Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches

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Abstract

The availability and spatial arrangement of habitat patches are known to strongly influence fauna in terrestrial ecosystems. The importance of patch arrangement is not well-studied within running-water systems where flow-induced movements of patches and of fauna could decouple habitat characteristics and faunal habitat preferences. Using small, stream-dwelling invertebrates, we asked if fauna in such systems can distinguish among patch types and if patch arrangement at their "landscape scale" (i.e., within a streambed across which they move and forage) can be linked to faunal abundance. We quantified the spatial distribution of sand and leaf patches at multiple sites on a streambed at regular intervals over a 1½yr period, estimated faunal abundance in the two patch types, and experimentally determined if faunal colonization varied among leaf patches that were similar structurally but differed in their potential microbial food resources. We show that despite their small size and limited swimming abilities, these stream invertebrates did respond to patch type, that specific characteristics of an individual patch influenced faunal colonization, and that the spatial arrangement of patches on the streambed was linked to field abundances. Larval chironomids and adult copepods were more abundant in leaves than in sand and preferentially colonized leaf patches made with rapidly decomposing leaves that harbored higher microbial (bacteria and fungi) abundances over leaf patches with more refractory leaves and lower microbial abundances. Further, statistical models that included spatially-explicit data on patch arrangement (e.g., patch contagion, distance between patches) explained significantly more variation in faunal abundance, than models that included only nonspatial information (e.g., date, time since last flood). Despite the fact that these fauna live in a highly dynamic environment with variable flow rates during the year, unstable patch configurations, and seasonal changes in total abundance, our findings suggest a need for aquatic ecologists to test the hypothesis that small-scale landscape attributes within streams (e.g., leaf patch aggregation) may be important to faunal dynamics. If patch aggregation has negative consequences for stream biota, streambed 'landscapes' may be fundamentally different from many terrestrial landscapes due to the inherent connectivity provided by the water and the over-riding importance of patch edges. Regardless of these differences, our findings suggest that the spatial configuration of patches in a landscape may have consequences for fauna even in highly dynamic systems, in which patches move and fauna periodically experience high levels of passive dispersal.

Introduction

Patchiness in habitat quality can affect virtually every aspect of population dynamics and stability (Johnson et al. 1992; Wiens et al. 1993). Availability of suitable habitat patches and the physical arrangement of those patches influence loss of species, shifting patterns of abundances, and population persistence in the face of disturbance (e.g., Hansson et al. 1995;
Individual patches can be characterized in a variety of ways including by their size and quality; similarly 'arrays' of patches (landscapes) can be characterized in many ways including by the relative abundance of patch types and the arrangement of patches (Wu and Loucks 1995). Empirical work from both terrestrial and aquatic systems has demonstrated the influence of patch type (i.e., patches that vary in structure, resource-availability, refuge value) on species composition and abundance, particularly with respect to those organisms that actively search for resources and habitat (Southwood 1977; Townsend 1989; Pahl-Wostl 1998). Empirical studies primarily on terrestrial vertebrates and insects have convincingly demonstrated that the arrangement of patches on the landscape (e.g., degree of fragmentation) also can influence the biota (Forman 1995; Hansson et al. 1995). Indeed, the field of landscape ecology has grown exponentially in the last decade as evidence has accrued that the spatial structure of entire, heterogeneous mosaics of patches may have profound ecological significance.

Though the majority of landscape ecology studies have focused on terrestrial systems, aquatic ecologists have long recognized that habitat heterogeneity is an important determinant of faunal dynamics. In running-water systems, most landscape studies have addressed how spatial attributes at the watershed scale and above relate to biological organization (Roth et al. 1996; Johnson and Gage 1997). So, while many stream ecologists recognize that the patch dynamics concept may be critical to understanding pattern and process in streams at multiple scales (Pringle et al. 1988; Townsend 1989; Crowl et al. 1997), few small-scale studies (within a stream) have included both patch type and patch arrangement as factors that might influence biological processes. Numerous studies have shown that patch type and availability influence invertebrate and fish populations in running-water systems (Hildrew and Giller 1994), and, certain patches (e.g., flood refugia) may be critical to the persistence of stream fauna (Sedell et al. 1990; Lancaster and Hildrew 1993; Lancaster and Belyea 1997). A few studies have quantified spatial heterogeneity in resources (at single or multiple scales) and shown that heterogeneity per se, not just mean resource levels, may influence the growth and distribution of stream invertebrates (e.g., T. Palmer 1995; Downes et al. 1993; Sarnelle et al. 1993).

The fact that stream ecologists have completed more work on the importance of particular patch types and less on the influence of spatial arrangement is probably related to the dynamic nature of streams — they are typically viewed as physically rigorous, open habitats. The response of stream fauna to patch arrangement can be obscured by flow-induced movements of fauna and even the patches themselves (Sih & Wooster 1994; Pahl-Wostl 1998). This does not mean stream ecologists believe their systems are controlled solely by physical processes. Stream ecology has a rich history of the study of biotic interactions (e.g., Peckarsky and Dodson 1980; McAuliffe 1984; Kohler 1992); however, relative to lakes and some terrestrial systems, physical disturbances are more pronounced and the study of flow-related phenomena has played a dominant role in stream ecology (Allan 1995). Stream fauna actively and passively enter the water column and once there may be dispersed great distances by flow (Poff and Ward 1991; Lancaster et al. 1996). Passive dispersal (i.e., animals drifting along with water currents) is particularly common for small stream fauna (Palmer 1992; Robertson et al. 1995; Palmer et al. 1996a). For such fauna, it is not clear that a response to patch type and arrangement would be detectable.

Our goal was to determine if the abundance of small stream invertebrates varies with the type and arrangement of habitat patches on a streambed. We used two groups of invertebrates that are abundant in streams throughout the world: copepods and larval chironomids. We tested two specific hypotheses: Hypothesis 1—fauna respond to differences among patches that vary structurally or in microbial abundance (potential food); and, Hypothesis 2—the spatial arrangement of patches influences faunal abundance on the streambed. We show that these small stream fauna do respond to patch type (leaf patches vs. sandy patches), that specific characteristics of an individual patch (leaf species and microbial resources within a patch) influence faunal colonization, and that the spatial arrangement of patches on the streambed is linked to field abundances.

Methods

General approach

For Hypothesis 1, we used two data sources: (1) a field survey that quantified the abundance of fauna in sand and leaf patches at regular intervals over 1½ years; and, (2) a field experiment to determine whether fauna preferentially colonized patches that had higher potential
food but were similar in their physical structure. The survey data allowed us to ask if faunal abundance was related to patch type (sand vs. leaf patches). The experimental data allowed us to ask if colonization varied between leaf patches made of rapidly decomposing leaves with high microbial biomass vs. patches with leaves that decompose more slowly and have lower microbial biomass.

For Hypothesis 2, we documented the amount and spatial arrangement of leaf material and sand each time we sampled invertebrates for the 1½-year field survey. Using a number of landscape metrics (e.g., measurements of patch size, shape, connectivity), we quantified patch arrangement on each sampling date and asked if faunal abundance was related to patch arrangement or, more simply, to total amount of leaf material at a site or other non-spatial factors (e.g., time since last flood). Since we were asking if there was any correlation between faunal abundance and patch arrangement, our ‘testing’ of Hypothesis 2 should be viewed as exploratory data analysis (Thomson et al. 1996). Our findings have since led us to test specific hypotheses using replicated landscapes in the lab (Silver et al. 2000).

Our study system is a low-gradient stream in northern Virginia (Goose Creek) that is characterized by long stretches of sandy channel in which sand and clusters of leaves are the two dominant patch types for stream fauna. The study site and fauna have been described extensively elsewhere (e.g., Palmer 1990, 1992; Poff et al. 1993; Palmer et al. 1996b).

Hypothesis 1: Faunal response to patch type

Faunal distribution across patch types: field survey data

Sampling the landscape. We surveyed the stream in 1994–1995 at ca. 2 month intervals during the winter and monthly between June and November. On each date, we sampled fauna in four, 20 × 6 m sites (separated by at least 75 m) and we mapped (see Hypothesis 2, methods) the distribution of leaf vs. sandy patches. For each site and on each date, we collected two invertebrate samples from leaf patches and two from sand patches; samples were paired, i.e., a leaf sample was collected from a randomly selected position in each site, and a sediment sample was collected at the nearest leaf-free (sandy) area (Figure 1).

Leaf patches were sampled by slipping all leafy material from a 15" × 15cm area (typically, leaf patches were ca.1 cm deep) into a Ziplock® bag held down-stream of the debris patch. Sand samples were collected using a corer (3 cm dia, 1 cm deep). Samples were rinsed with MgCl₂ to promote faunal relaxation, and animals washed into containers with Formalin and Rose Bengal®. In the laboratory, samples were examined at 50× magnification to enumerate all animals. Copepods were identified to species and chironomids to the lowest possible level, usually genus. The total number of animals per sample was standardized by surface available for settlement expressed per 100 cm² surface of streambed.

Statistical analysis. We considered a genus or species to show affinity for sand vs. leaf patches if it occurred there more often than could be explained by chance alone, e.g., the null expectation was that animals should appear in each patch type in proportion to the relative abundance of that patch type in the stream (i.e., % of streambed covered with leaves or sand) for any particular sampling date and site. We used a two-tailed sign rank test to determine if the proportion of animals in leafy debris differed significantly from the null expectation. We tested the 5 most abundant species/genera of each taxon as well as total chironomids and copepods (12 comparisons, with a Bonferroni corrected threshold of \( p = 0.004 \)).

Faunal response to leaf patch composition: field experiment

Faunal colonization of leaf patches. Leaf packs were made with freshly abscised leaves from the streambank from two tree species that vary greatly in their decomposition rates: flowering dogwood (Cornus florida, breakdown rate \( \approx 0.0075 \) day⁻¹) and sycamore (Platanus occidentalis, breakdown rate \( \approx 0.0038 \) day⁻¹) (Webster and Benfield 1986). Control leaf packs were constructed of plastic which provided a substrate much like a leaf, but offered little in the way of nutrition for the microbial/invertebrate community. Each leaf pack consisted of six leaf pieces (45.5 cm² each) supported with an H-shaped hackberry wood frame (Celtis occidentalis, also indigenous to Goose Creek) between the middle layers of leaves. The leaf/frame assembly was placed inside 1 cm-mesh plastic netting. Packs were attached to wooden stakes with nylon, and anchored to the streambed.

Five packs for each treatment (Cornus, Platanus, Control) - time combination were randomly placed onto the streambed in five rows in Nov 1996 and sampled after 1, 7, and 14 days. Individual leaf packs were
at least 1 m apart from each other and any naturally occurring leaf packs. Naturally occurring leaf packs were sampled randomly on days 7 (n = 4) and 14 (n = 3) to estimate invertebrate and microbial abundance on natural packs. On each sampling date, packs were removed (beginning downstream) onto a 63 μm sieve then 1/4 of the leaves from a pack placed in O₂-uptake chambers (see below) and the other 3/4 preserved in Rose Bengal®-stained formalin for enumeration of invertebrates. Faunal abundance was expressed per g dry leaf matter.

Leaf Pack Attributes: O₂ uptake and microbial biomass. O₂-uptake was measured as an indication of relative biological activity for each treatment on a given sampling date. Although not reflecting any single component of the biological community, this measure summarizes metabolism taking place on the leaf surface, which may relate to the quality of the resources (Petersen and Cummins 1974; Ward and Johnson 1996). Bacterial cell counts and fungal biomass were quantified since these are known food sources for these fauna (Perlmutter and Meyer 1991; Borchardt and Bott 1995; Hall 1995; Stanko-Mishic et al. 1999).

Sealed PVC chambers were used to measure O₂ consumption of each subsample taken from the packs at the time of each sampling and of water-only controls (Lampert 1984). At the beginning of the experiment there were instances in which O₂ consumption in the water-only controls was greater than on the leaves (with dry leaves, there is a lag time in microbial and fungal growth) which resulted in negative values for O₂ consumption early in the study.

To estimate fungal biomass on leaves, ergosterol was extracted and measured following Newell et al. (1988) and Suberkropp and Weyers (1996). Bacterial extraction and enumeration are after Epstein & Rossel (1995) with modifications. Briefly, detergent (ammonium phosphate) was added and the samples allowed to incubate for 15 min followed by sonication. Detergent was decanted, leaves washed with filtered (0.2 μm) distilled H₂O, and stained with filtered (0.2 μm) DAPI to a final concentration of 40 μg/ml (5 min incubation). Samples were filtered onto 0.2 μm black polycarbonate filters backed by 0.45 μm glass fiber filters. The bacteria in 10 fields of view were counted at 1000× using epifluorescence microscopy and are presented as the number of cells per g dry leaf material.

Statistical analysis. ANCOVA (3 treatments – Cor- nus, Platanus, and Control, with day treated as a covariate) was performed on three of the dependent variables: O₂-uptake, bacteria abundance, and chironomid abundance. For ergosterol biomass (μg/g leaf, square-root transformed), ANOVA was used since initial analysis with ANCOVA revealed no effect of day. LSD mean comparisons were performed on significant treatment x day interactions (Litell et al. 1991). For all tests, assumptions of normality and homogeneity of variances were met (Sokal and Rohlf 1981).
Hypothesis 2: Linking faunal abundance to patch arrangement

Mapping patch distribution in field survey and linking to faunal samples

On each sampling date for the field survey work, we mapped each of the 4 sampling sites by running transect lines across the width of the stream (ca. 20 m) at 1 m-intervals along a 6 m length of the stream; this created a grid of 120, 1 x 1 m cells (Figure 1). A individual recorded the distribution of leaves in 10 x 10 cm subcells within each of the 120, 1 m² cells (i.e., mapping resolution of the leaf material was ca. 100 cm²). Maps were digitized and every leaf patch individually measured in order to calculate indices quantifying three aspects of leaf patchiness: patch size, patch shape, and arrangement of patches across the landscape.

We characterized the distribution of patch sizes for each map using mean patch size and standard deviation of patch size. Because the distribution may be highly skewed, we used modal patch size to determine the most common patch size. We characterized patch shape for each map by measuring the absolute amount of perimeter (total perimeter per m²), the relative abundance of interior vs. edge habitat (average perimeter to area ratio), perimeter convolution (shape factor) and patch elongation (compactness) (Bosch 1978; Davis 1986). Because the largest patch in a landscape may have disproportionate effects on animals (R.H. Gardner, pers. comm.), we also determined the perimeter, shape factor and compactness of the largest patch. Finally, we characterized patch arrangement for each map using the number of patches per m², the downstream distance between patches, and contagion.

Contagion measures habitat continuity by assessing the degree of aggregation or clumping of patch types (O'Neill et al. 1988, Turner 1989). High values of contagion mean there are large contiguous areas of sand or leaves, while low values mean the landscape is divided into many small patches. Contagion required an adjacency matrix, A, whose members a_ij express the likelihood of patch types i and j being found adjacent to each other when the landscape is divided into a grid of cells. To calculate A, we divided the map into square cells 10 cm on edge and marked each cell as leaves or sand depending on which type habitat was more common in the cell.

Statistical analysis.

Our goal was to determine whether the spatial indices explained variation in faunal abundances in leaf and sand patches. The resolution of organismal sampling was lower than that of the landscape mapping (we did not take faunal samples in every grid cell); however, we were interested in whether we could detect landscape-level (= across a 120 m² site) differences in abundance, rather than differences among cells within a site. Therefore, for each date, we integrated faunal abundance across a landscape (=site) by multiplying the contribution of abundance in each patch type by the relative amount of that patch type in the map. We refer to this quantity as ‘landscape-level abundance’ of animals and use it as the dependent variable in the following analyses. Scaling-up of faunal abundances (from cores to site) should not have biased our search for a pattern since within a patch type in Goose Creek, small-scale aggregations of these fauna are typically less than the size of the core we used (Hakenkamp 1997; Swan and Palmer 2000).

To determine whether landscape characteristics were good predictors of landscape-level abundances, we conducted a series of regressions first using non-spatial descriptors only, then using both spatial and non-spatial descriptors. We used a stepwise model selection procedure (SAS Institute 1989). Landscape level abundances were log-transformed in order to meet the assumption of homogeneity of variance. We asked whether inclusion of spatial information (patch size, shape, and arrangement) significantly increased the explanatory power of the regression, as measured by adjusted $r^2$ (see below).

Non-spatial descriptors included time of year (date), days since last flood, magnitude of last flood, and availability of leaf patches (% of streambed covered by leaves). Spatial descriptors included those described above except standard deviation of patch size, which was highly correlated with mean patch size. A temporal relationship between time of leaffall (which could influence patch descriptors) and important life history events (e.g., synchronous emergence or egg laying) would confound our ability to interpret the relationship between patch descriptors and faunal abundance. Thus, we took care to determine that no descriptors were highly correlated with date. To guard against collinearity, we used the commonly accepted test that the Condition Number (square root of ratio of largest and smallest eigenvalues of the correlation matrix) for the model not exceed 30 (Kleinbaum et al.
1988); for independent variables that were collinear, we dropped one of them from the model before proceeding. To avoid inflation of $r^2$, we report the adjusted $r^2$, which reduces the $r^2$ by taking into account the number of regressors and the degrees of freedom (SAS Institute 1989).

Results

Hypothesis 1: Faunal response to patch type

Faunal distribution across patch types: field survey data

The abundance of chironomids (Figure 2A) varied during the 1994–1995 sampling period, averaging ca. 200 per 100 cm$^2$ in the leaves and ca. 80 per 100 cm$^2$ in the sand. Abundances of copepods (Figure 2B) were much lower: ca. 51 per 100 cm$^2$ in the leaves and 13 per 100 cm$^2$ in the sand. Species composition also varied among dates and patch types with the dominant taxa typically making up more than 80% of the individuals (proportions calculated by date and site). The dominant chironomids were Corynoneura sp., Orthocladius sp. Gp. A., Polypedilum spp., Glyptotendipes sp., and Tanytarsus spp. and the dominant copepods were Eucyclops elegans, Diacyclops albus, Elaphidiella bidens, Macrocylops albidos, and Parastenocaris palmerae.

Both chironomids and copepods were found disproportionately in the leaf patches (Figure 3, two-tailed sign rank test P<0.0001 for total chironomids, P = 0.017 for total copepods). The patterns were particularly influenced by several highly abundant copepods (Eucyclops elegans, Diacyclops albus) and chironomids (Corynoneura sp. and Orthocladius sp. Gp. A) that showed a strong affinity for the leaf patches. In general, the proportion of the total fauna (in sand + leaves) was less than for the copepods than for the chironomids (Figure 3) because two of the dominant copepod species, Elaphidiella bidens and Macrocylops albidos, were common in both sand and leaves.

Faunal response to leaf patch composition: field colonization experiment

Faunal colonization of leaf patches. Invertebrates colonized leaf patches rapidly. By Day 14, fauna were more abundant in Cornus than in either Platanus or control packs (Figure 4; ANCOVA: trt x day interaction, P<0.01; LSD mean comparisons: Cornus >
Table 1. Summary of measurements taken on naturally occurring leaves during the leaf pack colonization experiment. For biota, values are number per weight of leaf (g); for oxygen uptake, values are μg O₂ per g of leaf; for ergosterol, values are μg per g of leaf. Water velocity is in cm/s.

<table>
<thead>
<tr>
<th>Variable</th>
<th>n</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water velocity</td>
<td>7</td>
<td>24 ± 2.3</td>
</tr>
<tr>
<td>Invertebrate abundance</td>
<td>7</td>
<td>62 ± 26.7</td>
</tr>
<tr>
<td>Chironomid abundance</td>
<td>7</td>
<td>35 ± 19.1</td>
</tr>
<tr>
<td>O₂-uptake</td>
<td>7</td>
<td>73 ± 69.5</td>
</tr>
<tr>
<td>Bacterial abundance</td>
<td>7</td>
<td>1.3 (±0.37) x 10₁⁴</td>
</tr>
<tr>
<td>Ergosterol biomass</td>
<td>4</td>
<td>172.3 ± 54.52</td>
</tr>
</tbody>
</table>

Figure 4. Chironomid colonization of leaf packs differing in composition: Cornus leaves, Platanus leaves, or plastic (control ‘leaves’). Symbols are means (n = 5) ± SE.

Platanus ≈ Control , P < 0.05). Total invertebrates and chironomids (per g of leaf material) on ‘young’ (<1 week in the stream) experimental packs were within the range of values found on natural packs in the field that consisted of mixed species of leaves of unknown age (Table 1).

Figure 5. O₂ consumption rates (A), bacterial abundance (B), and ergosterol biomass (C) of each treatment over time in leaf packs differing in composition: Cornus leaves, Platanus leaves, or plastic (control). Symbols are means (n = 5) ± SE.

Leaf pack attributes: oxygen uptake and microbial biomass. O₂-uptake varied significantly (ANOVA: trt × day interaction, P<0.01) between treatments (Figure 5A) and increased over time at a greater rate for Cornus than Platanus or control packs; differences between Platanus and controls were notable only on day 14 (LSD mean comparisons: Cornus > Platanus > Control, P<0.05). O₂ consumption rates, bacterial abundance and ergosterol levels were within the range of values found in naturally-occurring leaf packs (Table 1) although, bacterial abundances in natural packs were most similar to abundances found in treatment packs early in the study.

Treatment effects were detected (ANCOVA) for both bacteria (P<0.05) and ergosterol (P<0.01). Bacterial abundance and ergosterol biomass were higher in Cornus packs than in Platanus or control packs (Figures 5B and 5C). Bacterial abundances on Cornus and Platanus were greatest on day 7 (Figure 5B), but ergosterol biomass on leaves was greatest just 24 h after initiating the experiment (Figure 5C). Measurable levels of ergosterol were found on Cornus and Platanus leaves at day 0 (dry leaves) suggesting leaves were colonized by fungi before entering the stream, and this colonization was higher on Cornus than Platanus. Despite the high ergosterol levels on Day 1, particularly for the Cornus packs, cells were presumably inactive since oxygen-uptake was insignificant (Figure 5A).

Hypothesis 2: Linking faunal abundance to patch arrangement

Seasonal changes in the arrangement of leaf patches on the streambed were reflected in the landscape indices (Figure 6, Table 2). In general, the maximum values for indices that were strongly influenced by
the size of the largest patch (mean and SD of patch size, largest patch perimeter) were found in the fall, when most leaves had already fallen but had not yet decomposed. Number of patches per m² also doubled at the start of leaffall, but remained high for several months. Perimeter-to-area ratio and modal patch size showed modest increases as large accumulations of leaves became fragmented in the months after leaffall. Despite these general seasonal trends, considerable differences in landscape indices remained between maps on every sampling date (even in the fall) so that we could explore potential relationships between patch arrangement and faunal abundance.

The regression models showed that the landscape indices (spatial descriptors) explained a significant fraction of variability in landscape-level faunal abundances throughout the survey period. For chironomids, inclusion of spatial descriptors increased the adjusted $r^2$ of the best regression model from 0.38 to 0.68 ($P=0.001$ for the spatial model, Table 3). For copepod abundances, no non-spatial model was significant, while the best spatial model had an adjusted $r^2$ of 0.42 ($P = 0.0006$, Table 3).

For both taxa, landscape-level abundances decreased as the perimeter of the largest patch increased (Table 3). Chironomids also decreased with increasing contagion, suggesting that subdivided (non-aggregated) patches were associated with increased abundances. Copepods decreased as the distance between patches decreased, and as modal patch size increased, suggesting that landscapes consisting of many small, evenly spaced patches were favorable.

Discussion

The availability and spatial arrangement of habitat patches are predicted to influence population dynamics (Fahrig and Merriam 1985; With et al. 1997) and this has been confirmed by many studies conducted in terrestrial systems (Fahrig and Paloeimo 1988; Hamazaki 1996). For running-water systems, there has been little work on how patch arrangement influences populations but the importance of patch type to community composition and species persistence of stream invertebrates has been shown (e.g., Downes 1990; Hildrew and Giller 1994). When fauna experience high levels of passive dispersal (as is frequently the case for small stream invertebrates) and patches have high turnover rates (as is common for leaf patches in streams), a link between faunal abundance and the spatial configuration of patches is not necessarily expected, even if biota are influenced by patch type. High levels of dispersal and changing patch structure may mask ‘landscape’ level responses to patch arrangement (Hansson et al. 1995; Pahl-Wostl 1998).

We provide evidence that stream-dwelling chironomids and copepods responded to patch type and arrangement. They were more abundant per unit area of streamed in leaf patches than in sand despite the wide variety of flow conditions that occurred over the course of our field survey period. Further, they colonized some types of leaves more rapidly than other types, even though flow velocity during the leaf colonization experiment was ca. 24 cm/s. Our mapping and regression results suggest that faunal abundances in the stream were greater when leaf patches were subdivided across the streamed landscape rather than aggregated into large clusters. So, even given the somewhat coarse approach we took to explore the influence of patch arrangement on these small fauna (correlative survey work), a pattern was detected. Since leaf patch aggregation is inextricably linked to season in the natural setting (more leaves streamwide and leaves more highly aggregated in the fall), field studies suggest but do not prove faunal responses to patch arrangement. Recently, we have used lab experiments in which we hold amount of leaf material constant and remove flow so that we could carefully test the hypothesis that chironomids respond to patch arrangement. We found that survival, developmental rate, and body size were significantly higher when raised in microcosms in which leaf patches are arranged in a subdivided as opposed to an aggregated fashion (Silver et al. 2000). These lab results provide support for our present interpretation that faunal abundance in the field may be lower when leaf patches are highly aggregated.

Hypothesis 1: Faunal response to patch type

Accumulations of leaves and wood in streams are well known to attract abundant biota whose composition may vary with leaf species (Webster and Benfield 1986; Leff and McArthur 1989; Dobson 1994). Murphy et al. (1998) recently concluded that patterns in the aggregation of stream macroinvertebrates imply active selection and rejection of certain patches 'in search for favored conditions.' Our field survey does not allow us to pinpoint the exact mechanism that led to higher copepod and chironomid abundances in leaf patches than in sand; however, the results are suggestive of active habitat selection. In low flows, animals
Table 2. Minimum, median, and maximum values for each measure of landscape pattern. When seen, qualitative seasonal 'trends' are provided but there were insufficient data to test statistically for seasonal effects. Note – within any date (or season), there was high variability in each parameter among the four mapping sites (see text); L.P. = leaf patch.

<table>
<thead>
<tr>
<th>Values</th>
<th>Min</th>
<th>Median</th>
<th>Max</th>
<th>Units</th>
<th>Seasonal trends</th>
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<td>(A) Measures of patch area</td>
<td></td>
<td></td>
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<tr>
<td>Mean patch area</td>
<td>167.0</td>
<td>362.7</td>
<td>2664.5</td>
<td>cm²</td>
<td>Fall (Oct.–Nov.) peak</td>
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<tr>
<td>Standard deviation of patch size</td>
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<td>626.2</td>
<td>23639.9</td>
<td>cm²</td>
<td>Fall (Oct.–Nov.) peak</td>
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<tr>
<td>Modal patch area</td>
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<td>130.0</td>
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<td>(B) Measures of patch shape</td>
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<tr>
<td>Total perimeter/meter²</td>
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<td>134.5</td>
<td>314.6</td>
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<td>Average perimeter to area ratio</td>
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<td>0.63</td>
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<td>Average shape factor</td>
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<td>0.36</td>
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<tr>
<td>Average compactness</td>
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<td>390.6</td>
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<tr>
<td>L.P. perimeter</td>
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<td>816.3</td>
<td>7788.3</td>
<td>cm</td>
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<td>(C) Measures of patch arrangement</td>
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<td></td>
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<tr>
<td>number patches/m²</td>
<td>64.1</td>
<td>237.5</td>
<td>517.6</td>
<td>none</td>
<td>highest in Sept., lowest in Feb.</td>
</tr>
<tr>
<td>Contagion</td>
<td>1.43</td>
<td>1.89</td>
<td>2.52</td>
<td>none</td>
<td>highest in Fall, lowest in Feb.</td>
</tr>
<tr>
<td>Average downstream distance between patches</td>
<td>1.18</td>
<td>5.37</td>
<td>44.85</td>
<td>cm</td>
<td>lowest in Fall, highest in May</td>
</tr>
</tbody>
</table>

are free to swim and move across the sediment 'selecting sites'. During higher flows (i.e., when passive dispersal dominates), habitat selection could occur via repeated rejection of sand patches until animals find themselves in leaf packs. Such a mechanism of habitat 'selection' has been found for some benthic marine invertebrate larvae: in the presence of flow, larvae are passively dispersed and actively reject sites after settling to the bottom; in low or zero flows, the larvae swim and actively select sites (Grassle et al. 1992). This mechanism, termed "ballooning behavior", could be a common way in which stream invertebrates exert control over which patch type they inhabit.

Alternative explanations for higher faunal abundances in leaves include not only active habitat selection/rejection, but passive accumulation in leaf patches due to flow effects, direct or indirect effects of predation, or higher reproductive rates in leaf packs. We found higher chironomid abundances in the leaf patches even when flow was extremely low (June – October) and fauna were not subjected to passive dispersal, thus passive accumulation in packs due to flow effects seem unlikely. Fish predation on chironomids and copepods in Goose Creek is higher in leaf patches than in sand (Shofner, 1999) and macroinvertebrate predators in Goose Creek are rare in the sandy channel yet found in leaves (Poff et al. 1993). Thus, leaf patches do not appear to be a refuge from predators. Reproduction as an explanation of enhanced abundances in leaf patches requires that individuals complete their entire life cycle in leaves. This may be the case for some copepods but it is inconsistent with chironomid life histories in which adults are aerial, and early instar larvae are dispersed in the drift (Oliver 1971). Further, in the colonization experiment, abundances were higher in Cornus packs yet the duration of the experiment was deliberately kept shorter than the time needed for colonists to reproduce.

The colonization experiment also allowed us to assess the possibility that higher abundances in some patch types are simply due to differences in habitat architecture. The quandary of how to compare faunal abundance between habitats that differ structurally is not new to ecologists – there is no simple solution. Because of this, we designed our leaf colonization experiments to hold habitat architecture constant across
treatments (same surface area of leaves in *Cornus*, *Platanus* and control packs) while varying patch type (leaf species and microbial resources differed). Faunal abundances were clearly higher on *Cornus* supporting the idea that the fauna do respond to patch type.

Response of fauna to patch type may be related to potential food availability. In Goose Creek, microbial abundances appear to be quite different in sand than on leaves (in sand: $< 8 \times 10^{10}$ bacterial cells/g of sand, ergosterol undetectable, no data on diatoms; on leaves: $10^{14}$bacteria cells/g of leaf, 172 $\mu$g ergosterol/g leaf, abundant diatoms; Swan 1997, Stanko-Mishic et al. 1999). Further, the leaf pack colonization experiment ‘offered’ potential colonists a choice of patch types that differed with respect to potential food sources. The higher microbial biomass on *Cornus* than on *Platanus* follows predictions from generally accepted models of leaf decomposition (Webster and Benfield 1986) and invertebrates may be responding to microbial differences that relate to decomposition. Stanko-Mishic et al. (1999) has shown that survivorship of chironomids living in sand amended with high ‘quality’ leaves (*Cornus*) is significantly greater than in sand amended with lower quality leaves (*Platanus*) or unamended sand. It is possible that some other aspect of the leaves (e.g., chemistry) could account for faunal responses. Carefully designed manipulative experiments are needed to unambiguously distinguish among the possible explanations. Our results certainly suggest it is worthwhile to test the hypothesis that high microbial resources reduces emigration of chironomids and copepods from high quality patches and enhances survivorship (Stanko-Mishic et al. 1999) thereby increasing abundance.

**Hypothesis 2: Linking faunal abundance to patch arrangement**

As in many streams, flow varies markedly throughout the year in Goose Creek and this has dramatic consequences for the frequency and magnitude of chironomid and copepod dispersal (Palmer 1992; Palmer
Table 3. ‘Best’ (highest adjusted $r^2$) non-spatial vs. spatial multiple regression model for explaining the landscape-level abundance of chironomids and copepods during the 1994-95 sampling dates. Descriptions of the spatial and non-spatial terms used are provided to the right and the direction of effect (sign) is shown. Terms included in each model vary since the best model was chosen using stepwise regression procedures and guarding against multicollinearity (see text).

<table>
<thead>
<tr>
<th>Model</th>
<th># of terms</th>
<th>Adjusted $r^2$</th>
<th>$p$</th>
<th>Descriptor</th>
<th>Sign</th>
<th>Term</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Chironomids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-spatial terms only</td>
<td>2</td>
<td>0.38</td>
<td>0.002</td>
<td>days since flood</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>flood size</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Non-spatial + spatial terms</td>
<td>4</td>
<td>0.68</td>
<td>0.001</td>
<td>largest patch perimeter</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>average compactness</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>contagion</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>days since leaf fall</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>(B) Copepods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-spatial terms only</td>
<td>2</td>
<td>0.01</td>
<td>N.S.</td>
<td>flood size debris cover</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Non-spatial + spatial terms</td>
<td>4</td>
<td>0.42</td>
<td>0.0006</td>
<td>largest patch perimeter</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>downstream distance between patches</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>modal patch size</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

et al. 1996a, b). Despite the potential for broad passive dispersal, our regressions suggest that copepod and chironomid abundances changed as the spatial arrangement of patches on the streambed changed. Models that included spatially-explicit data had significantly greater explanatory value than regression models that included only nonspatial information (e.g., date, time since last flood). This was true even after adjusting for the increased number of predictor variables in the model. The percent of variability in chironomid abundances explained by spatial and non-spatial indices together was almost double that explained by non-spatial indices alone, while copepod abundance could not be predicted at all without the use of spatial indices.

We took care to ensure collinearity was not indicated as a serious problem in the multiple regressions, and that the correlation coefficients were adjusted for the number of predictors (see Methods). It is difficult to unravel the effects of relative habitat amount vs. spatial arrangement in any landscape study (Gardner and O’Neill 1991) – patch aggregation was generally greater in the fall when there were also the most leaves streamwide. We can not exclude the possibility that the total amount of leaf material in the stream as a whole was linked to temporal changes in faunal abundance (a seasonal effect on leaffall is expected in streams!) but the amount of leaf material at a given site (i.e., the % of a 120 m$^2$ mapped area covered with leaves) was not significantly correlated with date in our study. On any given date, sites differed – sometimes dramatically – in the total amount of leaf material. Such differences among sites within a date are not surprising since many factors other than season (e.g., water level, local geomorphology, and flow) determine the amount and arrangement of leaf material at different sites along a stream. Thus, our work suggests that either total amount of leaf material in the entire stream or local arrangement of leaf material influence faunal abundance.

In laboratory experiments we have held the amount of leaf material constant while manipulating patch arrangement and found that chironomids responded negatively to leaf patch aggregation (Silver et al. 2000); similar work remains to be done in the field. The quantification of benthic resource heterogeneity represents an important step in the evolving view of running-water ecosystems (Pringle et al.
1988; Townsend 1989; Downes 1990), particularly since the growth and distribution of stream fauna has been shown to be linked to spatial variability in resources for many different running-water ecosystems (T. Palmer 1995; Downes et al. 1993; Sarnelle et al. 1993). We argue there is a need to experimentally assess the biotic importance of resource aggregation on streambeds at scales of cm's – m's while holding total resource levels constant. The small, within-stream scale is probably one of many possible 'landscape' scales relevant to stream fauna. Biotic responses to landscape attributes at many scales have been shown to have life history and population-level consequences for many terrestrial systems (e.g., Fahrig and Merriam 1994; Dooley and Bowers 1998) and we expect similar findings may apply to running-water systems once they have received additional study.

If patch aggregation proves generally to be disadvantageous for stream fauna, this is in contrast to results from studies in many terrestrial systems in which large (aggregated) patches are often advantageous. Large patches are credited with providing source populations, interior habitat, and sufficient space to support species requiring large amounts of contiguous habitat (Forman 1995). Streambed 'landscapes' may be fundamentally different from terrestrial landscapes.

First, connectivity may be provided through the water column rather than through continuous bottom habitat, neutralizing one positive effect of large patch size. Second, patch edges (which are more 'common' when leaves are in small numerous clusters rather than large aggregations) may have a special function in stream systems: they intercept the flow, increasing the probability of settlement for drifting animals. Third, while large leaf patches in streams contain a large amount of interior, which may be rich in detrital food resources, they could be low in oxygen and high in predation risk (schools of foraging minnows can routinely be seen aggregating near structures in streams). These are three interesting ideas that remain to be tested.

Regardless of the underlying mechanism, the spatial configuration of patches in a landscape may have consequences for fauna even in highly dynamic systems such as streams, in which patches move around frequently and fauna may periodically experience high levels of passive dispersal.

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