

Invertebrate colonization of leaves and roots within sediments of intermittent Coastal Plain streams across hydrologic phases

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Abstract Ecological flows between habitats are vital for predicting and understanding structure and function of recipient systems. Ecological flows across riparian areas and headwater intermittent streams are likely to be especially important in many river networks because of the shear extent of these interfaces, their high edge-to-width ratio, and the alternation of wet and dry conditions in intermittent channels. While there has been substantial research supporting the importance of riparian-stream linkages above-ground, comparatively less research has investigated below-ground linkages. We tested the hypothesis that riparian roots are colonized by invertebrates as a food source within stream beds of intermittent headwater streams. We compared benthic invertebrate assemblages colonizing three types of buried substrates (leaves, roots, and plastic roots) among three intermittent Coastal Plain streams, each with a different riparian management treatment (clearcut, thinned, and reference), over a 1-year period. Invertebrate density was significantly lower in root litterbags than in plastic roots litterbags, but neither differed from densities in leaf litterbags. Total invertebrate abundances, however, were significantly higher in leaf and root litterbags compared to abundances

in plastic root litterbags. Invertebrate biomass and richness did not vary among substrates, but invertebrate density, abundance, and richness all declined from the wet phase (September–December) through the dry phase (June–August). Meiofauna and aquatic dipterans were the primary colonizing invertebrates during the wet phase. Relative abundance of terrestrial taxa increased during the dry phase, but their absolute abundance remained lower than aquatic taxa during the wet phase. Invertebrate composition did not differ among substrate types, but was significantly different among streams and time periods. Cumulative number of dry days, degree days, and redox depth all strongly correlated with assemblage structure as indicated by ordination scores. Our results suggest that subsurface invertebrates respond to leaves and roots as food sources, but assemblage composition is not substrate specific. Colonization of leaves and roots within stream beds by aquatic and terrestrial taxa supports the idea that headwater intermittent streams are important interfaces for the reciprocal exchange of energy and materials between terrestrial and aquatic ecosystems.

Keywords Organic matter · Riparian · Temporary stream · Drying · Meiofauna · Terrestrial invertebrates

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Introduction

Headwater intermittent streams lie at the terrestrial-aquatic interface both spatially, because of their narrow channel widths and landscape position, and temporally, because of their relatively young geological age and recent transition from terrestrial to aquatic environments (Horton 1945; Montgomery and Dietrich 1989). Perhaps as important,

intermittent streams show physical similarities to both aquatic and terrestrial habitats because of their seasonal wet and dry phases, respectively. These spatial and temporal dynamics strongly link headwater intermittent channels to adjacent riparian vegetation, which, in turn, influence in-channel processes and associated biota to a greater extent than wider and deeper perennial streams (Dieterich and Anderson 1998).

Previous work in forested streams has shown that riparian vegetation influences streamwater temperature, primary production, surface runoff, and groundwater chemistry (e.g., Burton and Likens 1973; Murphy et al. 1981; Lowrance 1992; Pinay et al. 1998). Litter from riparian vegetation also compose a primary source of coarse particulate organic matter (CPOM) to streams (Conners and Naiman 1984). However, in low-gradient Coastal Plain streams much of the CPOM becomes buried within the sandy stream beds following floods (Metzler and Smock 1990; Smock 1990). Roots of riparian trees are important in stabilizing stream banks (e.g., Gregory and Gurnell 1988; Thorne 1990; Wynn et al. 2004), and they can also be common (24% of CPOM) within intermittent Coastal Plain stream beds (Fritz et al. 2006a). However, the role of roots as food or habitat for invertebrates within intermittent channels is unknown. Leaf litter on the surface of perennial stream beds function primarily as a food source (e.g., Egglisshaw 1964; Richardson 1992; Dudgeon and Wu 1999), whereas buried litter or wood additions have had strong invertebrate response (Smith and Lake 1993; Crenshaw et al. 2002), no response (Boulton and Foster 1998), or a variable response over time (Tillman et al. 2003). Buried CPOM (leaves, roots, and plastic roots) was deployed to test the hypothesis that invertebrates respond to roots as a potential food source and therefore respond more similarly to leaves than plastic roots. We predicted that greater numbers, biomass and diversity of invertebrates would colonize litterbags containing roots than those containing plastic roots. Associated with these expected differences, we also predicted that the fauna colonizing litterbags containing roots would be more similar to those colonizing litterbags containing leaves than those colonizing plastic roots.

Materials and methods

Study sites

The study streams were in three contiguous Coastal Plain sub-watersheds (lat 31°, 34'N, long 87°, 25'W) of the Lower Alabama River, Monroe County in SW Alabama, USA. Study sub-watersheds (area = 10 to 15 ha) each had different riparian management treatments within 15-m

wide zones bordering the channels in July 1999, a clear-cut, a thinned, and a reference treatment (Governo et al. 2004). For the clear-cut sub-watershed, all trees within the 15-m riparian zone were harvested followed by coppice regeneration of hardwoods. The thinned sub-watershed had 50% removal of hardwoods and pines within the riparian zone. In the reference sub-watershed, no trees were removed from the riparian zone. Upland trees were left intact within all three sub-watersheds during the present study. Sub-watersheds and their channels were small (channel width ~0.7 m) and in-stream habitats were predominantly (~75%) shallow (mean water depth ~0.03 m), low-gradient (mean channel gradient ~0.03%) runs. Streambed sediments were predominately coarse-fine sand (0.35–0.4 m deep) overlying hardpan clay. CPOM within stream beds (0–30 cm) of the three sub-watersheds was estimated to be ~1.9 kg m⁻² compared to 0.3 kg m⁻² on the streambed surface (Fritz et al. 2006a). Mean discharge of the streams ranged from 0.01 to 0.08 m³s⁻¹ and flowed discontinuously for ~6 months (Oct–May). Streams did not flow from June to September, except immediately following heavy rains, and streambed moisture was at least two times drier than during the wetter months (Fritz et al. 2006a).

Methods

Invertebrate colonization was measured using nylon mesh litter bags (15 × 30 cm, Nylon Net Co., Memphis, TN, USA) containing either 5 g of leaf litter (*Liquidambar styraciflua*: 41%, *Quercus nigra*: 30.3%, *Acer rubrum*: 12.3%, *Magnolia virginiana*: 8.3%, and *Vitis rotundifolia*: 8%), 6 g of *Q. nigra* roots (combination of size classes: 0.5–1, 1–2.5, 2.5–5, and 5–10 mm diam), or plastic roots (cut to same specifications as *Q. nigra* roots for the four size classes and presoaked in DI water for 2 weeks). Species composition of leaves in litter bags was consistent with average percentages collected in litter traps among the three streams (Governo et al. 2004). The initial surface area of substrate per litter bag was 0.105 m² for leaves, 0.019 m² for *Q. nigra* roots, and 0.017 m² for plastic roots, and initial quality of leaves and roots, as indicated by C:N, was 80.0 and 73.2, respectively. Litter bags were constructed with 6-mm openings on the upper mesh and 3-mm openings on the lower mesh. Additional information on construction of the litter bag treatments is provided in Fritz et al. (2006a).

Bags were buried and staked 5 cm below the streambed surface on 8 August 1999 within runs (length: ~5 m) of homogeneous depth and current velocity. Litter bags were arranged randomly across 15 rows of 3 bags per row (45 bags per stream). Invertebrates were allowed to colonize litter bags for periods of 18, 44, 112, 314, and 366 days.

On each sampling occasion, three litter bags (subsamples) of each substrate type were carefully excavated by hand from each stream, placed individually into plastic bags and transported on ice to the laboratory. There, litter bag contents were gently rinsed with tap water into a 125- μ m sieve to separate leaves, roots, or synthetic roots from sediment and fine particulate organic matter (FPOM). All invertebrates were removed (using a stereomicroscope 12–40 \times magnification), identified (primarily to genus), and invertebrate biomass was estimated using published allometric equations (e.g., Benke et al. 1999). We assigned each taxon to one of four functional feeding groups (shredder, collector-saprophagous, grazer-piercer-herbivore, predator-parasite) based on food habit descriptions in literature (Goodey and Goodey 1963; Krantz 1978; Pennak 1989; Merritt and Cummins 1996). Invertebrates also were classified as aquatic or terrestrial, and meiofauna (adults ≤ 1 mm body length) or macroinvertebrates (> 1 mm body length).

We measured local habitat (per bag or stream) conditions thought to be important in structuring invertebrate assemblages within litter bags (Strayer et al. 1997). Depth below sediment surface was measured for each litter bag at the time of collection, as streambed sediments sometimes shifted, further burying or exposing bags. Hydrologic condition (scored as presence/absence of surface water), sediment redox condition (depth of aerobic sediment, see Bridgham et al. 1991), ash-free dry mass (AFDM) of FPOM, % CPOM remaining, and % sediment moisture (gravimetric method, Fritz et al. 2006b) also were measured on each collection date. Discharge was measured continuously using V-notch weirs and pressure transducers (~ 250 – 300 m from channel origins and ~ 100 m downstream of study sites). Streambed temperature was measured at 5-h intervals using temperature dataloggers (HoboTemp, Onset[®] Computer Corp., Bourne, MA, USA) buried 5 cm below the sediment surface.

Data analysis

The statistical unit for all analyses was the pooled values from three litterbags for a substrate collected from a given stream for each time period (therefore $n = 3$ for each substrate type and period). Therefore, we compared invertebrate colonization across the three substrate types over time from unreplicated combinations of flow and riparian management. We used repeated analysis of variance (ANOVA, PROC MIXED with Kenward-Rogers adjustment for degrees of freedom; Wang and Goonewardene 2004) to compare invertebrate taxonomic richness, invertebrate abundance (number of individuals/litter bag), total invertebrate density (number of individuals/g AFDM remaining + g AFDM of FPOM), and total

invertebrate biomass across substrate types for each time period. We assumed that the plastic roots were not a food resource, so invertebrate density for plastic root litterbags was based on the number of invertebrates per g AFDM of FPOM in the litterbags upon collection. The best fit covariance structure was selected based on relevance to study design and corrected Akaike Information Criteria (Wang and Goonewardene 2004). Where significant differences were detected with ANOVA, multiple comparison tests (LSMEANS, Tukey adjustment) were done to identify where specific differences resided. Normality was confirmed using Shapiro–Wilk test, whereas residuals were plotted to assess inequality of variance (Zar 1984). Data were log transformed when they did not meet statistical assumptions, which then allowed parametric analyses. Significance level was set at $\alpha = 0.05$.

Taxonomic composition among substrate types, streams, and time periods was compared using nonmetric multidimensional scaling (NMS), multi-response permutation procedure (MRPP), and indicator species analysis (PC-ORD for Windows, Version 5.10, MjM Software Design, Gleneden Beach, OR, USA). For these analyses, we used abundances of taxa (root–root transformed; Field et al. 1982) that occurred in $> 5\%$ of the samples (146 of 256 taxa across 45 samples). Bray–Curtis coefficient was used as the distance measure in the NMS ordination (step length = 0.20) and MRPP. The dimensionality of the final ordination was determined by scree plots and Monte Carlo simulations (99 runs). The relationships between axes scores and environmental variables (above) were assessed using Spearman rank correlation. We used MRPP to test the hypothesis that taxonomic composition did not differ among groups of litterbags (substrate types, streams, and time periods). The test statistic, T , describes the separation among groups and is analogous to a student's t -test with greater separation indicated by more negative T values. The likelihood that an observed difference occurred randomly was evaluated by the p value associated with each T statistic. The chance-corrected within-group agreement (A) statistic describes the effect size independent of sample size. Statistical significance can result when effect is small, so we only considered $A > 0.1$ to be meaningful (McCune and Grace 2002). Indicator analysis identifies the affinity of taxa to groups of samples by incorporating relative abundance and occurrence frequencies of individual taxa (Dufrêne and Legendre 1997). Indicator values (IV) were produced for each taxa, which range from 0 (no affinity) to 100 (100% affinity to a particular group, here substrate type). The difference between the maximum observed IV for a particular group and the mean IV generated from random permutations (4,999) was then used to derive a significance test for each taxon (Dufrêne and Legendre 1997). Taxa with most of their relative abundance and

occurrences ($IV > 25$) associated with particular groups were presented.

Results

Hydrologic conditions varied among streams over the study, and weir hydrograph data were not consistent with conditions at the study reach because of discontinuous hydrology, likely associated with spring seeps (Fig. 1). Flow was present at all study sites when litterbags were deployed, although the thinned site was dry during all subsequent collection visits. Flow was present on the first collection date (day 18) at the clear-cut site and on the first and third collection dates (days 18 and 112) at the reference site. Based on the conditions at collection and periodic visits, the reference site was the wettest and clear-cut site was the driest. Streambed temperature at the clear-cut site showed higher daily fluctuation and maxima compared with those at the thinned and reference sites (Fig. 1).

A total of 21,035 invertebrates in 257 taxa were collected from 135 litterbags, with almost 80% of the total abundance occurring in 37 taxa (Table 1). Overall, taxa richness and total abundance were evenly divided between meiofauna and macroinvertebrates (49.3 and 50.7% of the total abundance, respectively). In contrast, macroinvertebrates dominated the invertebrate biomass (97% of total). Aquatic invertebrates composed 57% of richness, 83% of the total abundance, and 67% of the invertebrate biomass.

Both aquatic taxa and meiofauna declined in relative abundance over the study (Fig. 2). Over the study, Ceratopogonidae, Chironomidae, and Tipulidae were the most dominant and diverse aquatic macroinvertebrates, whereas Enchytraeidae, Collembola, Sciaridae, and Cecidomyiidae dominated the terrestrial macroinvertebrates (Table 1). Among aquatic meiofauna, nematodes (particularly *Ironus*, *Labronema*, and *Eudorylaimus*), *Lobohalacarus* (halacarid mite), and crustaceans (*Attheyella*, *Candona*, *Parastenocaris*, and *Paracyclops chiltoni*) were most abundant, whereas oribatid mites and nematodes (*Hemicyclophora* and *Xiphenema*) were the dominant terrestrial meiofauna. Collectors and predators were the primary functional feeding groups across streams, substrate types and time periods, with grazers and shredders together usually representing only ~5% of invertebrates collected (Fig. 3). The higher proportion of grazers at the thinned site than at the clear cut and reference sites was primarily attributed to high relative abundances of the terrestrial taxa, Cecidomyiidae and *Hemicyclophora*.

Invertebrate density and abundance differed among substrate types and across time periods, whereas invertebrate biomass and richness only varied across time periods (Table 2, Fig. 4). Density of invertebrates colonizing plastic root litterbags was higher than root litterbags (adjusted Tukey's test, $p = 0.04$), although neither differed from invertebrate density in leaf litterbags ($p > 0.05$). Invertebrate abundance did not differ between litterbags with leaves and roots ($p > 0.05$), but both substrates had

Fig. 1 Discharge (measured downstream from study reaches at V-notch weirs), observations of hydrologic conditions at study reaches (symbols along x axis), and streambed temperature measured (5-h intervals) at the study reaches over the study period. *ND* no data

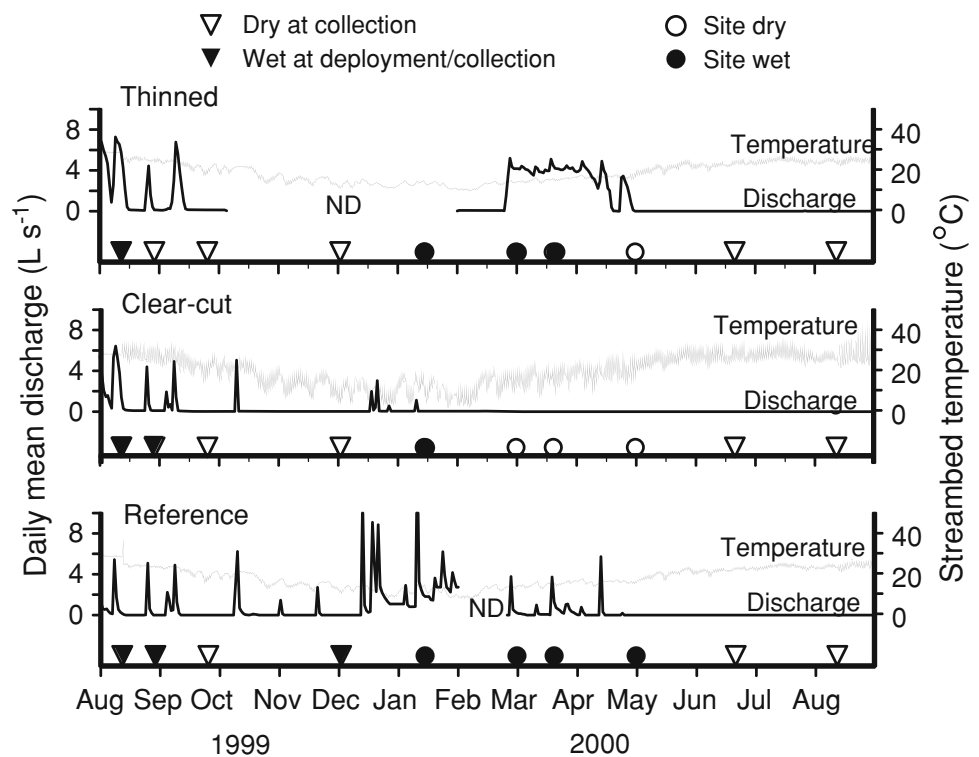


Table 1 Percent frequency and abundance of taxa collected from 45 pooled litter bags (subsamples of each substrate type from each stream and date) buried in three intermittent headwater streams in south-central Alabama, USA

Taxon	Frequency (%)	Abundance (%)
<i>Enchytraeus/Marionna</i> (Oligochaeta: Enchytraeidae)	93	5
<i>Labronema</i> (Nematoda: Dorylaimida)	87	5
<i>Eudorylaimus</i> (Nematoda: Dorylaimida)	82	6
<i>Ormosia</i> (Diptera: Tipulidae)	78	2
<i>Culicoides</i> (Diptera: Ceratopogonidae)	76	10
<i>Ironus</i> (Nematoda: Enoplida)	73	8
<i>Bezzia/Palpomyia</i> (Diptera: Ceratopogonidae)	71	4
<i>Pseudorthocladius/Parachaetocladus</i> (Diptera: Chironomidae)	69	2
<i>Gonomyia/Molophilus</i> (Diptera: Tipulidae)	60	2
<i>Lobohalacarus</i> (Acarina: Halacaridae)	60	1
Cecidiomyiidae (Diptera)	58	2
<i>Ceratopogon</i> (Diptera: Ceratopogonidae)	58	3
<i>Stilobezzia</i> (Diptera: Ceratopogonidae)	56	3
<i>Tabanus fairchildi</i> (Diptera: Tabanidae)	53	<1
<i>Tanytarsus</i> (Diptera: Chironomidae)	51	1
<i>Dolichopus/Hydrophorus</i> (Diptera: Dolichopodidae)	49	<1
<i>Pseudosmittia</i> (Diptera: Chironomidae)	49	1
<i>Polypedilum</i> (Diptera: Chironomidae)	44	2
<i>Attheyella</i> (Crustacea: Harpacticoida)	44	2
<i>Isotoma viridis</i> (Collembola: Isotomidae)	42	<1
<i>Paratendipes subaequalis</i> (Diptera: Chironomidae)	42	<1
<i>Hexatoma</i> (Diptera: Tipulidae)	40	<1
<i>Alaimus</i> (Nematoda: Dorylaimida)	40	2
<i>Bryocamptus</i> (Crustacea: Harpacticoida)	38	1
<i>Candona</i> cf. <i>annae</i> (Crustacea: Ostracoda)	38	2
<i>Mononchus</i> (Nematoda: Mononchida)	38	1
<i>Stegamacarus</i> (Acarina: Oribatida)	36	<1
<i>Mucronothrus</i> (Acarina: Oribatida)	36	1
<i>Proisotoma schoetii</i> (Collembola: Isotomidae)	33	2
Sciaridae (Diptera)	33	1
<i>Parametriocnemus</i> (Diptera: Chironomidae)	33	<1
<i>Pristinella osborni</i> (Oligochaeta: Naididae)	33	<1
<i>Pseudolimnophila</i> (Diptera: Tipulidae)	31	<1
<i>Rheosmittia</i> (Diptera: Chironomidae)	31	2
<i>Paracyclops chiltoni</i> (Crustacea: Cyclopoida)	31	5
<i>Dorylaimus</i> (Nematoda: Dorylaimida)	31	<1
<i>Mylonchulus</i> (Nematoda: Mononchida)	31	<1
Total		78.7

higher abundance than plastic root litterbags ($p < 0.05$). Density, abundance, and richness were highest on day 18 and declined significantly by day 44 (Fig. 4), coinciding with the first substantial dry period of the study (Fig. 1). Further declines in density, abundance, and richness were evident by day 366, but not for biomass.

A two-dimensional solution best described the data used in the NMS ordination as additional dimensions provided only a small reduction in stress (stress for two-dimensional

solution = 13%). The ordination of litterbag samples revealed that invertebrate composition did not cluster by substrate treatment (Fig. 5a), but showed separation among streams along Axis 1 (Fig. 5b) and across time periods primarily along Axis 2 (Fig. 5c). The distinct separation among time periods was associated with season, with autumn and winter samples (days 18, 44, and 112) being separated from summer samples (days 314 and 366) across Axis 2. Also significantly correlated to Axis 2 scores were

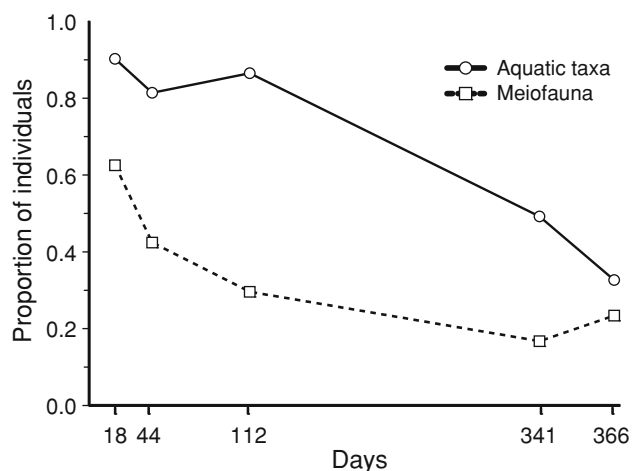


Fig. 2 Relative abundance of aquatic and meiofauna invertebrates collected across all streams and substrate types over the study period

four environmental variables (Fig. 5d). Samples with low Axis 2 scores had shallower depths to the anoxic sediment ($r_s = -0.84$) and higher sediment moisture ($r_s = -0.64$) than samples with higher Axis 2 scores. In contrast, samples with high Axis 2 scores had higher degree days ($r_s = 0.90$) and more days without flow ($r_s = 0.82$) than samples with low Axis 2 scores. Amount of FPOM within litterbags showed the strongest correlation with Axis 1 scores ($r_s = -0.69$).

MRPP confirmed compositional differences among streams and time periods seen in the NMS ordination (Table 3). Invertebrate composition from the thinned stream was more similar to the reference stream assemblage than the clear cut assemblage. Across time periods, the strongest differences occurred between the autumn–winter period (days 18, 44, and 112) and the summer period (days 314 and 366). Invertebrate composition did not differ among litter types, again supporting patterns from the NMS ordination.

Only 13 of 146 taxa examined were predominately ($IV > 25$, majority of relative abundance and occurrence frequency) associated with either leaves or roots, and none were associated with plastic roots (Table 4). However, only one taxon (*Mylonchulus*) had a significant association with a particular substrate (roots). When data from root and leaf litterbags were combined into a single category and compared to plastic roots, 25 taxa had $IV > 25$, but none of these had significant associations with either category (Table 3).

Discussion

Effect of substrate type

Invertebrate density was highest in litterbags containing plastic roots, but that was primarily a function of FPOM

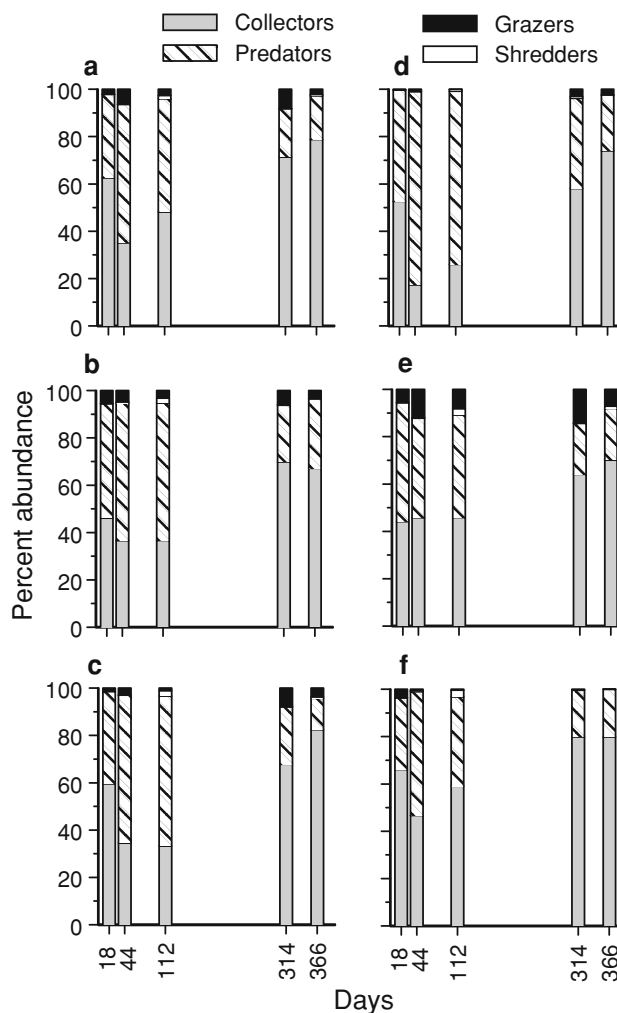


Fig. 3 Percent abundance of invertebrate functional feeding groups across leaf (a), root (b), plastic root (c) litter bags and streams (clear-cut, d; thinned, e; and reference, f). Litterbags for each treatment and date were pooled across subsamples. Collectors include both collector-gatherers and collector-filterers, grazers include algal scrapers, plant parasites, piercers, and herbivores, predators also include animal parasites

representing all of the organic matter in plastic root litterbags, but only ~37 and 30% of the organic matter in leaf and root litter bags, respectively. Abundance of invertebrates colonizing litterbags with roots and leaves was higher than those colonizing litterbags with plastic roots. This result suggests buried leaves and roots offered more suitable habitat than plastic roots or were also being used as a food source. However, we did not find differences in taxon richness, biomass, and assemblage composition among substrate types. These results indicate that invertebrate assemblages showed an overall response to subsurface detritus, albeit not through shifts in composition. The lack of consistent differences across assemblage measures by substrate type may be attributable to the paucity of shredders, the predominance of meiofauna, and

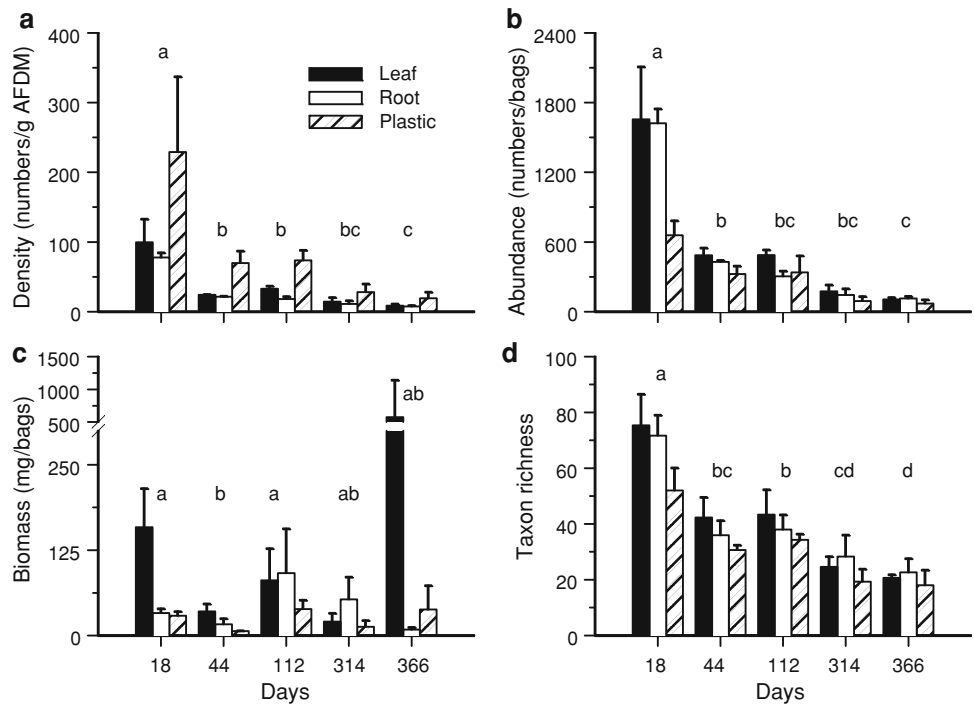
Table 2 *F* values (degrees of freedom) for repeated measures analysis of variance (ANOVA, PROC MIXED) comparing assemblage characteristics across substrate type (fixed) and time (random)

Effect	Density ^a (CSH)	Abundance ^a (CSH)	Biomass ^a (ANT1)	Richness ^a (ANT1)
Substrate	5.10* (2, 6.93)	11.21* (2, 5.54)	1.30 (2, 6.3)	1.40 (2, 6.87)
Time	22.01*** (4, 11.1)	22.48*** (4, 10.8)	15.91** (4, 6.05)	16.15** (4, 7.2)
Substrate × time	0.47 (8, 11.8)	0.48 (8, 11.2)	0.66 (8, 6.59)	0.17 (8, 7.82)

The best-fit covariance structure is shown in parenthesis below variable names (CSH heterogeneous compound symmetry and ANT1 1st order antedependence). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.0001$

^a Log transformed

Fig. 4 Mean invertebrate density (number of invertebrates per g AFDM remaining + AFDM FPOM) (a), invertebrate abundance (b), biomass (c), and richness (d) by substrate type across collection periods. Bars with different letters indicate significant differences (Tukey's post-hoc test, $\alpha = 0.05$) across collection periods. Error bars represent +1 SE

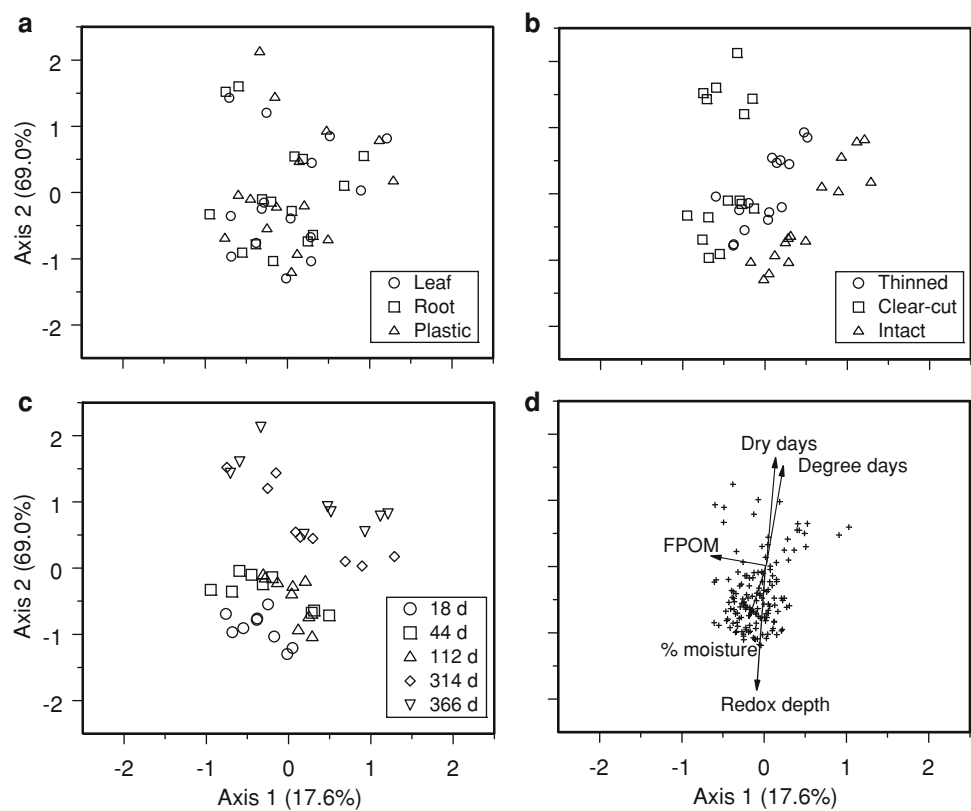


the temporally contrasting hydrology of the streams. Despite being qualitatively different (i.e., C:N, lignin content), leaves and roots in litterbags did not differ in rate of decay in these streams (Fritz et al. 2006a). Shredders can be a dominant component of the invertebrate community in high-gradient, forested streams regardless of hydrologic permanence (e.g., Dieterich et al. 1997; Price et al. 2003), although in low-gradient, sandy streams shredders often are a minor component (e.g., Kedzierski and Smock 2001; Wright and Smock 2001; Entekin et al. 2007), particularly in subsurface sediments (Strommer and Smock 1989; Traylor and Davis 1998) where conditions may be unsuitable for many macroinvertebrate shredders (Whitman and Clark 1984). In an Alaskan stream, meiofaunal densities and richness did not differ between plastic and natural substrates on the streambed surface (Robertson and Milner 2001). The authors concluded that CPOM was primarily a habitat rather than a food resource for meiofauna. In an

Australian, pebble-cobble dominated river, invertebrate abundance, richness, and composition did not differ among hyporheic patches (30 cm deep) amended with real or plastic leaves (Boulton and Foster 1998). Our results indicate that season- and stream-specific differences in environmental conditions appeared to be more important in structuring the composition of invertebrate assemblages than local difference in substrate type.

Hydrologic variability and lack of replication complicates the assessment of the effects of riparian management on the subsurface invertebrate assemblage. The taxonomic composition of the invertebrate assemblage clustered more strongly by stream than by substrate, where assemblage similarity was highest between the reference and thinned streams and least between reference and clear-cut streams. In addition, compositional differences between the clear-cut stream and the other treatments expanded over time. This pattern suggests that riparian vegetation affects the

Fig. 5 Ordination (NMS) of invertebrate assemblages (taxa occurring in >3 of the 45 pooled litterbag samples) by substrate type (a), stream (b), and time period (c). Final stress was 13% and percent variation accounted by the two axes are shown in parentheses. Environmental factors (d) correlated with NMS axes are shown as vectors, with vector length proportional to relationship strength and symbols (+) representing taxa



composition of terrestrial invertebrate assemblages that colonize dry stream beds and supports findings of others relating terrestrial insect subsidies and riparian vegetation (Mason and MacDonald 1982; Kawaguchi and Nakano 2001). Although these results may represent differences among streams rather than differences due to their associated riparian management, there is some circumstantial evidence to suggest riparian management may have influenced the taxonomic composition of the invertebrate assemblages. For instance, differences in streambed temperature patterns among streams (Fig. 1) was consistent with expected changes associated with riparian management treatment and may have contributed to compositional differences among streams. In particular, higher temperature variability and daily maxima in the clear-cut stream may have affected survival of aquatic taxa (e.g., *Ormosia*, *Stilobezzia*) that oversummer in streambed sediments, potentially exacerbating compositional differences among streams. Although all 3 study sites were dry during the summer collection periods, the clear-cut site was dry for the longest period of time prior to the summer collection dates (Fig. 1). However, differences in hydrology among streams do not explain why the thinned stream was more similar to the reference than the clear-cut stream during the autumn–winter collection periods, when the clear-cut stream was intermediate to the thinned and reference stream in hydrologic permanence (Fig. 1).

The invertebrate community

Sandy stream beds and intermittent hydrology are two physical features that stand out as important influences on subsurface invertebrate assemblage in the study streams. The low porosity associated with low-gradient, sandy stream beds coupled with low discharge when streams were flowing may limit oxygen supply to subsurface sediments. Other studies in low-gradient, sandy streams have shown that meiofauna and dipterans compose a significant portion of the invertebrate community (Whitman and Clark 1984; Strommer and Smock 1989). The biomass and metabolism of the invertebrate community (excluding the non-indigenous clam, *Corbicula fluminea*) in a sandy Virginia stream was dominated by meiofauna (Poff et al. 1993). The intermittent hydrology of the streams also selects for aquatic taxa, such as ceratopogonids, nematodes, and copepods with short life histories and life stages able to tolerate frequent and extended dry periods (Williams 2006).

The study streams were dry during many of the collection periods, which provided an opportunity to record colonization of dry stream beds by terrestrial invertebrates. Most studies investigating invertebrate communities of intermittent streams focus on the aquatic phase and few have recorded terrestrial fauna colonizing during the dry phase. The longitudinal contraction of surface water during

Table 3 Results of multi-response permutation procedure (MRPP) tests comparing invertebrate composition among substrate types, streams, and time periods

Comparison	<i>T</i>	<i>p</i>	<i>A</i>
Substrate types			
All treatments	2.0	1.00	-0.016
Plastic vs. root	1.1	0.91	-0.009
Plastic vs. leaf	1.7	1.00	-0.014
Root vs. leaf	1.5	0.99	-0.014
Streams			
All treatments	-10.3	<0.0001	0.085
Reference vs. clearcut	-8.0	<0.0001	0.080
Reference vs. thinned	-6.9	0.0002	0.069
Thinned vs. clearcut	-5.0	0.0012	0.048
Time periods			
All periods	-14.1	<0.0001	0.168
18 vs. 44 days	-5.1	0.0006	0.085
18 vs. 112 days	-6.0	0.0002	0.098
18 vs. 314 days	-9.4	<0.0001	0.177
18 vs. 366 days	-9.9	<0.0001	0.202
44 vs. 112 days	-1.0	0.14	0.018
44 vs. 314 days	-6.8	<0.0001	0.111
44 vs. 366 days	-8.2	<0.0001	0.142
112 vs. 314 days	-7.4	<0.0001	0.122
112 vs. 366 days	-8.8	<0.0001	0.154
314 vs. 314 days	1.5	0.27	0.007

Shown are MRPP test statistic (*T*), associated *p* values, and the chance-corrected within-group agreement statistic (*A*). *n* = 45 for each comparison

dry periods provides opportunity for terrestrial scavengers to take advantage of stranded aquatic taxa and conditioned organic matter (Moon 1956; Williams 2006). The duration, frequency, and predictability of drying likely influence the terrestrial invertebrate colonization in much the same way as lateral expansion and contraction along flood plains (Adis and Junk 2002). During our study, there was an increase in the relative abundance of terrestrial invertebrates coinciding with a decline in total invertebrate abundance and diversity. However, terrestrial invertebrates never attained as high a density in dry stream beds as aquatic species when streams were flowing. Similar patterns were found in a Moroccan river, where the abundance of terrestrial invertebrates during dry conditions was only 10–33% of the abundance of aquatic invertebrates during wetted conditions (Maamri et al. 1997). The density of colonizing terrestrial taxa will likely vary with their mobility, resource availability, and time since drying. Using pitfall traps in a dry South African stream, Wishart (2000) found most terrestrial invertebrates to be aerial, but the biomass of aerial and non-aerial taxa did not differ. Most of the terrestrial taxa colonizing our study streams were

Table 4 Indicator values (IV) for taxa across litterbag substrate types

Substrate type	Taxon	IV	<i>p</i>	
Leaves	<i>Enchytraeus/Marionna</i>	37.8	0.17	
	<i>Bezzia/Palpomyia</i>	30.4	0.51	
	<i>Culicoides</i>	28.1	0.85	
	<i>Ironus</i>	27.2	0.87	
	<i>Mononchus</i>	25.3	0.21	
Roots	<i>Mylonchulus</i>	40.4	0.003	
	<i>Labronema</i>	40.0	0.10	
	<i>Eudorylaimus</i>	37.0	0.19	
	<i>Ormosia</i>	30.2	0.71	
	<i>Pseudosmittia</i>	29.9	0.17	
	<i>Tabanus fairchildi</i>	27.9	0.33	
	<i>Isotoma viridis</i>	27.6	0.20	
	<i>Pseudorthocladius/Parachaetocladus</i>	27.5	0.72	
	Plastic roots	None	n/a	n/a
	Leaves + roots	<i>Enchytraeus/Marionna</i>	54.3	0.12
<i>Eudorylaimus</i>		50.7	0.18	
<i>Labronema</i>		50.0	0.31	
<i>Ormosia</i>		47.1	0.28	
<i>Bezzia/Palpomyia</i>		42.8	0.36	
<i>Ironus</i>		40.6	0.59	
<i>Pseudosmittia</i>		38.0	0.14	
<i>Tabanus fairchildi</i>		37.7	0.23	
<i>Polypedilum</i>		34.8	0.18	
<i>Candona cf. annae</i>		34.8	0.10	
<i>Lobohalacarus</i>		34.7	0.58	
<i>Isotoma viridis</i>		33.9	0.13	
<i>Mononchus</i>		33.8	0.11	
<i>Gonomyia/Molophilus</i>		32.5	0.76	
<i>Ceratopogon</i>		32.0	0.69	
<i>Dolichopus/Hydrophorus</i>		31.2	0.41	
<i>Tanytarsus</i>		29.6	0.60	
cf. <i>Cosmochthonoidea</i>		29.2	0.07	
Ologamasidae		28.0	0.09	
<i>Parametricnemus</i>		26.5	0.26	
<i>Alaimus</i>	25.9	0.51		
Plastic roots only	<i>Culicoides</i>	39.3	0.83	
	<i>Pseudorthocladius/Parachaetocladus</i>	36.2	0.82	
	Cecidiomyiidae	34.0	0.54	
	<i>Stilobezzia</i>	33.2	0.53	

Only taxa having the majority of their relative abundance and frequency occurrence associated with a particular substrate type are shown

non-aerial (e.g., Enchytraeidae, Collembola, Oribatida) or were the larvae of aerial insects (e.g., Cecidiomyiidae, *Pseudosmittia*, Sciaridae). This result suggests that terrestrial fauna in our study colonized the stream channel

predominately from the immediate banks or from oviposition by aerial adults. Several studies have shown that terrestrial invertebrates represent a significant link between terrestrial and perennial aquatic ecosystems (e.g., Cloe and Garman 1996; Nakano and Murakami 2001). Our findings indicate that colonization of dry stream beds by terrestrial fauna also can be substantial. Further research is needed to determine if activities of terrestrial fauna (e.g., scavenging, organic matter processing) can mediate or subsidize subsequent aquatic assemblages either locally or downstream. Because of their wet and dry phases and their abundance and position in the stream network, headwater intermittent streams play an important role as an interface for the reciprocal exchange of energy and materials between terrestrial and aquatic ecosystems.

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