Ecosystem Linkages between Southern Appalachian Headwater Streams and Their Banks: Leaf Litter Breakdown and Invertebrate Assemblages

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ABSTRACT

We examined red maple (*Acer rubrum* L.) leaf litter breakdown in streams and riparian zones at two sites in the southern Appalachian Mountains to understand how differences in abiotic and biotic factors influence leaf breakdown rates. Litterbags were placed in three riparian habitats differing in litter layer moisture: stream > bank > upland. Invertebrates colonizing litterbags at one site were also examined to determine how variations in community and functional structure affect breakdown rates. Leaves broke down fastest in streams and slowest in upland habitats, whereas bank habitats were intermediate and characterized by high variability. Faster leaf breakdown rates in streams appeared to be a function of greater moisture availability, a more stable thermal regime, and a higher biomass of leaf-shredding invertebrates, especially the stonefly *Tallaperla*. In addition, patterns of leaf breakdown and invertebrate community structure provided evidence for a stronger than expected ecological connection between the stream and the bank. Overall, detritus processing within this narrow riparian ecosystem varied considerably depending on the availability of moisture. Results from this study show that stream channel–floodplain interactions in riparian ecosystems of steep forested mountains are analogous to ones in larger downstream or low-gradient systems. Riparian zones throughout a river network display a remarkable heterogeneity in their ability to process organic matter, which is ultimately driven by changes in hydrological conditions.

Key words: moisture; community structure; stream; bank; upland; decomposition; detritus; heterogeneity; macroinvertebrate; shredder.

INTRODUCTION

Aquatic–terrestrial interfaces or riparian zones form a critical transition zone in landscapes, controlling the movement of nutrients and energy between adjacent ecosystems and containing relatively high levels of biodiversity (Malanson 1995; Risser 1995; Naiman and Décamps 1997). Viewed from an ecosystem perspective, riparian zones integrate the linkages among the geomorphic processes that create valley floor landforms, patterns of plant succession, and structural and functional attributes of stream ecosystems (Gregory and others 1991). The juxtaposition of these multiple landscape elements creates remarkable heterogeneity in both ecosystem structure and function within a narrow corridor. To improve our understanding of these complex sys-

tems, we need to make comparisons that incorporate both terrestrial and aquatic components (Freckman and others 1997; Wagener and others 1998; Groffman and Bohlen 1999).

One of the shared functions of terrestrial and aquatic ecosystems is the breakdown of detritus. Detritus is an essential resource in most aquatic and terrestrial ecosystems (Odum and de la Cruz 1963). For example, the exclusion of leaf detritus from streams (Wallace and others 1997b, 1999) and forest floors (David and others 1991; Arpin and others 1995) can alter food webs and productivity. Riparian zones provide an ideal setting for the identification of factors that have a significant effect on detritus breakdown because they contain a series of relatively distinct zones that differ in abiotic and biotic factors across a relatively short distance. Most studies of leaf breakdown in riparian zones that have incorporated both stream and terrestrial habitats have been done in portions of stream drainages that have relatively large, active floodplains (for example, see Merritt and Lawson 1979, 1992). These studies have found that decomposition in the floodplain can be either hindered by anoxic conditions due to standing water or sediment deposition (Cuffney and Wallace 1987; Chauvet 1988) or enhanced by both physical processes (that is, leaching and fragmentation from the stream flow) and biological processes (that is, microbial activity and invertebrate consumption) (Brinson 1977; Shure and others 1986; Gurtz and Tate 1988; Merritt and Lawson 1979, 1992; Molles and others 1995; Lockaby and others 1996; Ellis and others 1999). However, it is unclear whether riparian zones of mountain streams with little or no floodplain development have such a wide range in leaf breakdown dynamics. We hypothesized that there may be considerable heterogeneity in breakdown even in riparian zones of small steep mountain streams because of previous observations of litter movement dynamics within the riparian zone that were analogous to those in larger streams (Wallace and others 1995). We also examined invertebrates colonizing leaf litter because we expected that differences in leaf-consuming invertebrate assemblages within the riparian zone would influence breakdown rates.

The objective of this experiment was to examine leaf litter breakdown across an elevation gradient in riparian ecosystems at two sites in the southern Appalachian Mountains. Litterbags containing red maple (*Acer rubrum* L.) leaves were placed in three habitats differing in litter layer moisture: stream, bank, and upland. Invertebrates colonizing litterbags at one site were also studied to determine how abundance, biomass, and community and functional structure varied among habitats and over time.

STUDY SITES

This study took place in the Wine Spring Creek Ecosystem Management Demonstration Project area, an 1820-ha basin in the Wayah Ranger District of the Nantahala National Forest in western North Carolina, USA. The basin (35°11′00″N, 83°36′30″W) is in the Blue Ridge Physiographic Province and flows into the Nantahala–Little Tennessee River drainage. Mean annual air temperature in the Wine Spring Basin is 10.4°C; mean annual precipitation is 191.7 cm (4-y mean); (US Forest Service unpublished). One reach in each of two second-order streams, Bearpen Creek (BP) and Upper Wine Spring (UW), were chosen as study sites. Each stream reach is shallow (<10 cm at baseflow), 5–10 m wide, and bordered by steep slopes. Substrate composition in each reach consists primarily of cobble riffles and some depositional areas dominated by sand. Temperature in both stream reaches was monitored with Ryan Thermographs (Ryan Instruments, Redmond, WA, USA). Both streams have similar thermal regimes (mean: 8.9°C and 9.3°C; annual degree days: 3234 and 3381, respectively; 4-y mean) (J. B. Wallace unpublished). Mean annual discharge at BP was 47.2 L/s (3-y mean) (US Forest Service unpublished); discharge at UW was not measured but appeared to be similar to BP. Stream flow is perennial, with storm flows occurring throughout the year. Litter layer moisture and temperature in the bank and upland habitats were not available during the leaf breakdown experiment. However, these data were monitored at BP after the leaf breakdown experiment to provide information about environmental conditions in these habitats.

Moisture and temperature were measured continuously with electronic sensors (Electronically Monitored Ecosystems, Inc., Berkeley, CA, USA) from 1 July 1996 to 31 May 1997. Mean precipitation during 1996 and 1997 was higher (196 cm) than in 1995 (166 cm) when the experiment took place. Some moisture and temperature data for bank and upland habitats were lost due to equipment failure. However, missing bank and upland temperature data were estimated by significant regressions with stream temperature (bank: $P < 0.001$, $r^2 = 0.960$, $n = 219$; upland: $P < 0.001$, $r^2 = 0.943$, $n = 219$); similar strong explanatory relationships between terrestrial litter moisture and stream discharge or precipitation were not found.

Soils in the catchments are Typic Haplumbrepts

(Cullasaja series). Vegetation in bank and upland habitats consists of a mixed-hardwood forest dominated by birch (*Betula* spp.). A dense rhododendron (*Rhododendron maximum* L.) understory shades the streams yearround. Other important tree species are red maple, white and red oaks (*Quercus* spp.), hickory (*Carya* spp.), and hemlock (*Tsuga canadensis* [L.] Carr.). Half of the catchment area drained by BP and UW was selectively logged in 1973 except for a 50-m riparian buffer strip. In 1986, 27% of the UW catchment beyond the buffer strip was also clear-cut. Bank and upland habitats used in this study were within the undisturbed buffer strip.

METHODS

Red maple leaves from the Wine Spring Creek catchment were collected in autumn 1994. About 8 g (air-dry weight) of leaves were placed into 20 × 35 cm plastic mesh bags (mesh size: approximately 5 mm). Twenty-five litterbags were placed in each of three habitats (cobble riffles in the stream; bank next to the stream at or just below bank full width; upland forest approximately 10 m above the stream) at each site on 15 December 1994 and secured to substrates. Three replicate litterbags were retrieved from each habitat at each site after 2 and 4 weeks and approximately monthly thereafter (1 January, 16 January, 4 March, 1 April, 7 May, 12 June, 14 July, and 12 August, 1995), washed of debris and invertebrates, air-dried, weighed, and subsampled for ash-free dry mass (AFDM) determination. Initial leaf mass was corrected for mass loss due to handling and breakage during pack construction (Benfield 1996). Leaf breakdown rates (−k) were computed using an exponential decay model (Olson 1963; Petersen and Cummins 1974) and compared among habitats in each stream separately using a general linear model (GLM) with dummy variables (Zar 1998) using SAS (Release 6.03; SAS Institute Inc., Cary, NC, USA).

Invertebrates colonizing litterbags at BP were examined for differences among habitats. Invertebrates were washed from litterbags through nested 1000- and 125-μm–mesh sieves and preserved in a 6%–8% formalin solution containing phloxine B dye to facilitate the sorting of macroinvertebrates from debris. All macroinvertebrates retained on the 1000-μm sieve were removed using a dissecting microscope at 15×. The sample retained on the 125-μm sieve was subsampled as needed using a sample splitter (Waters 1969), and invertebrates were removed as above.

Insects were identified to genus or order; other invertebrates were identified as Aranae, Copepoda, Chilopoda, Diplopoda, Nematoda, Hydracarina, Oribatei, miscellaneous Acarina, Gastropoda, or Oligochaeta. All invertebrates were counted and measured to the nearest 1 mm for conversion to AFDM using taxon-specific length–mass regressions (Hodar 1996; Benke and others 1999). Invertebrates belonging to the shredder functional feeding group (FFG) were assigned using Merritt and Cummins (1996), Coleman and Crossley (1996) or by the examination of mouth parts.

Log$_{10}$ (x + 1)–transformed means of abundance and biomass of total invertebrates and shredders were compared among habitats with repeated-measures analysis of variance (ANOVA) using a general linear model in SAS. Individual habitats were compared using contrast statements. Only the first six dates were used in these analyses because stream litter had completely decayed in this time. Major groups of invertebrates comprising 5% or more of total abundance or biomass in any habitat were compared similarly. Arcsin-transformed proportions of shredders were also analyzed. Community structure of litterbag invertebrates was examined by ordinating the log$_{10}$ (x + 1)–transformed mean abundance and biomass on each collection date of the major groups compared above. Detrended correspondence analysis (DCA) (Hill and Gauch 1980) run with MVSP (Version 3.0; Kovach Computing Services, Anglesey, Wales, UK) was used to ordinate the data. DCA produces a similarity matrix based on chi-square distances.

RESULTS

Percent moisture in the litter was higher in the bank habitat than in the upland habitat of BP (Figure 1), especially from March to May. Bank moisture rose through the winter as stream baseflow increased (Figure 1). Moisture in the bank litter was significantly related to mean daily discharge at BP ($P < 0.001$, $r^2 = 0.210$, $n = 304$). Litter moisture in the upland habitat was not related to stream flow ($P = 0.892$, $r^2 < 0.001$, $n = 304$), and little variation was explained by daily precipitation ($P = 0.128$, $r^2 = 0.008$, $n = 304$).

Mean daily temperatures in the bank, upland, and stream habitats were more similar among habitats than was moisture (Figure 2), although seasonal differences were noted. Upland litter was warmer than bank and stream litter during summer, but it was cooler in autumn and winter (Table 1). Temperature in the upland habitat was more variable than in the bank or stream, ranging 28.2°C over 11 months, whereas bank and stream habitats
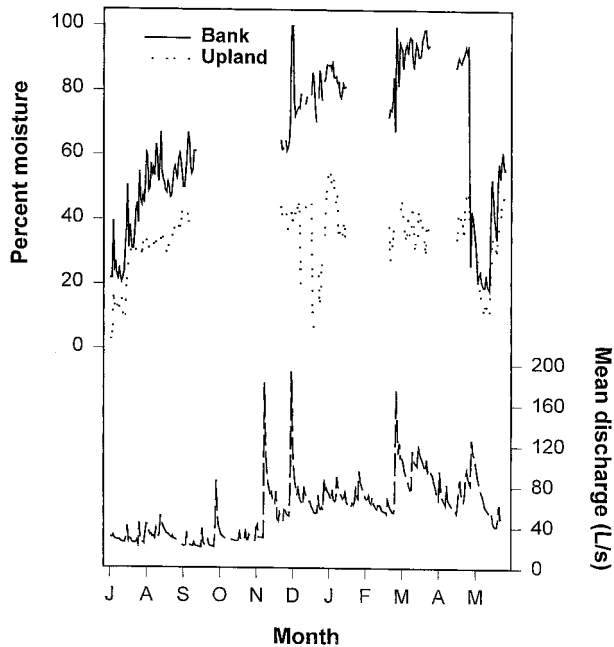
Figure 1. *Top*: Percent moisture in litter layer in bank and upland habitats at the Bearpen Creek site from 1 July 1996 to 31 May 1997. Breaks indicate missing data. *Bottom*: Mean daily discharge (L/s) for Bearpen Creek over the same period.
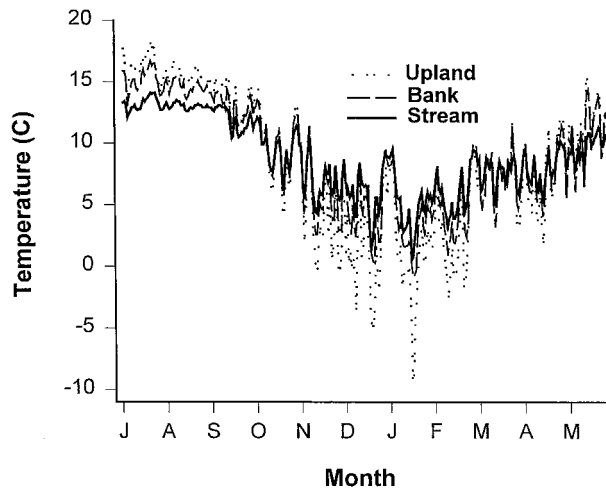

Figure 2. Temperature (°C) in litter layer in stream, bank, and upland habitats at the Bearpen Creek site from 1 July 1996 to 31 May 1997.

ranged 17.6°C and 14.7°C, respectively (Table 1). Total degree days were very similar between bank and stream habitats. The more moderate thermal regime in the bank litter during autumn and winter was probably a result of higher percent moisture from the rising stream hydrograph (Figure 1). Tem-

peratures were similar among habitats in spring (Table 1).

Breakdown rates for maple leaves differed significantly among habitats in BP ($P = 0.050$, $n = 66$) and UW ($P < 0.001$, $n = 66$). Leaves broke down fastest in streams and slowest in upland habitats (Figure 3 and Table 2). Significant differences among habitats for leaves in BP were obscured by high variation in the bank habitat (Figure 3).

Total invertebrate abundance was highest in stream and bank habitats (Figure 4) and was significantly different than the upland habitat (Table 3). There was a gradient among habitats in the importance of insects to total invertebrate abundance (Figure 4). Insects were most abundant in streams and least abundant in upland litterbags, and these habitats were significantly different from one another (Table 3). Noninsects were most abundant in bank litterbags. Unlike total abundance, total invertebrate biomass was markedly higher in the stream bags than in either the bank or upland litterbags (Figure 4). This significant difference among habitats (Table 3) was due to a predominance of insect biomass in stream litter (Figure 4). In contrast, noninsect biomass was more important in terrestrial habitats, although it was not significantly different among habitats (Table 3).

Taxa that dominated insect abundance in stream litterbags included midge fly larvae (Diptera: Chironomidae), the stoneflies *Tallaperla* and *Leuctra* (Plecoptera), and Collembola (Table 4). Collembolans were the only abundant insects in bank and upland litterbags (Table 4). The mites, especially Oribatei, and nematodes were the dominant noninsect groups in bank and upland habitats. Copepods were also highly abundant in the stream and on the bank. The peltoperlid stonefly, *Tallaperla*, comprised almost three-fourths of the total invertebrate biomass in stream litterbags (Table 4). Centipedes (Chilopoda) were the most important invertebrates in terms of biomass for both bank and upland habitats. Other important groups in terrestrial habitats were Coleoptera larvae, isopods, spiders (Aranae), and millipedes (Diplopoda). Interestingly, the stream stonefly, *Tallaperla*, was among the top five taxa in terms of biomass in the bank litterbags.

Detrended correspondence analysis (DCA) results for invertebrate abundance revealed a fairly distinct separation among habitats in community structure (Figure 5). Stream litterbags were characterized by low scores on axes 1 and 2, which corresponded to the ordination scores for aquatic invertebrates such as stoneflies, caddisflies, and copepods. Litterbags in upland habitats scored higher on both axes and were characterized by spiders, mites, and beetle

Table 1.   Litter-Layer Temperature (°C) for Each Habitat at the Bearpen Creek Site

Interval	Parameter	Stream	Bank	Upland
Summer	Mean ± SE	12.7 ± 0.1	14.2 ± 0.1	15.2 ± 0.2
1 Jul 96–30 Sept 96	Minimum	10.4	11.2	11.3
	Maximum	14.1	16.7	18.4
	Degree days	1170	1309	1397
Autumn	Mean ± SE	7.5 ± 0.2	5.2 ± 0.5	6.9 ± 0.3
1 Oct 96–31 Dec 96	Minimum	1.6	0.3	−5.0
	Maximum	12.1	13.5	14.5
	Degree days	689	634	476
Winter	Mean ± SE	6.2 ± 0.2	3.6 ± 0.5	5.2 ± 0.3
1 Jan 97–31 Mar 97	Minimum	0.6	−0.9	−9.8
	Maximum	9.5	11.4	11.7
	Degree days	559	469	328
Spring	Mean ± SE	8.7 ± 0.2	9.1 ± 0.4	9.0 ± 0.3
1 Apr 97–31 May 97	Minimum	5.4	4.1	1.9
	Maximum	11.3	14.4	15.7
	Degree days	533	547	556
All data (11 mo)	Mean ± SE	8.8 ± 0.2	8.8 ± 0.2	8.2 ± 0.3
	Minimum	0.6	−0.9	−9.8
	Maximum	14.1	16.7	18.4
	Degree days	2950	2958	2756

SE, standard error.

larvae. Axis 1 explained 52% of the variance in abundance, whereas axis 2 explained 9%. Terrestrial fauna such as snails, isopods, centipedes, and millipedes scored high on axis 1. Most of the variation in axis 2 was driven by high scores for spiders and low scores for isopods. Community structure in bank habitats was between that of stream and upland habitats, although it overlapped somewhat at different times. Invertebrate communities in bank litterbags collected in spring (March to May) resembled those in the stream that were collected in May and June (Figure 5). These late winter–early spring samples had a prevalence of oligochaetes and dipteran larvae. Invertebrates collected in bank litterbags at the beginning of the experiment were similar to upland habitats and had a high proportion of collembolans. Bank litter invertebrates at the end of the experiment had high numbers of nematodes, isopods, snails, centipedes, and millipedes.

Ordination results for community structure based on biomass showed that the stream was very different from the bank and upland habitats (Figure 5). This difference was driven by the dominance of stonefly and caddisfly biomass in stream litterbags. Bank and upland community structure based on biomass overlapped more than it did for abundance. Bank samples collected in the spring were again somewhat similar to stream samples, although less

than they were for abundance. Oligochaetes, copepods, and dipteran larvae characterized spring samples. Less variation was explained by the biomass ordination than by abundance: Axis 1 accounted for 36% and axis 2 accounted for 11%. Most of the bank and upland litterbags were characterized by high scores on axis 1 and intermediate scores on axis 2 (Figure 5). Centipedes, snails, isopods, mites, and nematodes dominated community structure in these habitats. Most of the variation in axis 2 was the result of millipede biomass having high ordination scores whereas spiders and collembolans had low scores.

Functional structure of colonizing invertebrates also varied by habitat. Shredders, especially *Tallaperla*, were more abundant and had higher biomass in the stream than in bank and upland habitats (Figure 6). Although the proportion of shredder abundance was also significantly higher in the stream, shredders comprised only 18% of total abundance (Figure 6). Conversely, shredder taxa dominated (72%) total biomass in the stream.

DISCUSSION

Litter breakdown varied among the different habitats within the riparian ecosystem of both sites. Leaves broke down fastest in streams compared to
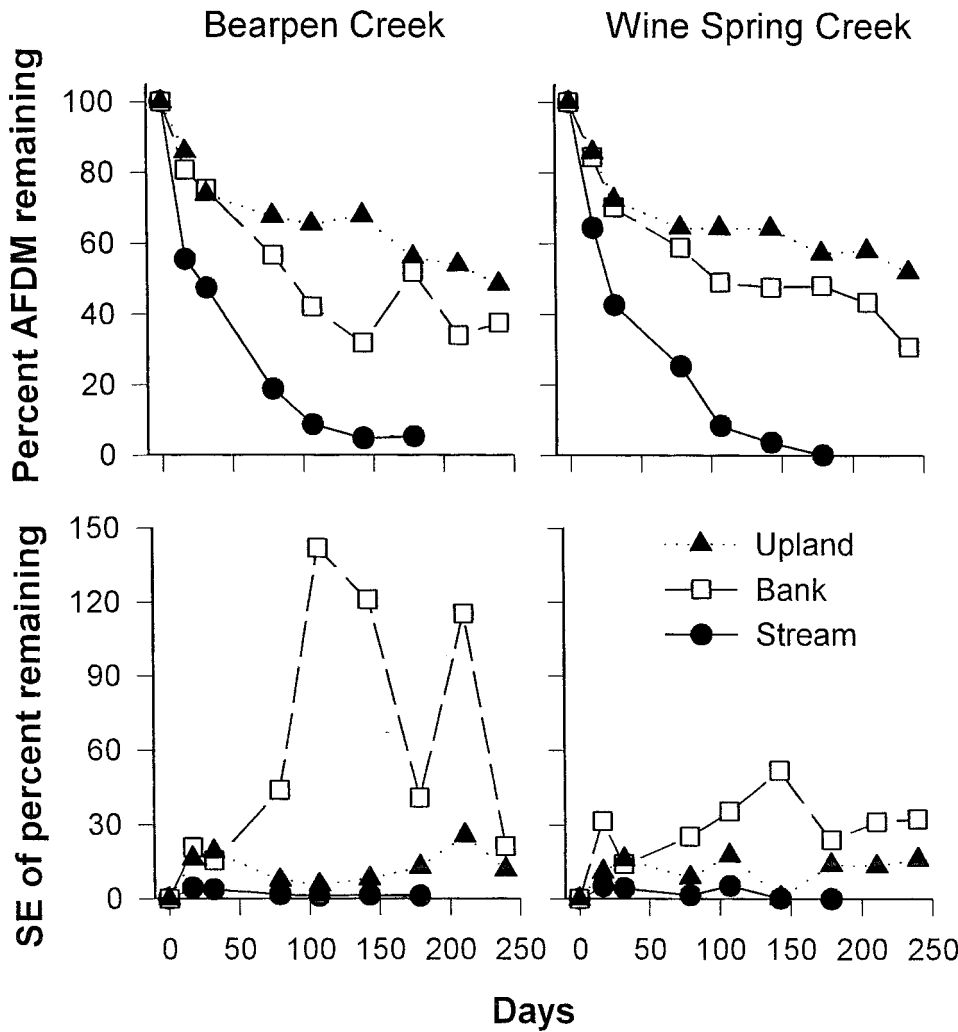
Figure 3. Mean (*top*) and standard error (SE) (*bottom*) of percent ash-free dry mass (AFDM) remaining on each collection date of red maple leaves in stream, bank, and upland habitats at the Bearpen Creek and Wine Spring Creek sites.

Table 2. Red Maple Leaf Breakdown Rates (–k; day^{-1}) for Each Habitat at Bearpen Creek and Upper Wine Spring Creek Sites

Site	Stream	Bank	Upland
Bearpen Creek	0.0175[a]	0.0044[a,b]	0.0022[b]
Upper Wine Spring Creek	0.0318[a]	0.0036[b]	0.0018[c]

Habitats were compared using a general linear model (GLM) with dummy variables.
Different superscripts indicate significant differences (P ≤ 0.05) among habitats at each site.

terrestrial habitats, a finding that agrees with those of other studies (Witkamp and Frank 1969; Thomas 1970; Brinson 1977; Merritt and Lawson 1979, 1992; Stout 1980; Cuffney and Wallace 1987; Gurtz and Tate 1988). Rapid leaf litter processing in streams is the result of many factors related to both physical and biological properties of water. For example, stream current promotes leaching (for ex-

ample, see Petersen and Cummins 1974) and fragmentation (for example, see Heard and others 1999). Also, the high specific heat capacity of water and local input of groundwater moderates the thermal range to which aquatic organisms are exposed. Stream temperatures at BP varied the least compared to bank and upland habitats. Furthermore, temperatures were warmer in the stream than in the terrestrial habitats during autumn and winter, which allows stream microbes and detritivorous invertebrates to actively process new leaf fall, whereas terrestrial biota must cope with extended periods of freezing temperatures. Differences in microclimatic variables such as air, soil, and surface air temperature and relative humidity have been found in riparian ecosystems associated with small streams in the northwestern United States (Brosofske and others 1997; Danehy and Kirpes 2000). These variations in microclimate are used to evaluate the effectiveness of riparian buffer strips
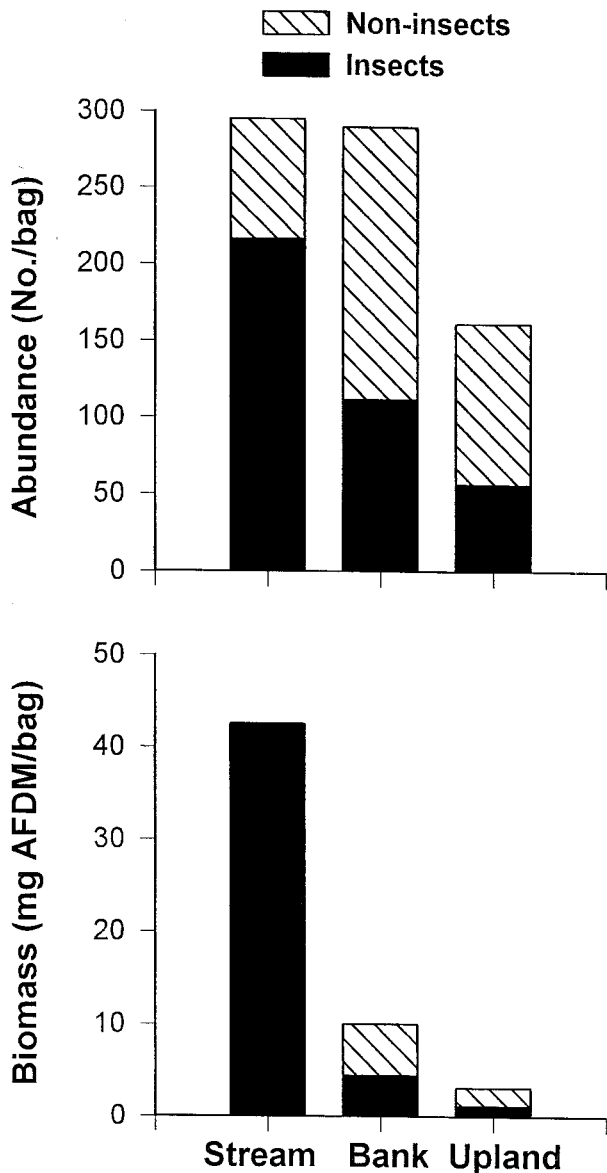
Figure 4. Abundance (No./bag) (*top*) and biomass (mg AFDM/bag) (*bottom*) of insects and noninsects colonizing red maple litterbags in stream, bank, and upland habitats of the Bearpen Creek site.

(Brosofske and others 1997; Dong and others 1998; Chen and others 1999), as well as to detect changes in ecosystem function and landscape structure at multiple spatial and temporal scales (Chen and others 1999). The importance of moisture as a controlling variable for litter decomposition is not limited to freshwater riparian ecosystems. It has also been noted for other environments such as nonriverine wetlands (Day 1982), salt marshes (Halupa and Howes 1995), tropical forest floors (Wieder and

Wright 1995), and alpine tundra (O'Lear and Seastedt 1994).

Differences in invertebrate assemblage and functional structure among habitats also appeared to help explain why stream litter broke down more rapidly than terrestrial litter. Three-fourths of the high invertebrate biomass in stream litterbags was comprised of a single insect taxon, *Tallaperla*, which functions as a shredder that feeds on coarse particulate detritus (Wallace and others 1970). In fact, the biomass of *Tallaperla* in stream litterbags was three and six times higher than the total invertebrate biomass in bank and upland litterbags, respectively. Thus, shredders dominated invertebrate community biomass in litterbags from the stream compared to those in bank and upland habitats (Figure 6). We expect then that leaf consumption by *Tallaperla* likely contributed to the higher rates of maple leaf breakdown in the stream than in the terrestrial habitats. The importance of a single shredder taxon to leaf breakdown rates in streams has also been reported for caddisflies (Grafius and Anderson 1979; Whiles and others 1993), stoneflies (McDiffett 1970), and amphipods (Newman 1990). These data suggest that differences in invertebrate community and functional structure can alter rates of ecosystem processes (see review by Coleman and Hendrix 2000). An important next step, however, would be to experimentally assess the relative importance of various mechanisms (for example, fragmentation, microbial processing, and invertebrate consumption) contributing to leaf decomposition in riparian habitats (Gessner and others 1999).

Two lines of evidence demonstrate that ecosystem processes in steep headwater streams and their banks are more tightly linked than typically assumed. First, the breakdown rates of red maple in bank habitats were intermediate between the rates in stream and upland habitats and were characterized by high variability. This was a result of bank habitats experiencing both stream and upland conditions. Although bank litterbags were never inundated at the time of collection, rising stream flow periodically reached bank litterbags between collection dates, as evidenced by the high moisture levels and the stream organisms that colonized bank litter. These wetter periods (late winter to early spring) corresponded to more rapid decay of maple leaves and also contributed to the high variability, since some litterbags were more inundated than others depending on bank elevation. Although this high variation hindered statistical analyses, it provided evidence for a dynamic interaction between stream and bank habitats. Clearly, ecosystem processes in these two habitats are tied together by fluctuating

Table 3. Statistical Results (F values) for Repeated-Measures Analysis of Variance Comparing Abundance and Biomass of Litter Invertebrates in Red Maple Litterbags among Dates (df = 5) and Habitats (df = 2) at the Bearpen Creek Site

Invertebrate Group	Date	Habitat	Date × Habitat	Individual Contrasts for Habitats
Abundance				
Acarina	25.68***	2.96	1.99	U[a]>B[a]>S[a]
Aranae	2.03	7.14*	0.90	U[a]>B[a]>S[b]
Chilopoda	1.00	1.75	0.72	B[a]>U[a]>S[a]
Coleoptera	1.10	10.85*	0.53	B[a]>U[b]=S[b]
Collembola	1.95	54.30***	2.41	B[a]>U[a]>S[b]
Copepoda	5.75*	51.85***	2.23*	S[a]>B[b]>U[c]
Diplopoda	20.17***	19.08**	21.59***	U[a]>B[b]>S[b]
Diptera	2.94*	56.92***	4.40***	S[a]>B[b]>U[c]
Gastropoda	2.26	8.37*	1.03	B[a]>U[a]>S[b]
Isopoda	0.92	8.56*	0.92	B[a]>S[b]=U[b]
Nematoda	14.20***	1.14	1.91	U[a]>B[a]>S[a]
Oligochaeta	10.57***	11.35**	4.04**	B[a]>S[a]>U[b]
Plecoptera	4.67**	50.26***	2.31*	S[a]>B[b]>U[b]
Trichoptera	1.87	16.13**	0.96	S[a]>B[b]>U[b]
Insects	3.93**	12.65**	3.81**	S[a]>B[a]>U[b]
Noninsects	17.34***	2.72*	2.67*	B[a]>U[b]>S[a]
Total	5.98***	6.17*	2.20*	S[a]>B[a]>U[b]
Biomass				
Plecoptera	2.37	137.04***	1.07	S[a]>B[b]>U[b]
Trichoptera	1.83	27.65***	0.84	S[a]>B[b]>U[b]
Diptera	1.17	9.35*	1.76	S[a]>B[ab]>U[b]
Coleoptera	0.35	1.33	0.83	B[a]>U[a]>S[a]
Acarina	43.64***	55.88***	10.22***	U[a]>B[a]>S[b]
Copepoda	3.93**	14.85**	1.29	S[a]>B[a]>U[b]
Oligochaeta	1.05	2.80	0.83	B[a]>S[a]>U[a]
Isopoda	1.31	5.58*	1.31	B[a]>S[b]=U[b]
Diplopoda	0.50	2.54	0.89	U[a]>B[a]>S[a]
Chilopoda	0.84	2.69	0.75	B[a]>U[a]>S[a]
Collembola	1.27	18.81**	2.01	B[a]>U[b]>S[c]
Aranae	1.24	2.00	0.84	U[a]>B[a]>S[a]
Nematoda	6.94**	3.36	2.15	U[a]>B[ab]>S[b]
Gastropoda	0.82	2.41	0.82	B[a]>U[a]>S[a]
Insects	1.22	57.15***	0.95	S[a]>B[b]>U[c]
Noninsects	1.25	4.61	0.50	B[a]>U[ab]>S[b]
Total	1.47	17.18**	1.01	S[a]>B[b]>U[b]

Habitats (stream [S], bank [B], upland [U] with different superscripts were significantly different ($P \leq 0.05$) using individual contrast statements.
Data were $\log_{10}(x + 1)$ transformed.
*$P \leq 0.05$
**$P \leq 0.01$
***$P \leq 0.001$

hydrology, which is associated with variations in seasonal climate and storm flow. Leaf breakdown rates along the banks of these headwater streams resemble that of the stream during periods of high flow and that of the uplands during low flow. Hence, our results show that the riparian zone of steep headwater streams have detritus-processing dynamics analogous to those in the floodplains of larger streams, although it is limited to a much narrower (≤ 1 m wide) region.

Invertebrates colonizing bank litterbags provide the second line of evidence for the ecological connection between stream and bank. The community structure in the bank litterbags during late winter

Table 4.   Top Five Taxonomic Groups from Each Habitat That Were Collected in Litterbags at the Bearpen Creek Site

Abundance			Biomass		
Stream	Bank	Upland	Stream	Bank	Upland
Chironomidae (41) Diptera	Oribatei (25)	Oribatei (41)	*Tallaperla* (74) Plecoptera	Chilopoda (29)	Chilopoda (40)
Copepoda (18)	Collembola (21)	Collembola (26)	*Isoperla* (5) Plecoptera	Coleoptera (13)	Aranae (15)
Tallaperla (10) Plecoptera	Copepoda (16)	Nematoda (16)	*Parapsyche* (5) Trichoptera	Isopoda (11)	Coleoptera (14)
Collembola (5)	Nematoda (9)	Misc. Acarina (9)	*Hexatoma* (2) Diptera	Gastropoda (7)	Diplopoda (13)
Leuctra (4) Plecoptera	Oligochaeta (8)	Diplopoda (2)	*Rhyacophila* (2) Trichoptera	*Tallaperla* (6) Plecoptera	Collembola (5)

Values in parentheses are the percent of total abundance or biomass represented by each group.

and early spring (March–May) was similar to that of the stream as reflected by the ordination results for abundance. In addition, a stream stonefly, *Tallaperla*, was among the top five taxa in terms of biomass in bank litterbags even though these litterbags had not been inundated with stream water at the actual time of sample collection. Thus, some stream invertebrates can move to bank habitats during periods of high base flow, even in streams with little or no floodplain, and these invertebrates can reside in moist bank habitats even after stream discharge has declined. These invertebrates presumably use the wetted banks as refugia from adverse hydrologic conditions in the stream, and some (for example, *Tallaperla*) can consume bank leaf litter, which was previously unavailable. In small low-gradient Coastal Plain streams with forested floodplains, invertebrates move frequently between stream channels and floodplains when discharge is rising during February–April (Smock 1994). Even though the numbers and biomass of invertebrates moving between habitats in the study by Smock were undoubtedly greater than in the present study, Smock (1994) considered the movements too low to affect the overall trophic dynamics of either the stream or the floodplain. Although the overall impact on trophic dynamics of the movement of stream invertebrates to the BP bank was probably low also, this type of movement has been overlooked in mountainous regions and probably influences leaf breakdown. In general, our results show that some invertebrates in steep headwater streams may not be limited to foraging between the banks; it is possible that they also participate in food webs and ecosystem processes in relatively moist

riparian systems. Furthermore, this movement by immature aquatic insects allows a two-way transfer of energy between the stream and the riparian zone, whereas emergent adult insects can be viewed primarily as a one-way loss of energy to the riparian zone. Thus, our study extends to small mountain streams the idea that streams and riparian zones should be viewed as integrated ecosystems.

Although our results show that riparian zones in steep mountain streams can have ecosystem dynamics analogous to that of downstream riparian zones, it is important to consider these lateral interactions in a long-term hydrologic context. For example, Wallace and others (1997a) found that the annual export of organic matter in a very small mountain stream could range ± 30% of total annual inputs during a period that encompassed record wet and dry years. Moreover, some of this variation was due to the retention of organic matter inputs along riparian margins during large storms (Wallace and others 1995). Precipitation during our leaf breakdown experiment was 166 cm, which is similar to the 55-y mean (170 cm) at a nearby climate station at Nantahala Dam (Nantahala Power and Light Company and L. Swift, personal communication). Thus, the leaf processing linkages between stream and bank observed in this study may be typical for years with normal precipitation. However, if this study had been conducted in a dry year, we might have reached the opposite conclusion about the importance of stream–bank linkages in mountain streams. Furthermore, during wet years, litter may either be flushed from the stream during spates without appreciable breakdown or deposited
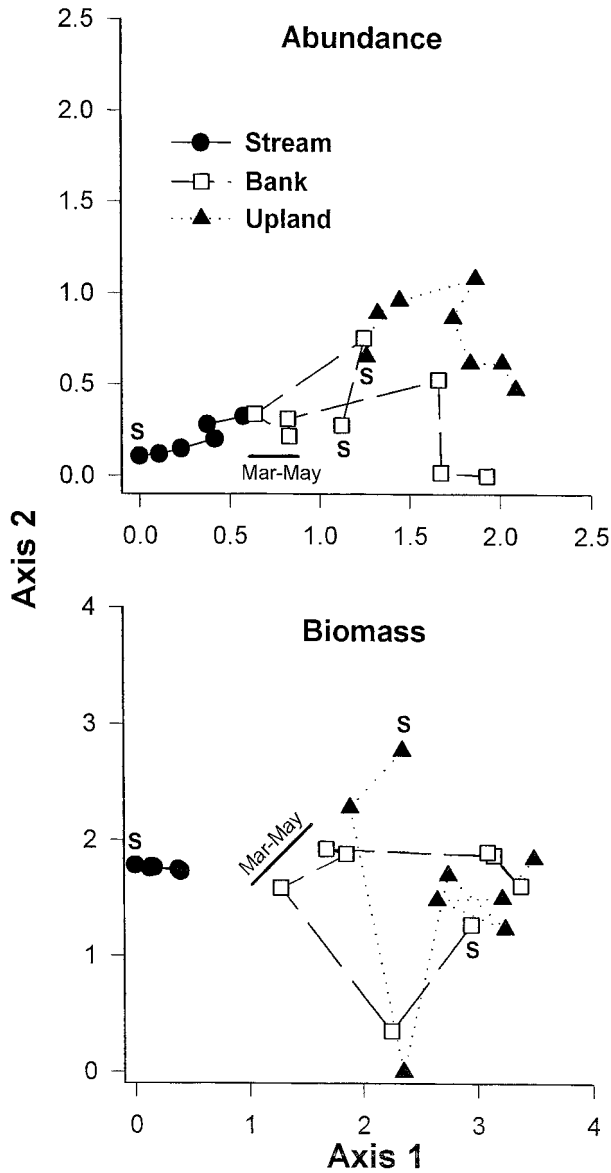
Figure 5. Ordination plots of the first two axes from detrended correspondence analyses (DCA) for the abundance (*top*) and biomass (*bottom*) of the major invertebrate groups in red maple litterbags in stream, bank, and upland habitats of the Bearpen Creek site. S denotes the first collection date; a line connects the subsequent collections. The bar denotes the bank litterbags collected from March to May.

Figure 6. Mean + SE (*top*) and proportion + SE of total (*bottom*) abundance (No./bag) and biomass (mg AFDM/bag) of the shredder functional feeding group colonizing red maple litterbags in stream, bank, and upland habitats of the Bearpen Creek site. Bars with the same letters were not significantly different among habitats ($P>0.05$).

laterally on banks. Ultimately, the fate of allochthonous leaf litter in riparian ecosystems is complex and varies with climate.

Overall, detritus processing within this narrow riparian ecosystem varied considerably depending on the availability of moisture. The likely mechanisms 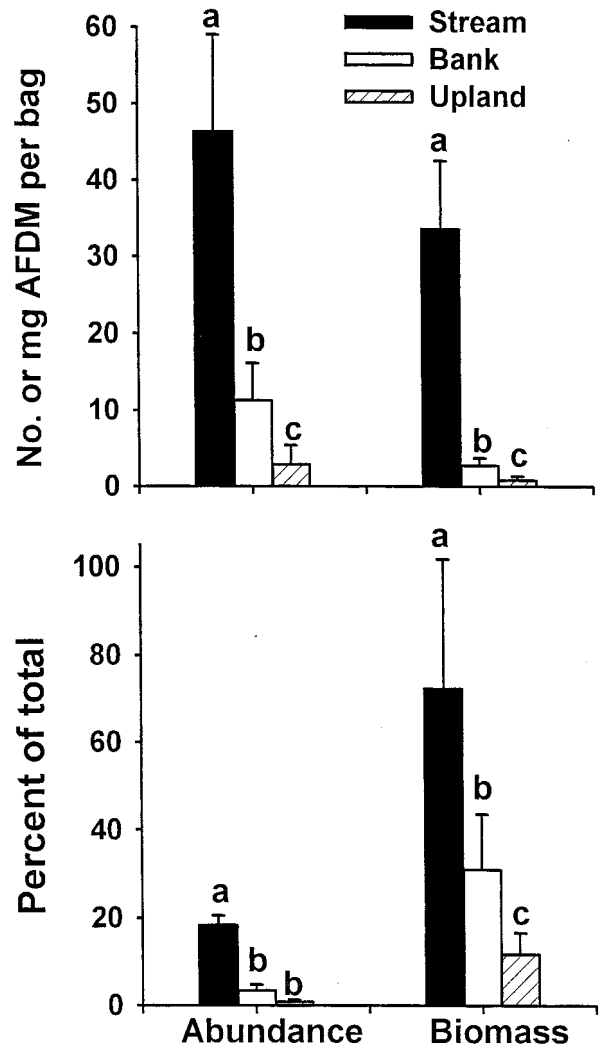underlying this phenomenon are differences in physical factors such as leaching and physical disturbance, as well as differences in biological factors such as microbial activity and invertebrate community and functional structure. Results from this study show that stream channel–floodplain interactions in riparian ecosystems of steep forested mountains are analogous to ones in larger downstream or low-gradient systems. As a result, riparian zones throughout a river network display a remarkable heterogeneity in their ability to process organic matter, which is ultimately driven by changes in hydrological conditions.

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