Using cylindrical PVC cores 4 cm deep and 5 cm in diameter (approx. 75 cm^3), one sample was taken from 1 of 12 randomly selected locations within each $1 \text{ m} \times 2 \text{ m}$ plot during each sampling period. Samples were collected in August 2004, December 2004, May 2005, and August 2005. Soil temperature was measured with a standard soil temperature probe at 5 cm depth, adjacent to soil core collection. Soil microarthropods were extracted in the laboratory, using a modified Tullgren funnel procedure (Moldenke 1994). Soil and litterbag microarthropods were stored as described above and later sorted under a stereomicroscope into the following categories: oribatid, prostigmatid, and mesostigmatid mites; Collembola; and others. Oribatid mites in litterbags were further sorted into mature and immature categories because mature oribatids have greater sclerotization and thus greater protection from predators (Walter and Proctor 1999). In addition, the adult and immature forms of some oribatid species feed on entirely different litter (or fungal) material (Schneider et al. 2004). Prostigmatida and mesostigmatida mites were lumped together for analysis because their numbers were so few and they frequently play similar roles as predators (Coleman et al. 2004). Microarthropod abundances are reported as the mean number of microarthropods per gram of dry litter or mean number of microarthropods per soil core.

Data analysis and experimental design

The general experimental design was based on four catchments (fixed factor), variable numbers of transects (random factor) within each catchment, and distance (fixed factor) from the stream within a transect. The exact number of transects and distance intervals varied depending on the variables measured. This corresponds to a traditional split-plot design with catchment as the main plot factor and transects representing replication within catchments. Distance from the stream is then the subplot factor. When an analysis in-

cluded season (fixed factor), then the design became a split-split-plot design.

We analyzed downed woody debris; forest floor mass, N, and C; total soil N and C; soil solution chemistry; soil CO₂ efflux; and litter and soil microarthropod data, using a split-plot design using PROC MIXED (SAS Institute Inc. 2004) with the Kenward–Roger’s method to estimate the denominator degrees of freedom. When main effects or interactions were significant, least square means were computed and Tukey’s pairwise comparisons were performed using an experimentwise alpha of 0.05. When interactions for a variable were not significant, only main effects were presented and interpreted. Transition points for parameters along transects were identified by visual inspection to be where changes in the distance relationship appeared most pronounced. To provide additional evidence for each transition, a contrast was defined to statistically test for a significant difference ($\alpha = 0.05$) between the means of the distances on both sides of the transition. For some parameters, more than one transition was visually identified, in which case the contrast with the most significant *P* value was selected for the test result. Because the abundance values of soil microarthropods typically follow a Poisson distribution, those data were analyzed using a generalized linear model (PROC Genmod, SAS version 9.1, SAS Institute Inc. 2004; Littell et al. 2002). This analysis does not yield tests for pairwise comparisons so that reported statistical significance is for overall main effects of distance, site, and their interactions.

Results

Structural characteristics

Vegetation

Overstory density, basal area, and aboveground biomass were similar from the near-stream to upper slope positions (Appendix A, Table A1). Twenty-nine tree species, six shrubs, and two woody vines were recorded in the overstory across the four headwater catchments. Of these, only 12 tree species were abundant (i.e., >1000 kg·ha⁻¹ total biomass) or present in more than one catchment (Appendix A, Table A1). Less common (i.e., occurring in only one of the four catchments) species were *Lindera benzoin*, *Ilex opaca*, *Acer pensylvanicum*, *Quercus coccinea*, and *Sassafras albidum*.

Some overstory species were preferentially distributed across the stream-to-upslope gradient (Appendix A, Table A1). For example, *Quercus* species had a significantly higher density at upper slope than near-stream locations ($t = -3.28$, $P = 0.039$), *A. rubrum* density was higher at mid-slope and upper slope ($t = 2.64$, $P = 0.077$) and significantly lower at lower slope positions ($t = -3.60$, $P = 0.022$) compared with near the stream, and *Oxydendrum arboreum* density was significantly higher at upper slope locations than either midslope ($t = -4.24$, $P = 0.013$) or near-stream locations ($t = -4.95$, $P = 0.006$) (Appendix A, Table A1). In contrast, *Betula lenta* density ($t = 2.59$, $P = 0.069$) and basal area ($t = 3.70$, $P = 0.011$) were significantly higher at near-stream than at upper slope positions.

In the ground layer, we recorded 138 species; 24 of these had $\geq 2.0\%$ average percent cover (Appendix B, Table B1), and only 70 occurred on more than 5% of the 160 quadrats

Table 1. PROC MIXED split-plot analysis of ground layer diversity (*H'*, Shannon’s index), richness (number of species per 1.0 m²), and percent cover.

Parameter	Main factor	df	<i>F</i>	<i>P</i> value
<i>H'</i>	Catchment	3	4.56	0.0235
	Distance	9	1.59	0.1289
	Catchment×distance	27	1.44	0.0997
Richness	Catchment	3	6.91	0.0057
	Distance	9	1.06	0.3961
	Catchment×distance	27	1.31	0.1685
% Cover	Catchment	3	5.75	0.0111
	Distance	9	0.56	0.8634
	Catchment×distance	27	1.14	0.3103

Note: Catchment represents four study sites and distance values range from 0 to 45 m at 5 m increments ($n = 10$).

across the four catchments. More than half of these 138 species were perennial forbs (52%), and the remaining species were tree seedlings (20%), woody shrubs (10%), woody vines (4%), ferns (8%), graminoids (4%), or annual forbs (1%). We did not detect any significant differences in diversity (*H'*), richness (*S*), or percent cover in the ground layer with distance from stream (Table 1). However, similar to findings for the overstory, some individual species in the ground layer had greater cover or frequency near the stream than farther away from the stream (Appendix B, Table B1). *Laportia canadensis*, *Astilbe biternata*, *Viola rotundifolia*, and *Tiarella cordifolia* were clearly more abundant near the stream (≤ 15 m). *Desmodium nudiflorum* was more abundant farther away from the stream (≥ 20 m). *Aristolochia macrophylla*, *Quercus rubra*, *Pyrolaria pubera*, *Collinsonia canadensis*, *Viola* spp., *Eupatorium purpureum*, and *Carya glabra* had low cover and low frequency adjacent to the stream (0 m), increased abruptly at 5 m, and then were relatively abundant across the hillslope (Appendix B, Table B1). Other species showed no affinity for any distance along the 50 m transect from the stream.

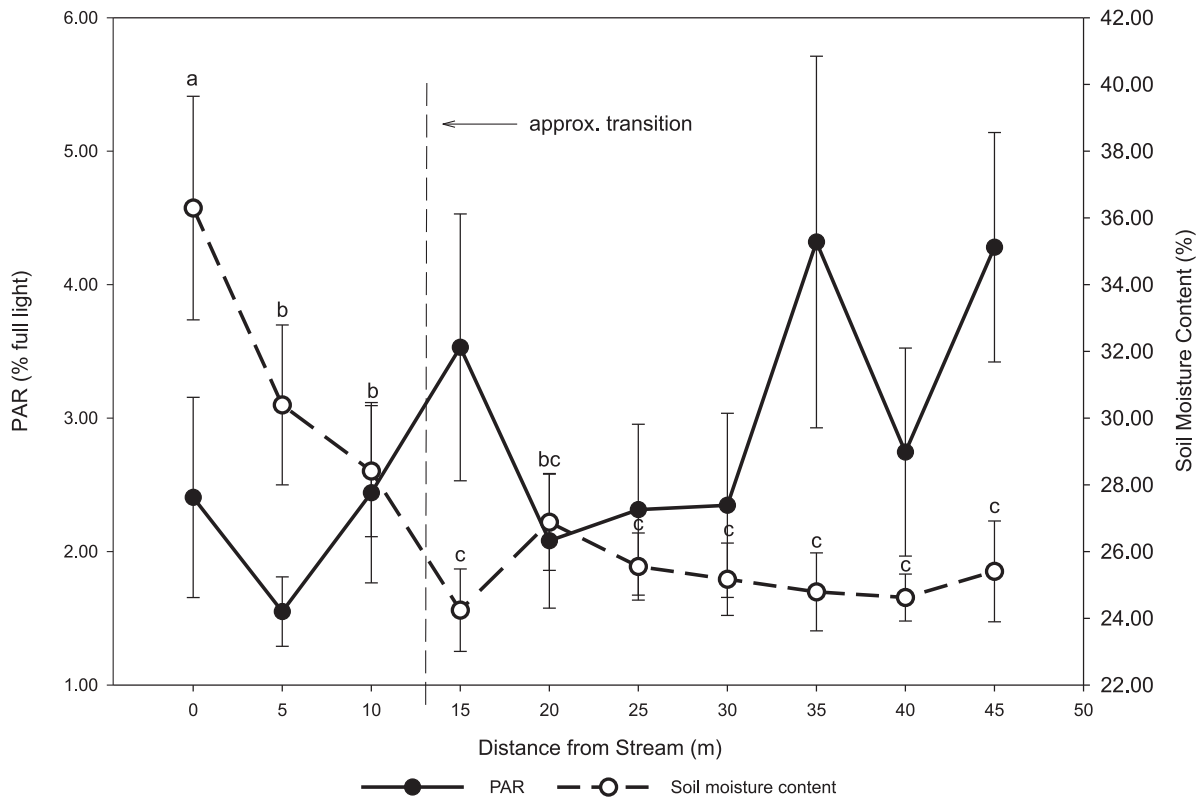
Microclimate

We found no differences in percent full sun (% photosynthetically active radiation) along the transect from near stream to the uplands (Fig. 2). Understory light levels were low; average full sun ranged from 1.56% to 4.22% across the hillslope. In contrast, average soil moisture was significantly higher near the stream (36%), compared with that at distances of 10 m or more from the stream channel (24%–26%; Fig. 2). Average soil temperature ranged from 12.9 °C near the stream to 12.2 °C in the uplands during the dormant season, and 16.3 °C near the stream to 17.6 °C in the uplands during the growing season. Absolute maxima and minima recorded were 29.0 and 5.2 °C, respectively.

Litterfall

Litterfall patterns by species generally followed overstory species distributions discussed in a previous section. Total litterfall mass, C, and N (kg·ha⁻¹) did not vary significantly along the 50 m transect (Table 2). Rates of litterfall (kg·ha⁻¹·day⁻¹) did not vary significantly along transects for either mass or C. Rates of litterfall N (kg N·ha⁻¹·day⁻¹) inputs suggested a trend of greater inputs near the stream;

Fig. 2. Average percent volumetric soil moisture content (over 20 cm) and percent full sun (photosynthetically active radiation; PAR) across seasons measured at 5 m intervals from streamside to uplands. Significant differences were evaluated at $\alpha = 0.05$.



however, differences among transect locations were not significant ($F = 2.24$, $P = 0.057$) (Fig. 3).

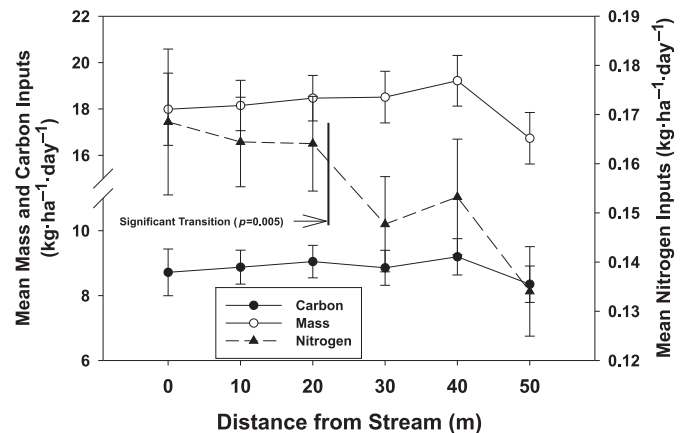
Forest floor

Total forest floor mass (small wood, Oi, plus Oe+Oa) did not vary significantly along the 50 m transects, but the opposite was true when analyzed separately by forest floor components. For example, total Oi mass, C, and N all increased significantly with distance from stream (mass: $F = 6.81$, $P < 0.0001$; C: $F = 7.23$, $P < 0.0001$; N: $F = 5.23$, $P < 0.0001$) (Fig. 4). The lowest values were observed near the stream and did not vary within the first 20 m, but then increased significantly beyond 20 m. In the humus (Oe+Oa) layer, mass and total C increased significantly with distance from stream (mass: $F = 2.72$, $P = 0.014$; C: $F = 2.40$, $P = 0.030$), while N content did not. However, humus mass did not increase with distance from stream in the same manner on all catchments (catchment by distance from stream interaction, $F = 1.88$, $P = 0.023$). We found no significant differences in the amount of small wood (<7 cm diameter) mass, total C, or total N with distance from stream.

Downed woody debris

Downed woody debris mass and C varied considerably with distance from stream and ranged from 26.4 Mg·ha⁻¹ (12.5 Mg C·ha⁻¹, for C) near the stream to 16.3 Mg·ha⁻¹ (7.8 Mg C·ha⁻¹, for C) at 50 m from the stream (Table 3), but there were statistically significant differences among transect locations. In contrast, total downed woody debris N was significantly greater at streamside ($P = 0.028$) compared

Fig. 3. Rates of litterfall inputs for total mass, carbon, and nitrogen. Values are based on total annual inputs for all species groups combined. Means to the right of the vertical thick solid line for N are significantly different from those to the left of the line ($\alpha = 0.05$). Error bars represent one standard error of the mean.



with 30 m from the stream (29.0 kg·ha⁻¹) and varied along the transect from 71.2 kg·ha⁻¹ at streamside to 31.7 kg·ha⁻¹ at 50 m from the stream (Table 3).

Soils and nutrient pools

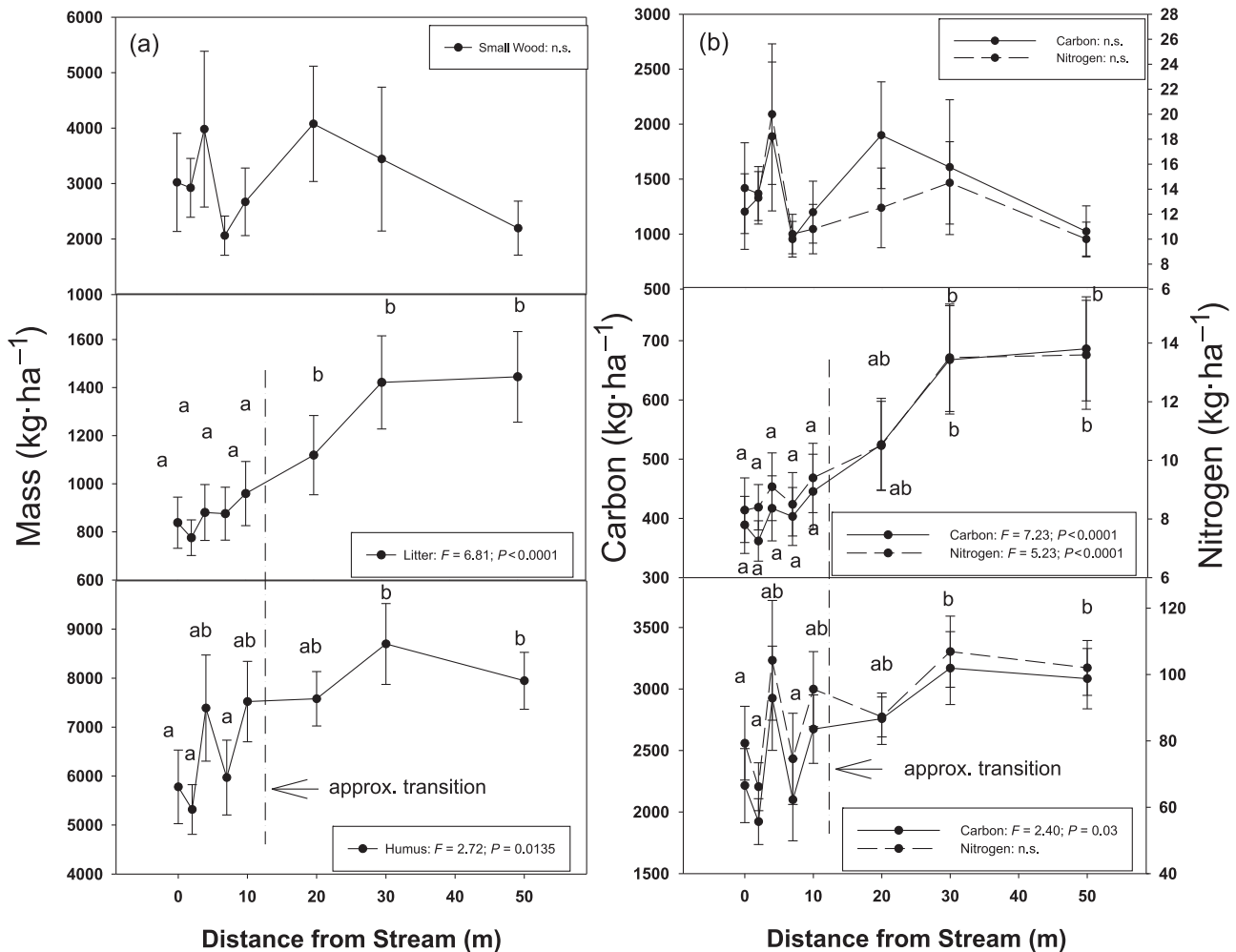
Soil depth increased significantly with distance from stream ($F = 4.82$, $P < 0.0001$) and ranged from 40 cm at streamside to near 75 cm at the 50 m transect location, an

Table 2. Results from PROC MIXED split-plot analysis of total litterfall mass, carbon, and nitrogen by species group.

Pool	Factor	df	P value						
			Small wood	Red maple	Oaks	Evergreens	Magnolias	Others	Total
Mass	Catchment	3	0.1796	0.0036	0.0289	0.8648	0.0590	0.0199	0.1199
	Distance	5	0.9893	0.0032	<0.0001	0.9866	0.0101	0.1645	0.5872
	Catchment×distance	15	0.4604	0.5574	0.0003	0.7689	0.0739	0.0094	0.0734
Carbon	Catchment	3	0.2048	0.0033	0.0289	0.8273	0.0543	0.0151	0.1595
	Distance	5	0.9905	0.0021	<0.0001	0.9793	0.0069	0.1682	0.8792
	Catchment×distance	15	0.4568	0.4097	0.0008	0.7988	0.0477	0.0078	0.0187
Nitrogen	Catchment	3	0.1326	0.0072	0.0203	0.8802	0.0357	0.0051	0.3260
	Distance	5	0.9554	0.0244	<0.0001	0.9816	0.0033	0.0033	0.0983
	Catchment×distance	15	0.7372	0.5267	<0.0001	0.7260	0.0297	0.0005	0.0022

Note: Oaks include white oak, chestnut oak, black oak, northern red oak, and scarlet oak. Evergreens are mostly eastern white pine but include a smaller proportion of eastern hemlock and rhododendron. Magnolias are dominated by yellow poplar but include Fraser magnolia and cucumber magnolia. Others includes a variety of species: basswood, black birch, grape species, hickory, and other less abundant woody species. Significant differences are evaluated at $\alpha = 0.05$ level.

Fig. 4. (a) Forest floor mass and (b) forest floor carbon (C), and nitrogen (N) amount by small wood (<7 cm diameter), litter (Oi), and humus (Oa + Oe) layers. Means with the same letter above error bars within layer and pool (C or N) are not significantly different ($\alpha = 0.05$). Statistics within figure legends represent overall distance effects. Error bars represent one standard error of the mean.



increase of 86% (Fig. 5a). In contrast, total C and total N in the A horizon decreased significantly with distance (C: $F = 2.05, P = 0.041$; N: $F = 1.99, P = 0.048$) (Figs. 5b and 5c). C/N in the A horizon was significantly lower near the

stream compared with the uplands (1 m, 16.65; 50 m, 18.35; $F = 2.34, P = 0.019$). There were no significant differences in total C, total N, or C/N with distance from stream in the B horizon. In addition, there was a negative

Table 3. Least square means for downed woody debris (≥ 2 cm) mass and carbon and nitrogen pools ($\text{kg}\cdot\text{ha}^{-1}$) by distance from stream.

Distance from stream (m)	Mass	Carbon	Nitrogen
0	26 367a (15 255)	12 453a (6 928)	71.19a (53.96)
10	14 641a (10 187)	7 057a (4 892)	33.63ab (24.62)
20	15 900a (6 508)	7 574a (3 096)	39.13ab (25.77)
30	14 496a (5 345)	7 052a (2 866)	28.98b (10.52)
40	18 662a (12 565)	9 076a (6 274)	39.31ab (21.21)
50	16 265a (10 751)	7 841a (5 154)	31.66ab (11.16)

Note: Means within pool with the same letter are not significantly different ($\alpha = 0.05$).

relationship between total soil C and humus C content ($R = -0.36$; $P = 0.036$) and soil N and humus N content ($R = -0.37$; $P = 0.039$) within 2 m of the stream.

Functional characteristics

Soil nutrient availability

Soil nutrient availability determined using exchange resin sheets for NO_3 , NH_4 , PO_4 , potassium, calcium, and magnesium did not vary with distance from the stream in either the dormant or growing seasons. Most solutes measured in soil solution, collected from either shallow or deep lysimeters, did not vary significantly with distance from stream during the dormant or growing seasons. $\text{NH}_4\text{-N}$ concentration at shallow depths increased significantly with distance from stream during both dormant and growing seasons (dormant: $F = 2.30$, $P = 0.034$; growing: $F = 2.20$, $P = 0.046$) (Fig. 6); whereas, due to high values adjacent to the stream, NH_4 concentrations in deep lysimeters significantly decreased with distance from stream during both seasons (dormant: $F = 67.66$, $P < 0.0001$; growing: $F = 161.79$, $P < 0.0001$) (Fig. 6). $\text{NO}_3\text{-N}$ concentrations did not vary significantly within depth with overall distance from stream.

Soil CO_2 efflux

There were no significant differences in soil CO_2 efflux along the stream-slope transect. Rates of soil CO_2 evolution ranged from a minimum of $0.02 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during the dormant season to a maximum of $22.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during the growing season. Temperature directly affected the soil CO_2 evolution (linearized relationship $r = 0.63$, $P < 0.0001$), while volumetric soil moisture content was inversely related to soil temperature ($r = -0.30$, $P < 0.0001$) and soil CO_2 evolution ($r = -0.18$, $P < 0.0001$).

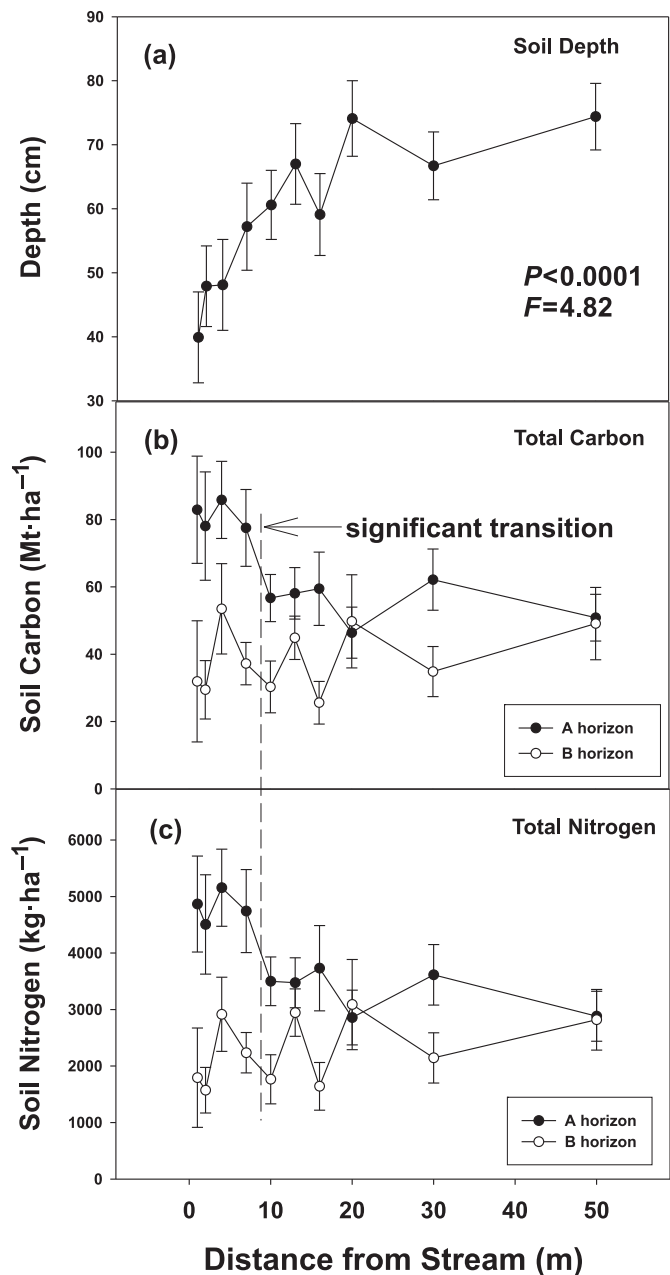
Litter decomposition

Overall, red maple litter decomposed at different rates depending on the location with respect to the stream ($F = 3.64$, $P = 0.017$) (Fig. 7). Decomposition constants ($-k$) ranged from -0.65 at streamside to -0.74 upslope. Litter mass loss was significantly faster at the 10 and 30 m locations than at the streamside locations ($P = 0.014$ and 0.034 , respectively). In contrast, there were no significant differences in N or C loss with distance from stream.

Microarthropods

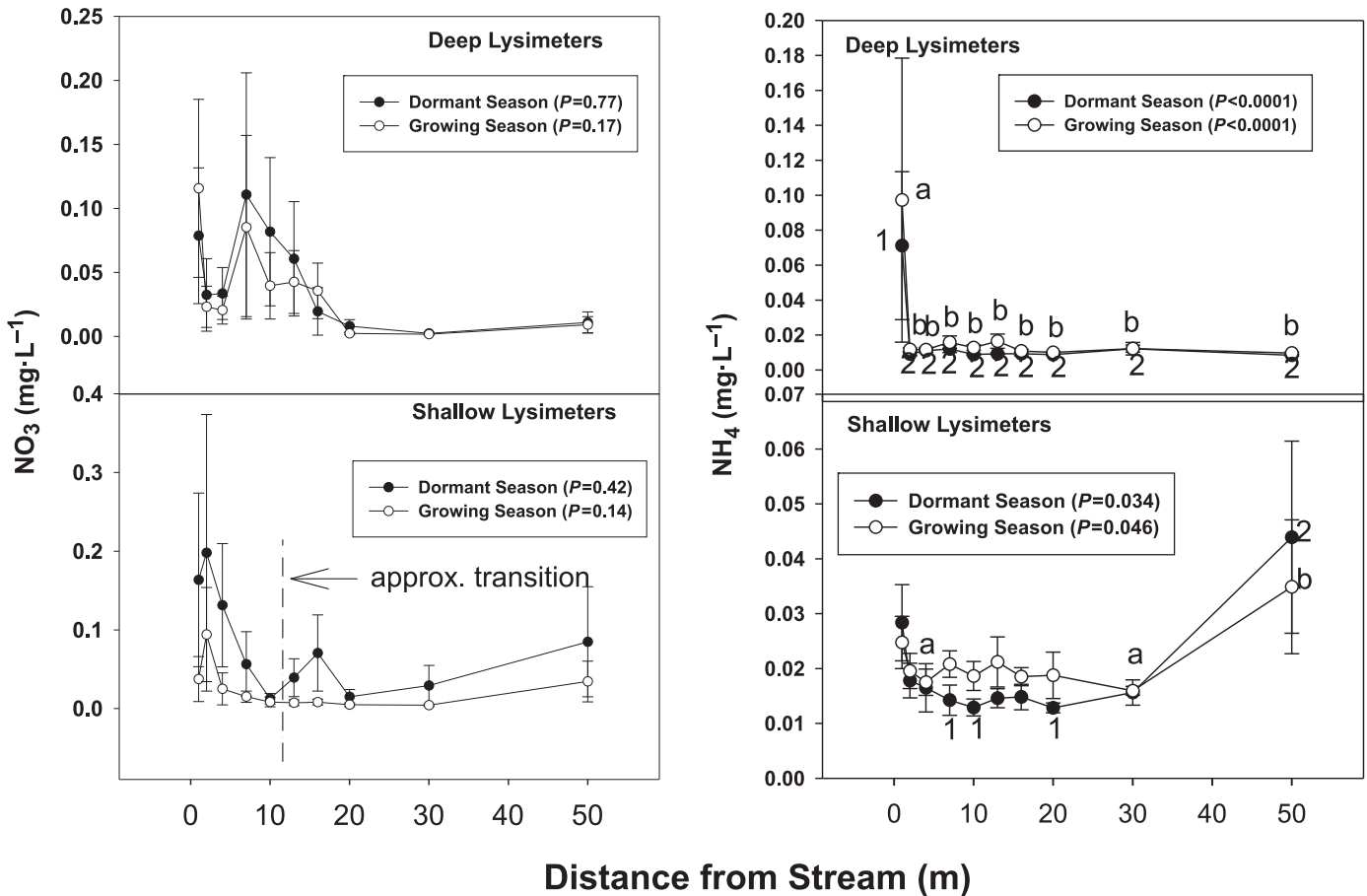
There were no significant differences in microarthropod

Fig. 5. Soil depth (a) and total soil carbon (b) and nitrogen (c) in the A and B horizons. For the A horizon, means to the right of the vertical dashed line are significantly different from those to the left of the dashed line ($\alpha = 0.05$). Error bars represent one standard error of the mean.



counts (totals ranged from 32 to 65 counts·(g dry mass) $^{-1}$) in litterbags along transects; however, oribatid mites sampled in soil cores displayed significant differences among transect locations (Table 4). The highest numbers were at 1 m distance, the lowest at 4 m (Fig. 8). For the combined taxa of prostigmatida and mesostigmatida, and also for collembola, there were no significant differences with distance from the stream (Table 4, Fig. 8). Soil oribatid numbers differed significantly for date and catchment (Table 4), with sharply greater numbers in May 2005 compared with the other three dates. Similar to the oribatids, collembolan numbers were significantly higher in May 2005

Fig. 6. Mean NO_3 and NH_4 concentration soil solution by season, lysimeter depth, and distance from stream. Means with the same letter are not significantly different during the growing season, and means with the same number are not different during the dormant season. In shallow lysimeters, only those means that are different are so designated. Statistics within legend box are for overall distance effects. No superscript indicates no difference (PROC MIXED with Tukey's adjustment, $\alpha = 0.05$). Error bars represent one standard error of the mean.



compared with the other three dates sampled and also varied significantly with catchment (Table 4).

Transitions in key parameters

Soil chemistry

The A horizon total soil N transitioned between 7 and 10 m (Fig. 5; Table 5) with a significant reduction in N upslope ($P = 0.0001$). Similarly, A horizon total C exhibited the same significant reduction at 7–10 m from the stream ($P < 0.0001$) (Table 5). This transition was not evident in the B horizon for either N or C. Soil solution chemistry also displayed significant transitions. $\text{NO}_3\text{-N}$ concentration in shallow lysimeters (A horizon) decreased significantly beyond 10 to 13 m from the stream, during both dormant ($P = 0.024$) and growing ($P = 0.027$) seasons (Table 5; Fig. 6). Although the direction of change remained the same, the transition in deep lysimeters (lower B horizon) was farther upslope, 16 and 20 m from the stream during the dormant season ($P = 0.031$) (Table 5); differences were not significant ($P = 0.095$) during the growing season.

Forest floor and aboveground

Forest floor exhibited a significant transition between 10 and 20 m from the stream for Oi mass ($P < 0.0001$), total

Oi C ($P < 0.0001$), total Oi N ($P < 0.0001$), Oe+Oa mass ($P = 0.002$), and total Oe+Oa C ($P = 0.005$) (Table 5), resulting in greater forest floor mass upslope relative to near-stream locations, as well as larger pools of total C and N. Downed woody debris also revealed a significant transition with greater mass ($P = 0.001$), total C ($P = 0.019$), and total N ($P = 0.025$) within 10 m of the stream (Table 5). Soil moisture (v/v , %) decreased with distance and transitioned between 10 and 15 m from the stream ($P < 0.0001$). Rates of N inputs in litterfall ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$) increased significantly with distance from stream and exhibited a significant transition around 20 m from the stream ($P = 0.005$) (Fig. 3).

Discussion

Vegetation

In the southern Appalachians, numerous authors (Whittaker 1956; Day and Monk 1974; Elliott et al. 1999) have described landscape-scale species distributions as a predictable mosaic related to soil moisture. Indeed, some woody species, such as *Rhododendron maximum*, *Tsuga canadensis*, and *Betula lenta*, have been recognized as being more abundant in riparian areas than in the upland forest (Hedman and Van Lear 1995; Vandermast and Van Lear 2002). In our study, *B. lenta* was the only tree species that was signifi-

Fig. 7. Litter (red maple) mass, carbon, and nitrogen loss rates ($-k$) by distance from stream. Error bars represent one standard error of the mean. For mass loss, means with the same letter are not significantly different ($\alpha = 0.05$).

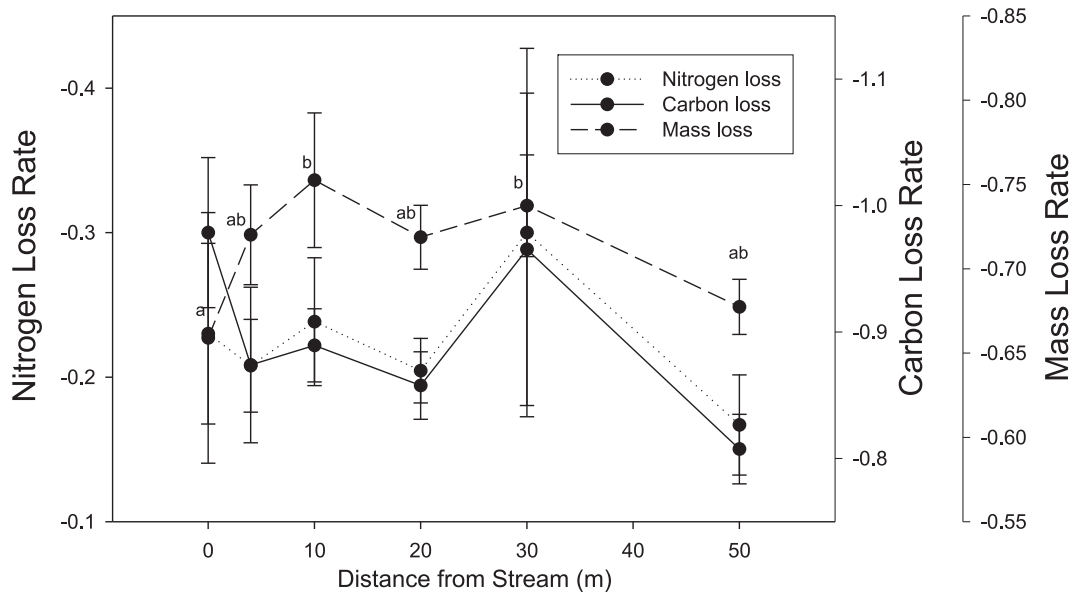


Table 4. Soil microarthropod response to date, site, and location (distance) from stream (PROC GENMOD, SAS Institute Inc. 2004).

Organism	Log-likelihood	Term	χ^2	df	P value
Oribatid mites	690.97	Date	186.12	3	<0.0001
		Catchment	17.00	3	0.0007
		Location	16.69	4	0.0022
Collembola	426.07	Date	30.31	3	<0.0001
		Catchment	8.50	3	0.0367
		Location	3.41	4	0.4914
Prostigmatid/mesostigmatid mites	506.89	Date	43.86	3	<0.0001
		Catchment	8.01	3	0.0457
		Location	6.01	4	0.1985
		Date \times catchment	23.12	9	0.0059
		Date \times catchment \times location	80.94	60	0.0371

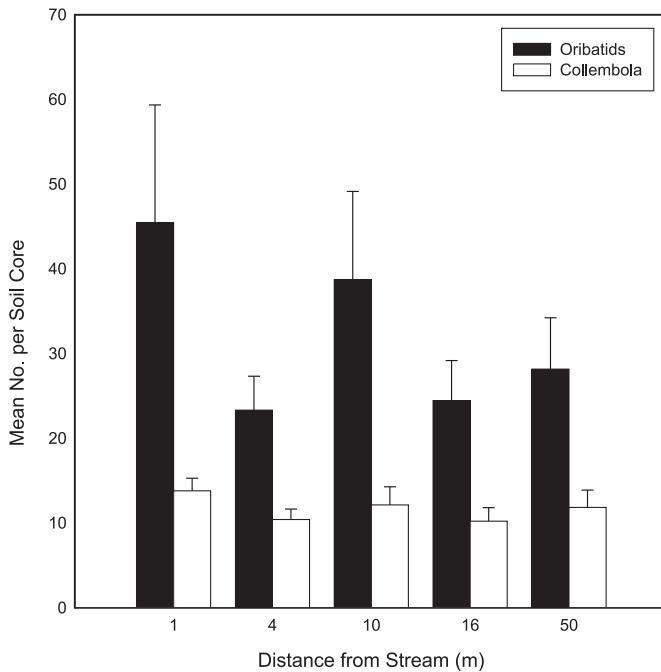
Note: Collection dates were August and December 2004, May and August 2005. The models presented are the most parsimonious; large log-likelihood values indicate a good fit to the model (Agresti 1996).

cantly more abundant near the stream and could indicate a riparian area condition. *Rhododendron maximum* occurred infrequently, i.e., it was present in only 17% of the near-stream plots and absent from all the upland forest plots. *Tsuga canadensis* was relatively abundant from near stream to upper slope; and *L. tulipifera*, a species often associated with mesic, cove (concave terrain and high soil moisture), and riparian forests (Hedman and Van Lear 1995), was also abundant across the hillslope.

In general, riparian ecosystems are noted for having high levels of plant diversity (Dieterich et al. 2006; Richardson et al. 2007). For example, in contrast to our results, Brown and Peet (2003) surveyed the Little Tennessee, the New, and the Nolichucky rivers in the southern Appalachians and found that riparian areas had more exotic and native species and higher species diversity than upland areas, and species diversity increased with flood frequency within the riparian zone. Other authors have found significantly higher richness of

herbs in the riparian zone (<12 m from the stream channel) than in the uplands (>20 m from the channel) (Dieterich et al. 2006). Goebel et al. (2003) showed in higher-order streams that important contributions to overall plant species diversity may occur beyond the protected riparian zone where rigid riparian definition is used. They reported that fluvial landforms outside the protected riparian zone, such as terraces and connecting hillslopes, may receive inadequate protection, particularly if those landforms contained unique plant assemblages or rare plant species. Our study was restricted to small perennial streams in headwater catchments that lack alluvial benches, have steeper sideslopes, and have a closed canopy cover (relative to larger streams), all of which diminish the distinction between riparian areas and the surrounding forest. As a result, we observed few exotic species and found no differences in overstory or ground layer diversity between near-stream and upland areas. Only a few individual overstory and ground layer spe-

Fig. 8. Average number of soil microarthropods per soil core. Averages are over four dates: August and December 2004, May and August 2005. Error bars represent one standard error of the mean.



cies were identified as being indicators of riparian or upland forest conditions.

Carbon, mass, and nutrient pools

We found a significantly greater pool of N in downed woody debris nearer the stream on our study catchments, perhaps the result of years of sustained accumulation of wood that serves as long-term storage of N. This large pool of N is likely the result of (i) inherent instability of near-stream large trees due to shallow soils, (ii) the presence of eastern hemlock in riparian zones, and (iii) the accumulation of N in slowly decomposing wood. Eastern hemlock is known to decompose slowly so that inputs of large wood by this species remain for longer periods of time (Harmon 1982). Downed woody debris performs critical functions in riparian habitats. For example, Southerland (1986) demonstrated experimentally that additions of downed woody debris along stream banks increased the number of salamanders as a result of reduced predation. Brunner and Kimmins (2003) reported the influence of downed woody debris on asymbiotic N fixation. They hypothesized that higher rates of observed asymbiotic N fixation associated with downed woody debris is likely to represent an important contribution to the N balance over the long term, particularly in forest ecosystems where N fixation and deposition are low. Further, Creed et al. (2004) reported large increases in N in coarse wood with increasing stage of decomposition in a southern Appalachian spruce–fir forest.

Forest floor and nutrient turnover

As with most ecosystems in the southern Appalachians, we found that the majority of forest floor mass resided in the humus layer and represented a large and important be-

Table 5. Parameters exhibiting significant transitions along the 50 m stream to upland transects.

Parameter	Approximate transition (m)	Direction of change*	P value
Aboveground			
Forest floor			
Humus mass (Oe+Oa)	10–20	Increase	0.0020
Humus C	10–20	Increase	0.0052
Litter mass (Oi)	10–20	Increase	<0.0001
Litter N	10–20	Increase	<0.0001
Litter C	10–20	Increase	<0.0001
Litterfall			
N input rate [†]	20–30	Decrease	0.0051
Woody debris			
Mass	<10	Decrease	0.0014
N	<10	Decrease	0.0245
C	<10	Decrease	0.0190
Belowground			
Soil moisture			
0–20 cm	10–15	Decrease	<0.0001
Soil A horizon			
Total C	7–10	Decrease	<0.0001
Total N	7–10	Decrease	0.0001
Soil solution [‡]			
NO ₃ — Do, S	10–13	Decrease	0.0237
NO ₃ — G, S	10–13	Decrease	0.0274
NO ₃ — Do, D	16–20	Decrease	0.0308

Note: Significance is based on $\alpha = 0.05$.

*Direction of change represents streamside to uplands.

[†]Litterfall input rate is in $\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$.

[‡]For soil solution concentration, Do, G, S, and D denote dormant season, growing season, shallow lysimeters, and deep lysimeters, respectively.

lowground pool of site nutrients (Vose and Swank 1993). Across a range of sites in the region, the humus layer accounts for 70% of total forest floor mass (Clinton and Vose 2007). In this study, the proportion of total mass in small wood, litter, and humus varied with distance from stream. Even though large differences in mass were observed along transects, high spatial variability in this parameter made statistically significant differences rare. When examining forest floor components (i.e., small wood, litter, humus) and nutrient content, some of the differences were statistically significant. For example, there was significantly less total litter mass, N, and C in near-stream locations (<20 m) relative to more distance locations. Similar patterns were observed for humus mass and C. Although our estimates of decomposition rates were lowest at streamside, in general there appears to be a tendency in these systems for detritus and coarse and fine forms of organic matter to cycle at greater rates nearer the stream compared with the uplands because of stream water temperature moderated microclimate that favors certain decomposers (Hutchens and Wallace 2002).

We found increased soil nutrient concentrations near the stream in A-horizon soils that corresponded with a decline in humus layer mass. There was a significant negative relationship between humus layer total C and N and total soil C and N within 2 m of the stream. As C and N pools increased in the soil, there was a decrease in the amount of C and N in the forest floor, suggesting rapid incorporation of fine and coarse organic material. Increased nutrient concentrations also re-

sulted in greater amounts of plant-available nutrients in the A horizon near the stream as evidenced by increased soil solution NH_4 concentrations. Increased N and C concentrations in riparian soils are commonly found across the country, as documented in regional and county soils surveys (Natural Resources Conservation Service; <<http://soils.usda.gov/contact/nssc/>>). Research studies examining soils across topographic and elevation gradients have also shown that cove and riparian soils commonly have greater N concentrations and availability (Garten et al. 1994; Knoepp et al. 2000) than upland soils, which is attributed to differences in both vegetation and higher moisture content of riparian soils (Knoepp et al. 2000).

Nutrient cycling

The internal cycling of C and other plant nutrients via decomposition is fundamentally important to ecosystems (Cadish and Giller 1997). These processes have a major influence on plant growth and community structure (Bardgett 2005) through the regulation of nutrient availability (Perala and Alban 1982). Hutchens and Wallace (2002) demonstrated variation in decomposition of *A. rubrum* along the stream to upland gradient in southern Appalachian headwater catchments. Their results indicated greater fluxes of material closer to the stream compared with upland habitats because of stream-water-moderated microclimate, which favored several macroinvertebrate taxa important in decomposition. In our study, rates of decomposition at streamside (1 m) were the lowest; the highest rates occurred close to the stream (≤ 10 m) compared with the uplands. Further, our estimates of decomposition are based on a single tree species, and there is evidence of a link between leaf litter diversity and regulation of litter decomposition rates (Hector et al. 2000; Ball et al. 2008) and ecosystem function, in general (Meier and Bowman 2008). We found the variety of leaf litterfall to be much higher near the stream than in the uplands, which may be related to finding less mass, N, and C in forest floor litter near the stream than in the uplands.

Soil respiration rates, an indicator of belowground microbial and root activity, did not vary significantly with distance from stream. Within a vegetation type, rates of soil respiration have been shown to be largely dependent on soil temperature and moisture conditions (Singh and Gupta 1977; Schlentner and Van Cleve 1985). In our study, soil temperature was correlated with soil CO_2 evolution but did little to explain variation along the streamside to upland gradient. Soil moisture did not provide additional explanatory information regarding variation in rates of soil CO_2 efflux either overall or along the gradient. Studies at a similar site in the southern Appalachians have shown a positive relationship between increased soil moisture and soil respiration (Reynolds and Hunter 2001). However, the effect of soil moisture on soil CO_2 efflux has been shown to be negative for amounts greater than 20% by volume (Luo and Zhou 2006; Nuckolls et al. 2009) and positive under drier conditions (Davidson and Janssens 2006), particularly following a wetting period. In our study, the influence of soil moisture, although important in autotrophic and heterotrophic respiration, may have been muted by other factors along the gradient, such as soil temperature, as well as the fact that soil moisture values were consistently $>20\%$. In addition, CO_2 derived from the decomposition of soil organic compounds is tightly linked to

the intrinsic kinetic properties of the various compounds that determine temperature sensitivity to decomposition and, hence, the release of CO_2 (Davidson and Janssens 2006).

Soil fauna and decomposition

The composition of soil and litterbag microarthropods were characteristic for this region (i.e., collembola and mites from the suborders oribatid, mesostigmatid, and prostigmatid) (Reynolds et al. 2003). Soil and litter microarthropods are critical to the decomposition process, as they fragment litter, feed on and transport fungi, and link components of soil food webs (Coleman et al. 2004). Recent modeling of soil food webs indicates that fungal-feeding microarthropods are important participants in the production of dissolved organic matter (Osler and Sommerkorn 2007); however, we did not find any significant differences in microarthropod abundance in litter from the near stream to the upland forest. In contrast, Reynolds et al. (2003, 2007) found that oribatid mites were positively correlated with litter decomposition rates and that they were the most common microarthropod in moist areas. Hutchens and Wallace (2002) hypothesized that the faster litter decomposition rates they measured closer to the stream were due to stream-moderated microclimate, which favored several macroinvertebrate taxa important in decomposition; however, like the results in our study, they also found no significant differences for collembola and mite numbers between upland and bankside litterbags. Significant variation in the numbers of soil oribatids and other soil microarthropods among transect locations was probably due to the inherent patchiness of soil resources and the notorious clumped distribution of soil microarthropods (Coleman et al. 2004). The lack of significant or predictable variation in litter and soil microarthropod populations indicates that these descriptors are insufficient by themselves for defining riparian width.

Transitions in key parameters

Our second objective was to determine if structural and functional attributes could be used to objectively identify the extent of the riparian zone. For some parameters, we were able to identify significant zones of transition (Table 5) occurring between 7 and 30 m from the stream, with the majority of the parameters transitioning between 10 and 20 m from the stream. We found total soil N and C, soil A-horizon depth, soil solution $[\text{NO}_3]$, litterfall N, and total downed woody debris N and C to be greatest near the stream. The forest floor exhibited the opposite trend — lower mass, total N, and total C in litter and lower total mass and C in the humus layer near the stream, compared with the forest floor on the uplands. The inverse relationship between belowground and forest floor N and C pools may be the result of varying rates of forest floor turnover from the near-stream positions to the uplands; i.e., faster rates of incorporation of N and C and greater longevity of downed woody debris near the stream.

Some of these observed transitions may be caused by riparian zones acting as sinks for nutrients in solution moving along subsurface hydrologic flowpaths. This inherent capacity to buffer against inputs from the uplands results from several processes: nutrient sequestration in vegetation, soil adsorption, volatilization, and microbial immobilization

(Naiman and Décamps 1997; Naiman et al. 2005). These processes significantly modify the amount, form, and timing of nutrient export from watersheds (Gregory et al. 1991). For example, Knoepp and Clinton (2009) demonstrated the ability of riparian buffers to sequester inputs of N and other solutes from upland forest management activities. They concluded that riparian buffers are effective at removing soil solution NO_3 resulting from timber harvest activity and at preventing N from reaching the stream. The riparian zones' function as a regulator of nutrient export is considered one of the most important benefits of undisturbed riparian areas, particularly in agricultural systems where nutrient fluxes are often well in excess of natural conditions (Lowrance et al. 1984). Hence, riparian zones play a critical role in moderating the migration of dissolved materials from terrestrial to aquatic ecosystems. Knowledge of the capacity of the riparian ecosystem to buffer and mitigate fluxes of nutrients and other materials to the stream is critical for conserving this important function.

Conclusions

Our hypothesis that riparian zones in headwater catchments could be distinguished from the uplands by structural and functional characteristics was generally supported. Significant transition zones were identified for some parameters; however, other parameters were unrelated to topographic position and were not useful for identifying a distinct riparian zone in this setting. It is particularly noteworthy that the "traditional" riparian indicator used in larger stream systems — vegetation composition — was a poor parameter for defining riparian zone width here. Instead, more basic abiotic (e.g., soil moisture) and structural and functional parameters (e.g., downed woody debris N content, forest floor, soil and soil solution chemistry) were significant indicators (Table 5) of transition from near-stream conditions to upland conditions. Overall, our results showed that important transitions occur in the range of 10–20 m from stream edge. The range in the location of these transition zones suggests that the distinction between riparian and upland conditions is more accurately described as an 'ecotone' in these headwater systems rather than as a well-defined riparian zone boundary. This knowledge should improve our ability to develop principles and techniques essential to identifying riparian structure and sustaining riparian zone function. This requires a better than cursory understanding of the role of riparian zones in protecting critical aquatic and terrestrial habitats and important ecosystem characteristics that influence water quality and habitat protection.

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Appendices

Appendices A and B begin on the following page.

Appendix A

Table A1. Summary of average density, basal area, and foliage, and total aboveground biomass of the most abundant tree species at each of three distances from stream plot locations (near stream (0–10 m), midslope (20–30 m), and upper slope (40–50 m)).

Species	Distance	Density (stems·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	Biomass (kg·ha ⁻¹)	
				Foliage	Total
<i>Acer rubrum</i>	Near stream	56 (16)a	0.8 (0.5)	141 (82)	5 396 (4 082)
	Midslope	125 (51)b	3.5 (2.6)	551 (395)	27 092 (22 241)
	Upper slope	150 (39)b	2.6 (0.9)	431 (149)	16 101 (5 863)
<i>Betula lenta</i>	Near stream	62 (47)a	2.7 (2.1)a	235 (195)	21 925 (18 289)
	Midslope	31 (16)ab	1.2 (0.8)ab	101 (75)	9 305 (7 031)
	Upper slope	12 (12)b	0.1 (0.1)b	6 (6)	476 (476)
<i>Carya</i> sp.	Near stream	56 (21)	1.7 (0.7)	202 (100)	11 434 (5 993)
	Mid slope	94 (24)	1.6 (0.9)	187 (115)	10 140 (7 016)
	Upper slope	100 (35)	0.8 (0.3)	77 (30)	3 470 (1 411)
<i>Cornus florida</i>	Near stream	38 (30)	0.2 (0.1)	26 (17)	752 (538)
	Midslope	88 (33)	0.4 (0.2)	51 (23)	1 351 (665)
	Upper slope	69 (37)	0.2 (0.2)	29 (19)	702 (500)
<i>Fagus grandifolia</i>	Near stream	194 (177)	2.0 (1.9)	239 (235)	12 279 (12 216)
	Midslope	62 (41)	0.4 (0.2)	49 (29)	1 572 (920)
	Upper slope	75 (43)	0.9 (0.8)	111 (100)	6 882 (6 665)
<i>Liriodendron tulipifera</i>	Near stream	119 (31)	10.7 (1.7)	878 (140)	89 068 (12 863)
	Midslope	75 (23)	6.0 (2.0)	498 (164)	46 514 (14 912)
	Upper slope	88 (33)	7.1 (2.5)	585 (210)	54 957 (19 435)
<i>Oxydendrum arboreum</i>	Near stream	0a	0a	0a	0
	Midslope	6 (6)a	0.01 (0.01)b	0.56 (0.56)b	4.14 (4.14)
	Upper slope	44 (21)b	0.4 (0.2)b	36 (16)b	1 722 (804)
<i>Quercus alba</i>	Near stream	6 (6)a	0.2 (0.2)	28 (28)	730 (730)
	Midslope	31 (15)b	2.8 (1.0)	366 (142)	17 926 (6 516)
	Upper slope	25 (10)b	2.5 (1.7)	298 (183)	19 808 (16 239)
<i>Quercus montana</i>	Near stream	12 (12)a	0.4 (0.4)a	48 (48)	1 855 (1 855)
	Midslope	0a	0a	0	0
	Upper slope	62 (16)b	5.5 (1.9)b	871 (340)	66 722 (34 787)
<i>Quercus rubra</i>	Near stream	12 (12)	4.1 (4.1)	694 (694)	61 057 (61 057)
	Midslope	44 (6)	9.8 (2.5)	1 621 (447)	137 970 (44 456)
	Upper slope	44 (19)	6.8 (3.9)	1 094 (664)	86 270 (60 051)
<i>Tilia americana</i>	Near stream	56 (36)	3.4 (2.9)	411 (347)	28 001 (25 062)
	Midslope	69 (40)	0.5 (0.4)	59 (45)	2 248 (1 888)
	Upper slope	6 (6)	0.3 (0.3)	38 (38)	2 010 (2 010)
<i>Tsuga canadensis</i>	Near stream	100 (57)	1.06 (0.9)	2 293 (1 815)	14 184 (11 679)
	Midslope	75 (10)	0.7 (0.3)	1 588 (695)	9 479 (4 458)
	Upper slope	50 (27)	1.64 (1.1)	3 286 (2 168)	22 707 (16 120)
All <i>Quercus</i> species	Near stream	38 (30)a	5.5 (5.3)	854 (818)	71 110 (70 103)
	Midslope	81 (26)ab	13.6 (4.2)	2 158 (700)	167 778 (57 849)
	Upper slope	138 (30)b	15.5 (3.9)	2 365 (669)	178 941 (66 313)
Total of all species	Near stream	1068 (163)	30.6 (7.6)	9 865 (4 190)	285 850 (98 595)
	Midslope	956 (154)	29.3 (3.8)	14 602 (18 200)	278 270 (54 945)
	Upper slope	994 (194)	30.8 (4.8)	10 156 (4 242)	303 699 (83 563)

Note: Standard errors are in parentheses. Minor species with <1000 kg·ha⁻¹ total biomass or occurring in only one plot were not included in table. Values with standard errors equal to the average represent species that were found in only one of the 16 plots per slope position. For the same species within a column, values followed by different letters denote significant differences ($P < 0.05$) among slope positions.

Appendix B

Table B1. Average percent cover and percent frequency of ground layer species (across all transects and catchments) related to distance

Species	0 m	5 m	10 m	15 m
	% Cover (SE); % frequency			
<i>Polystichum acrostichoides</i>	7.68 (3.53); 56	4.06 (2.00); 31	3.19 (1.48); 38	4.19 (1.58); 44
<i>Laportia canadensis</i>	7.50 (3.97); 50	2.44 (1.35); 31	1.12 (0.94); 12	0.19 (0.19); 6
<i>Viola rotundifolia</i>	6.44 (1.41); 88	3.44 (1.27); 50	2.25 (1.36); 25	1.06 (0.64); 25
<i>Parthenocissus quinquefolia</i>	3.06 (1.42); 38	0.75 (0.43); 19	2.69 (1.25); 44	4.75 (1.64); 62
<i>Astilbe biternata</i>	2.81 (1.58); 19	2.50 (2.50); 6	1.88 (1.88); 6	2.81 (2.50); 12
<i>Solidago curtisii</i>	2.62 (1.27); 38	1.88 (1.26); 25	0.81 (0.36); 31	0.62 (0.43); 12
<i>Thelypteris noveboracensis</i>	2.50 (1.51); 19	5.62 (5.00); 12	4.31 (1.50); 44	5.19 (3.24); 6
<i>Tiarella cordifolia</i>	2.31 (0.45); 69	2.81 (0.91); 44	1.62 (0.54); 44	0.44 (0.24); 25
<i>Disporum lanuginosum</i>	1.50 (0.87); 19	1.19 (0.48); 31	1.06 (0.45); 31	2.50 (1.02); 31
<i>Hamamelis virginiana</i>	1.25 (0.45); 44	1.50 (0.69); 31	2.00 (0.54); 56	1.25 (0.68); 25
<i>Amphicarpaea bracteata</i>	1.19 (0.53); 25	1.25 (0.97); 12	2.88 (1.35); 38	1.25 (0.69); 25
<i>Desmodium nudiflorum</i>	1.19 (0.65); 31	1.06 (0.40); 38	2.12 (0.74); 44	6.06 (2.01); 75
<i>Aster divaricatus</i>	1.00 (0.40); 38	1.88 (0.68); 50	2.44 (0.86); 44	1.88 (0.57); 44
<i>Acer rubrum</i>	0.81 (0.36); 56	2.12 (0.69); 75	1.81 (0.57); 62	2.31 (0.87); 62
<i>Prenanthes</i> sp.	0.81 (0.40); 25	0.88 (0.44); 25	1.75 (0.70); 50	1.06 (0.45); 31
<i>Calycanthus floridus</i>	0.75 (0.63); 12	0.94 (0.50); 19	—	—
<i>Aristolochia macrophylla</i>	0.56 (0.22); 31	2.31 (1.36); 31	2.75 (2.49); 19	2.56 (1.44); 31
<i>Quercus rubra</i>	0.38 (0.22); 19	1.06 (0.41); 31	1.88 (0.94); 44	1.18 (0.48); 31
<i>Pyrolaria pubera</i>	0.31 (0.31); 6	3.25 (1.56); 31	0.75 (0.43); 19	3.69 (1.68); 38
<i>Collinsonia canadensis</i>	0.25 (0.25); 6	0.25 (0.25); 6	0.56 (0.39); 12	0.19 (0.19); 6
<i>Viola</i> spp.	0.25 (0.17); 12	1.12 (0.29); 62	2.88 (1.24); 62	1.31 (0.47); 50
<i>Eupatorium purpureum</i>	0.19 (0.19); 6	1.00 (0.44); 31	0.50 (0.35); 12	4.12 (2.50); 44
<i>Carya glabra</i>	—	1.25 (0.70); 25	2.69 (1.28); 31	0.88 (0.66); 12
<i>Medeola virginiana</i>	—	0.56 (0.39); 12	0.06 (0.06); 6	1.75 (0.98); 25
	Total percent cover (SE)			
	66.0 (8.7)	67.6 (9.8)	69.1 (8.1)	81.0 (10.0)
	H' (SE)			
	1.986 (0.107)	2.076 (0.135)	2.269 (0.109)	2.220 (0.131)
	Mean richness: no. of species per 1.0 m quadrat (SE)			
	12.8 (1.1)	13.4 (1.3)	15.1 (1.2)	15.5 (1.4)
	Total richness: no. of species per distance from stream location			
	71	73	82	77

Note: $N = 16$ quadrats for each distance. Only the 24 ground layer species with ≥ 2.00 mean percent cover for at least one distance from stream location accounted for 82.6% of the total species present across the four catchments. H' is Shannon's index of diversity.

from stream.

20 m	25 m	30 m	35 m	40 m	45 m
7.81 (3.50); 31 —	2.19 (1.12); 25 —	5.94 (2.82); 31 —	4.06 (1.60); 38 —	1.88 (1.28); 12 —	2.62 (1.36); 25 —
1.06 (0.68); 19 1.88 (0.97); 38 —	1.38 (0.97); 19 2.87 (1.20); 38 —	0.38 (0.22); 19 1.88 (0.88); 31 2.50 (2.50); 6	1.56 (1.27); 12 1.38 (0.55); 31 0.31 (0.31); 6	0.12 (0.12); 6 0.94 (0.68); 12 —	— 1.38 (0.69); 31 —
1.56 (1.27); 12 2.62 (1.88); 25 0.56 (0.32); 19 4.25 (3.12); 31 0.38 (0.26); 12 5.56 (4.97); 31 4.25 (1.68); 50 2.75 (0.95); 56 2.88 (1.25); 56 1.12 (0.38); 50 —	1.50 (0.70); 31 5.31 (2.79); 25 1.19 (0.68); 25 2.50 (0.91); 38 1.12 (0.94); 12 0.69 (0.42); 19 6.25 (1.84); 62 1.31 (0.42); 50 1.81 (0.52); 69 1.62 (0.70); 44 1.25 (0.97); 12	1.06 (0.68); 19 3.75 (1.74); 25 0.69 (0.42); 19 2.50 (1.27); 31 0.88 (0.40); 31 0.62 (0.36); 19 6.19 (1.39); 75 3.69 (2.46); 44 2.19 (0.98); 69 0.56 (0.26); 25 —	2.25 (1.25); 38 2.81 (1.29); 25 0.81 (0.45); 19 2.19 (1.02); 31 0.88 (0.44); 25 0.94 (0.68); 12 4.00 (0.80); 75 3.31 (1.07); 56 2.19 (0.95); 69 2.25 (0.74); 50 —	2.81 (1.71); 19 4.38 (3.73); 19 0.44 (0.33); 12 0.50 (0.30); 19 0.44 (0.33); 12 2.06 (1.10); 25 4.00 (1.14); 56 2.44 (0.88); 44 1.81 (0.66); 62 0.88 (0.38); 31 —	3.12 (1.51); 31 1.75 (0.88); 25 0.31 (0.22); 12 1.12 (0.69); 19 0.69 (0.62); 19 0.81 (0.44); 19 5.75 (1.71); 75 1.62 (0.71); 38 2.31 (0.79); 75 1.12 (0.45); 38 3.00 (1.50); 25 1.25 (1.25); 6 1.31 (0.69); 25 7.19 (2.09); 56 0.62 (0.62); 6 1.81 (0.55); 56 1.75 (0.75); 38 2.06 (1.36); 19 1.88 (0.98); 31
0.19 (0.19); 12 1.75 (0.88); 25 5.62 (2.28); 38 0.25 (0.25); 6 0.81 (0.36); 31 1.25 (0.67); 25 0.12 (0.12); 6 0.001 (0.001); 6	1.56 (1.09); 12 1.25 (0.68); 25 4.31 (1.57); 44 0.62 (0.62); 6 1.25 (0.49); 50 3.12 (1.48); 44 2.81 (1.29); 25 0.75 (0.63); 12	0.19 (0.14); 12 1.56 (0.88); 19 4.62 (2.01); 31 0.25 (0.25); 6 0.75 (0.25); 44 0.75 (0.41); 19 1.44 (0.70); 31 3.00 (1.34); 44	1.38 (0.96); 19 0.69 (0.31); 25 5.62 (2.18); 38 0.62 (0.62); 6 1.75 (0.66); 62 1.38 (0.55); 38 1.12 (0.51); 25 0.75 (0.39); 25	1.94 (1.28); 19 2.88 (1.16); 44 3.12 (1.01); 44 3.38 (2.52); 19 1.44 (0.43); 62 2.69 (0.99); 50 0.62 (0.62); 6 1.06 (0.45); 31	1.25 (1.25); 6 1.31 (0.69); 25 7.19 (2.09); 56 0.62 (0.62); 6 1.81 (0.55); 56 1.75 (0.75); 38 2.06 (1.36); 19 1.88 (0.98); 31
76.1 (11.6)	71.7 (8.2)	71.5 (10.3)	80.9 (7.6)	71.4 (12.8)	67.8 (7.4)
1.921 (0.158)	2.229 (0.124)	2.072 (0.134)	2.404 (0.116)	2.120 (0.188)	2.237 (0.088)
13.1 (1.3)	14.9 (1.2)	13.5 (1.7)	16.4 (1.2)	14.3 (1.9)	14.2 (1.1)
82	78	80	85	82	81

are included in table. Total number of ground layer species observed is 138. Minor species (<2.00 mean percent cover at any distance from the stream)