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Spatial distributional patterns of macroinvertebrates along rivers within and among biomes

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Abstract

This study was designed to test the biome dependency hypothesis, which predicts that similar assemblages of macroinvertebrates occur along rivers both within and among drainage basins if the basins occupy the same biome. Benthic macroinvertebrates were collected from three drainage basins within each of three biomes in Canada, the eastern deciduous forests (EDF) of southwestern Ontario, the grasslands of south-central Alberta, and the montane coniferous forests (MCF) of southeastern British Columbia. A total of 225 benthic samples (3 biomes x 3 rivers/biome x 5 sites/river x 5 samples/site) was collected in spring using a cylinder sampler.

The significant interaction effect between biome and a site's location along a river indicated that spatial patterns of variation in total density and taxonomic composition were not spatially consistent among sites along rivers or among biomes. Total macroinvertebrate densities were equivalent between the EDF and grassland sites. However, total density was substantially lower at the MCF sites than at sites in the other two biomes. The greatest differences in taxonomic composition occurred among biomes, although significant differences also occurred for all other sources of variation examined. Macroinvertebrate composition was more strongly associated with local, site-specific factors (riparian vegetation and land use) than with longitudinal gradients. Distinct site-specific taxonomic assemblages were evident in EDF, but not in the other two biomes where land use was more homogeneous.

Introduction

Perhaps it is because rivers flow through such varied landscapes that researchers have had difficulty in predicting spatial distributional patterns of lotic macroinvertebrates and in applying these predictions successfully to other drainage basins (Corkum, 1989). The applicability of relationships derived in one study area to other study areas depends on similarity of environmental components and scale (Seifert, 1984) as well as taxonomic resolution. Historically, empirical relationships between riverine fauna and environmental factors were based on the classification of rivers into distinct units or zones from headwaters to mouth (Hawkes, 1975). Although attempts were made to associate the invertebrate fauna with fish zones, the distributional replacement patterns of invertebrate species along rivers appear to be continuous rather than discrete (Ide, 1935; Maitland, 1966).

Drainage basins have been used as a framework to relate an integrated series of physical gradients along a river with associated changes in functional feeding mechanisms of macroinvertebrates (Vannote *et al.*, 1980). Cummins *et al.* (1984, 1989) demonstrated a strong association between riparian vegetation, the relative proportion of allochthonous and autochthonous matter, and feeding groups of aquatic insects along the lengths of rivers. Although general patterns in the river continuum concept may exist, deviations from the model that are found in nature have been explained by variations in several environmental factors including climate, riparian vegetation, tributaries, site-specific lithology and geomorphology features (Minshall *et al.*, 1983, 1985).

I (Corkum, 1989) evaluated the relative contribution of landscape or biogeographical features and on-site hydrological variables to the spatial distribution of benthic macroinvertebrate assemblages at 100 river sites in northwestern North America. Although both types of variables were important, a model incorporating landscape features was more useful than a model that used only hydrological features in the correct classification of river sites characterized by distinct invertebrate assemblages. Earlier, Ross (1963) had noted a strong correspondence between certain caddisfly taxa and the terrestrial biome (defined by climate, but reflected by vegetation) through which small rivers flowed. Some caddisfly taxa were endemic to rivers in the western montane forests, whereas other caddisflies occurred only in rivers of the eastern deciduous forests.

Expanding on the work by Ross (1963), I (Corkum, 1989) suggested that similar assemblages of macroinvertebrates were most likely to occur at river sites within or among drainage basins if the drainages occurred within a single biome. Many researchers have stressed the importance of riparian vegetation to water quality and stream biota (Vannote *et al.*, 1980; Correll, 1986; Cummins *et al.*, 1989). However, if macroinvertebrates in rivers are biome dependent, there also should be a strong link between the lotic fauna and the climax vegetation that characterizes the biome.

Both the biome dependency (Ross, 1963; Corkum, 1989) and the longitudinal gradient or continuum concept models (Hawkes, 1975; Vannote *et al.*, 1980) may be used to predict the spatial distributional patterns of insects (at a coarse level of identification) along rivers. The biome dependency hypothesis predicts that similar assemblages of macroinvertebrates are most likely to occur at sites along rivers if the drainage basins occupy the same biome. The relationships that are derived for one biome are not expected to apply to other biomes because of the overriding importance of climate and vegetation (biome features) on the stream invertebrate community. In contrast, the longitudinal gradient or continuum models predict that invertebrate assemblages will change along the lengths of rivers. Moreover, these longitudinal spatial patterns are expected to be consistent from biome to biome.

I designed this study to determine if spatial distributional patterns of lotic macroinvertebrates (total density and taxonomic composition) differed most strongly among biomes or among sites along rivers within biomes. Specifically, I analysed benthic macroinvertebrates collected at sites along the lengths of rivers within each of three biomes in Canada, the eastern deciduous forests (EDF) of southwestern Ontario, the grasslands of south-central Alberta, and the montane coniferous forest (MCF) of southeastern British Columbia.

Description of sites studied

The three biomes selected for study are described and identified on maps presented in Udvardy (1975) and Danks (1979). Three drainages were examined within each of three biomes, the EDF (Ausable, Credit, Maitland), grasslands (Battle, Little Bow, Rosebud) and MCF (Cottonwood, Salmo, Salmon). In an earlier study on spatial distributional patterns of macroinvertebrates along the Ausable, Credit, and Maitland rivers of the EDF, I showed that macroinvertebrate composition (identified to the family level) at river sites did not differ among three sampling seasons (spring, summer, autumn) (Corkum, 1990). Since benthic composition did not differ seasonally at EDF sites, I chose to compare faunal patterns in spring before most overwintering taxa emerge (Hynes, 1970).

Drainage basins were selected within a narrow geographical range to avoid potential effects of latitudinal gradients on the macroinvertebrate community (EDF: 43° 04′ to 43° 51′ N; grasslands: 50° 08′ to 52° 51′ N; MCF: 49° 11′ to 53° 04′ N). The nine rivers were sampled at five sites from upstream (site 1) to downstream (site 5) locations. Sites were selected to correspond wherever possible to flow gauging stations (Water Resources Branch, Environment Canada). Site location, elevation and river distance from site to source were determined from 1:50000 National Topographic Series (NTS) maps (Fig. 1).

The biome study areas are characterized by distinctive temperature, total precipitation and degree days (Table 1). Data were obtained from five climatic stations located within the study area of each biome (Environment Canada, 1982). The EDF is the wettest biome; grassland sites are driest with some overlap with the moderate precipitation levels of the MCF. Mean annual temperature, mean daily January temperature and mean daily July temperature of the grasslands are lowest compared to the more moderate temperatures in the other biomes. Although the MCF is cooler in summer than the EDF, there is overlap in mean annual temperature and mean daily January temperature between the two regions (Table 1). Total number of degree days varies among biomes: 1128 DD (EDF), 939 DD (MCF), 667 DD (grasslands).

Criteria for river selection were based on de-

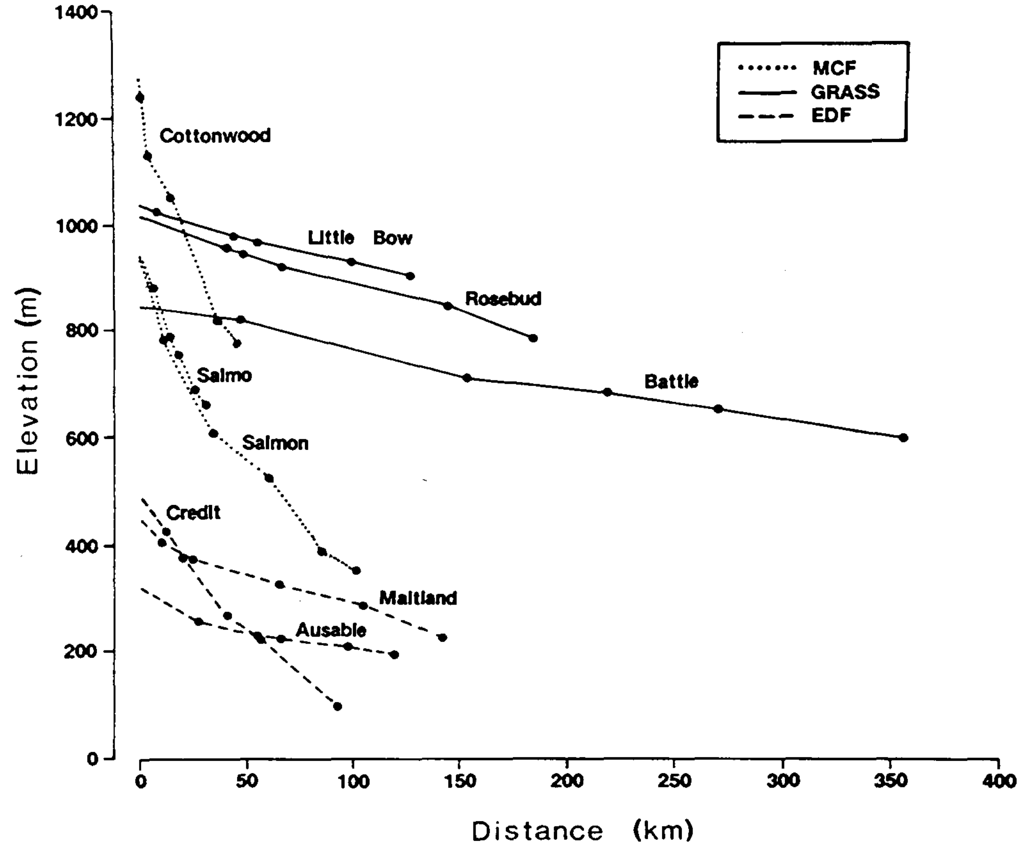

Fig. 1. Longitudinal profiles for the five study site locations on each river in terms of elevation and distance from source for rivers in the MCF (Cottonwood, Salmo, Salmon), grassland (Battle, Little Bow, Rosebud), and EDF (Ausable, Credit, Maitland) biomes.

Table 1. Thirty year summary (1951–1980) of mean annual air temperature, mean daily January and July air temperatures, total precipitation and degree days obtained from five (mean ± standard error) climate stations within each of the three biomes: eastern deciduous forest (EDF), grasslands (GRASS) and montane coniferous forests (MCF). Data were obtained from Environment Canada (1982).

	EDF	GRASS	MCF
Mean annual temp. (°C)	6.92 (0.43)	2.84 (0.38)	7.16 (0.73)
Mean daily Jan. temp. (°C)	- 6.84 (0.51)	- 14.38 (0.95)	- 5.78 (1.45)
Mean daily July temp. (°C)	19.70 (0.47)	16.80 (0.42)	18.78 (0.64)
Total precipitation (mm)	895.86 (34.74)	427.00 (22.06)	580.12 (46.59)
Degree days (above 10°C)	1127.90 (58.14)	666.54 (40.39)	939.22 (87.64)

velopment within the drainage basin. Minimal municipal or industrial development occurred within basins. With the exception of the Battle River, rivers were not interrupted by reservoirs. Battle River site 3 and site 4 were located 35 km and 26 km downstream from reservoir outflows, respectively. By chance, sites sampled occurred in different land use areas.

The three EDF drainages, located in southwestern Ontario, were sampled May 12–20, 1987. The Credit River (drainage area: 843 km^2) rises in a hilly region of moraines and flows south through deciduous forests for about 95 km before entering Lake Ontario (Chapman & Putnam, 1984). The Ausable (1645 km^2) and Maitland (2521 km^2) rivers flow west through agricultural cropland and enter Lake Huron.

The grassland rivers (Battle, Little Bow and Rosebud), located in south-central Alberta, were sampled May 10–16, 1988. The Battle River, a tributary of the North Saskatchewan River was the largest drainage basin sampled (9740 km^2 at site 5). The Battle River basin, located in the Groveland subregion of Aspen Parkland, is characterized by fescue (*Festuca* spp., a bunch grass), shrubs, and about a 15% cover of aspen (Strong & Leggat, 1981). Because much of this area is cultivated, the region has the appearance of grassland.

The Little Bow, a foothills stream, flows southeast to the Oldman River, a tributary of the South Saskatchewan River. The drainage area at Site 5 on the Little Bow was 2780 km^2. The Rosebud River drains 3990 km^2 of agricultural land before entering the Red Deer River, a tributary of the South Saskatchewan River. Both the Little Bow and Rosebud rivers flow through fescue grassland. This region occurs on moderately well-drained, black, chernozem soils and is one of the most productive agricultural zones in Alberta (Strong & Leggat, 1981).

The mountainous rivers, located in southeastern British Columbia, were sampled May 18–23, 1988. The Cottonwood River (drainage area: 1280 km^2) originates in the Quesnel Highlands on the western border of the Columbia Mountains and flows into the Fraser River. Interior western and subalpine mountain hemlocks occur throughout the basin. The Salmo River (drainage area: 1230 km^2), is a tributary of the Columbia River. Some sawmills operate in this region of interior western hemlock. The Salmon River (drainage area: 1510 km^2) flows from the Monte Hills Provincial Forest (Ponderosa Pine and bunchgrass) through farmland to Shuswap Lake just downstream from the town of Salmon Arm.

Materials and methods

Taxonomic resolution and sampling procedures

Macroinvertebrates can be identified using various biological classifications (size, behaviour, functional feeding group, taxonomic composition) each of which can be related to a set of environmental variables (Corkum & Ciborowski, 1988). In this study, I chose to work with taxonomic designations because such categorizations reflect broad environmental requirements as well as the biogeography of constituent groups. Other biological classifications also could have been used to test the study hypotheses, recognising that different categorizations depend on scale of resolution. For example, some familial classifications correspond well with trophic assignments, yet there are problem groups (e.g. Chironomidae) in which animals assigned to one familial classification may have representatives belonging to several different trophic levels.

Since distributional patterns of species are a function of biotic interactions, dispersal mechanisms, environmental tolerances, and historical factors (Carter *et al.*, 1980), the likelihood of a species being present throughout a drainage basin is low. Accordingly, use of a coarse taxonomic designation is justified when benthic distributional patterns are sought on a large study scale (interbasin comparisons) (Corkum & Ciborowski, 1988). For example, Illies (1961) designated families of aquatic insects that were associated with particular river zones (rhithron, potamon) on a world-wide basis. I also chose to compare macroinvertebrate communities among drainage basins using a familial classification.

Benthic macroinvertebrate samples were taken using a modified Hess cylinder sampler (0.1 m^2) with a 1-m trailing bag (mesh size: 250 μm). Since I collected all benthic samples, variation in sampling technique was minimal. Five samples were collected along a transect and preserved with Kahle's fluid (Pennak, 1978).

In the laboratory, macroinvertebrates were sorted from the detritus, identified using a dissecting microscope and stored in 70% ethanol. Insects were identified to family level; coarser designations were used for non-insect taxa. Microcrustaceans were not retrieved from samples.

Data analyses

A total of 225 macroinvertebrate samples (3 biomes × 3 rivers/biome × 5 sites/river × 5 samples/site) was included in the analysis. A replicated, mixed model nested analysis of variance (ANOVA) (Sokal & Rohlf, 1981) was used to test for significant differences in total benthic macroinvertebrate density among biomes, among rivers nested within biomes, among site locations along rivers as well as the interaction terms.

Macroinvertebrate composition was analysed using a nested multivariate analysis of variance (MANOVA) procedure outline in the statistical package, SPSSX (Norusis, 1985). In this study, 33 dependent variables (taxa) were selected for the MANOVA using a 1% rule; absolute density (number per 0.1 m^2) was determined for each taxon. A taxon that contributed to 1% of any one of the 225 samples or 1% of the entire collection was included in the analysis.

A discriminant analysis was used to identify those taxa whose densities contributed significantly to differences among treatment effects in the MANOVA. Finally, regression analyses were performed to examine response curves of given taxa (identified from the results of the discriminant analysis) along rivers using actual river distances rather than site location.

Results

Total density

Total density of macroinvertebrates (no. 0.1 m^{-2}) was recorded for all 225 samples. Results of the nested ANOVA indicated that total density differed significantly among biomes, among rivers within biomes, among sites and in the interaction terms (biomes × sites; rivers within biomes × sites) (Table 2). The significant interac-

Table 2. Summary of a nested analysis of variance (ANOVA) test to examine the influence of biomes, rivers within biome, sites, and interaction terms on total benthic density. F_s (biome) = MS(group)/MS(subgroup); F_s (other variables) = MS(group)/MS(within). Refer to Sokal & Rohlf (1981) to calculate degrees of freedom (*df*) for nested ANOVA.

Source of variation	*df*	*SS*	*MS*	*F*	*P*
Biomes	2	363.08	181.54	10.34	<0.001
Rivers within biomes	6	105.34	17.56	32.52	<0.001
Sites	4	7.77	1.94	3.59	0.008
Biomes × sites	8	32.83	4.10	7.59	<0.001
Rivers within biomes × sites	24	126.90	5.29	9.80	<0.001
Within group	180	91.31	0.54		

tion effect indicates that differences in total density were not spatially consistent and where consistent longitudinal among-river patterns were found, they were biome-specific.

There were no significant differences in total density of macroinvertebrates between grassland and EDF biomes (Student-Newman-Keuls (SNK) multiple comparison test, $P \geq 0.05$). By chance, river sites in these two biomes were sampled during periods of low flow.

The total density at river sites for the mountainous (MCF) region was noticeably less than for either grassland or EDF sites (Fig. 2). In the MCF biome, the Cottonwood River (which was in flood when sampled) exhibited the lowest benthic densities. The mean daily discharge for the Cottonwood River at Cinema (36 km downstream from site 5) was 114 (an increase in flow of 67% from the previous day) and 137 $m^3 s^{-1}$ (May 22 and 23, respectively) when sites were sampled compared with 78.9 $m^3 s^{-1}$, the mean daily discharge for May (Environment Canada, Water Survey Branch). The Salmo River near the town of Salmo (site 5) exhibited near normal flows [105 $m^3 s^{-1}$ (May 18) and 88.6 $m^3 s^{-1}$ (May 19)] when sampled compared with 97.5 $m^3 s^{-1}$, the mean daily discharge for May. The Salmon River with lower than mean annual flows when sampled [site 5: mean daily discharge, May 21, 7.13 $m^3 s^{-1}$; mean daily discharge for the month, 8.72 $m^3 s^{-1}$] also had low benthic densities compared with sites in the EDF and grassland biomes.

Despite significant differences in total benthic density among river sites, there were no discernible monotonic patterns in total density along river lengths (Fig. 2). Within the EDF biome, benthic density was lower for sites on the Credit River

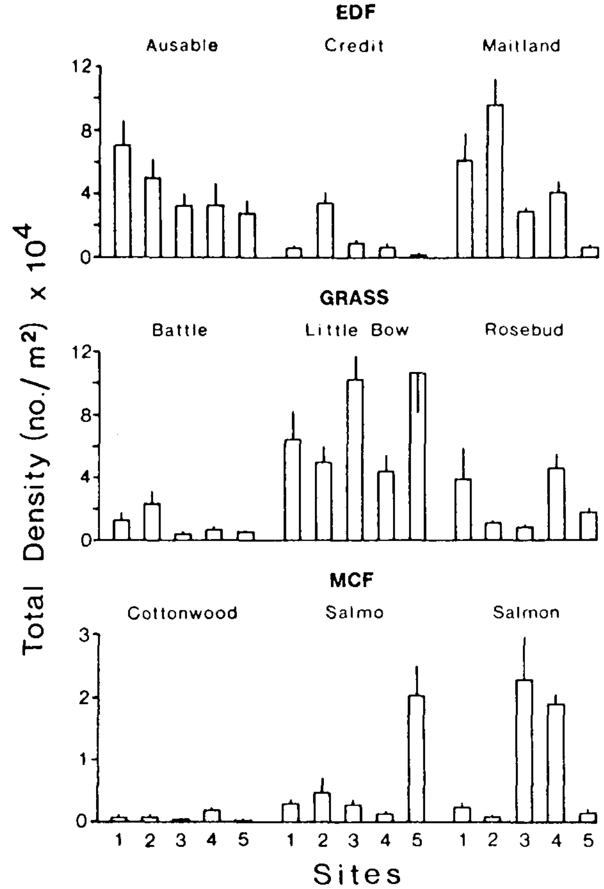

Fig. 2. Mean and standard errors of benthic macroinvertebrate density ($n = 5$ samples) for each of five sites on rivers within each of the three biomes. Sites are numbered from upstream (site 1) to downstream (site 5) locations.

Table 3. Summary of the nested multivariate analysis of variance to examine the influence of biomes, rivers within biomes, sites, and interaction terms on taxonomic composition.

Source of variation	Wilks' lambda	*F*	*P*
Biomes	0.00375	68.767	<0.001
Rivers within biomes	0.00398	6.897	<0.001
Sites	0.01758	7.891	<0.001
Biomes × sites	0.00027	8.310	<0.001
Rivers within biomes × sites	0.00000	6.926	<0.001

than sites on either the Ausable or Maitland rivers (Fig. 2). The Credit flows through deciduous forests, whereas the other two EDF rivers drain agricultural land. Within the grasslands, benthic density at Battle River sites was lower than at sites on the Little Bow or Rosebud rivers (Fig. 2). Riparian vegetation was noted at sites along the Battle, whereas cropland reached the river channel at most of the other river sites in the grasslands. Within the MCF biome, benthic densities at Salmon River (sites 3 and 4) and Salmo River (site 5) were about 10-fold higher than other montane river sites (Fig. 2). Salmo River site 5 was heavily forested; pine cones were present in the benthic samples. Salmon River sites 3 and 4 were located within pastureland.

Taxonomic composition

Results of the nested MANOVA indicated that there were significant differences in macroinvertebrate community composition among biomes, among rivers within biomes, among sites and the interaction terms (biomes × sites; rivers within biome × sites) (Table 3). The highest F-statistic was obtained for biomes (68.767) (Table 3) indicating that differences in density of individual taxa were most pronounced among the three biomes compared with the other sources of variation. The significant interaction between biomes and sites indicates that differences between the main effects were not consistent among all taxa. Accordingly, discriminant analysis was used to identify which taxa differed most consistently in benthic density among biomes and from site to site along rivers.

The first three discriminant functions were significant in that they contributed substantially to group differences (Table 4). A total of 19 taxa contributed (i.e., their densities were significantly correlated with the three discriminant functions) to the (biome × site) group interaction. The first discriminant function (DF1) explained most

Table 4. The correlation (corr) coefficients between the discriminant functions and each dependent variable (taxon). Probability of obtaining an observed correlation if the true value is zero (*$p < 0.01$). Taxa are listed in order of the strength of their correlations. Only those taxa that exhibit significant correlations with one of the three functions are listed.

Variable	Function 1 corr	Function 2 corr	Function 3 corr
Tricladida	−0.369*	−0.062	0.211*
Leptophlebiidae	−0.345*	−0.116	−0.366*
Tricorythidae	0.339*	0.172	0.148
Elmidae	−0.321*	0.005	−0.112
Brachycentridae	−0.305*	−0.087	0.075
Pulmonata	−0.236*	0.230*	0.192
Corixidae	−0.230*	0.105	0.177
Tipulidae	−0.218*	0.181	−0.190
Heptageniidae	0.207*	0.026	−0.226*
Ephemerellidae	−0.164	0.358*	−0.132
Hydropsychidae	−0.054	0.319*	−0.105
Amphipoda	0.181	−0.250*	−0.320
Tabanidae	−0.083	0.238*	0.072
Rhyacophilidae	−0.025	−0.215*	−0.045
Empididae	−0.018	0.209*	0.058
Limnephilidae	0.051	0.207*	−0.262
Psephenidae	−0.012	−0.134	−0.344*
Hirudinea	0.057	−0.049	−0.305*
Lepidostomatidae	−0.189	0.179	−0.274*
Wilks' lambda	0.00027	0.00171	0.00872
Probability	<0.0001	<0.0001	<0.0001
% Variance explained	31.23	23.75	15.38

(31.2%) of the between-group variability. Discriminant function correlations were used to determine the individual contribution of a taxon to each discriminant function. Taxa that had significant ($P < 0.01$) positive correlations with the first discriminant function were mayflies, Tricorythidae (0.339) and Heptageniidae (0.207). Tricladida (−0.369), Leptophlebiidae (−0.345), Elmidae (−0.321), Brachycentridae (−0.305), Pulmonata (−0.236), Corixidae (−0.230), and Tipulidae (−0.218) had significant negative correlations with DF1. The second and third discriminant functions, although significant, explained a low proportion of between-group variability.

Benthic differences among biomes and river locations

Differences in macroinvertebrate benthic density among river sites in the three biomes are presented for the nine taxa that best distinguished the biome × site interaction (i.e. were significantly correlated with DF1). There was considerable variation in benthic density of the nine taxa among biomes (Table 5). Results of the SNK multiple comparison tests showed that mean density of elmids, corixids, and tipulids differed among each of the three biomes. Highest mean densities of elmids and corixids occurred in the EDF; highest mean densities of tipulids occurred in the MCF. The mayfly families, Leptophlebiidae and Heptageniidae, were prevalent in the two forested biomes. Highest densities of Tricladida (flatworms) and the mayfly, Tricorythidae, occurred at EDF sites; there were no differences in mean densities of these organisms at grassland or mountain sites. Pulmonate snails were most abundant at grassland and EDF sites. Brachycentrid caddisfly larvae were most abundant at grassland sites.

Table 5. Results of the Student-Newman-Keuls multiple comparison tests ($p < 0.05$) used to compare mean densities among biomes (EDF, eastern deciduous forests; GRS, grasslands; MCF, mountains) for those taxa that were significantly correlated with DF1. Biomes are arranged from lowest to highest mean density for each taxon. Biomes linked by underlines are not significantly different from one another.

Taxon	Biome		
Elmidae	MCF	GRS	EDF
Corixidae	MCF	GRS	EDF
Tipulidae	GRS	EDF	MCF
Leptophlebiidae	GRS	MCF	EDF
Heptageniidae	GRS	EDF	MCF
Tricladida	GRS	MCF	EDF
Tricorythidaex	MCF	GRS	EDF
Brachycentridae	MCF	EDF	GRS
Pulmonata	MCF	GRS	EDF

More taxa differed significantly in mean density among sites in the EDF than in the other two biomes (Table 6). In the EDF, eight of nine taxa exhibited significant differences in mean density among river sites; mean density of tipulids did not differ among river sites. Overlap in mean density of leptophlebiids (sprawling mayflies), elmids (riffle beetles) and corixids (water boatmen) occurred among EDF river sites; highest mean densities occurred at upstream and mid-stream locations. There were five taxa (Brachycentridae, Heptageniidae, Pulmonata, Tricladida, Tricorythidae) in the EDF for which no significant differences among mean density occurred at four of five sites and a fifth, isolated site exhibited either the highest or lowest mean value.

Few differences in mean density of taxa among taxa were noted in the grasslands (Table 6). No differences in mean density were noted among river sites for six of nine taxa. For the remaining three taxa (Heptageniidae, Pulmonata, and Tipulidae), there were no significant differences in mean density among four of five sites, and the fifth, isolated upstream site (1 or 2) exhibited the highest mean densities (Table 6).

At mountainous river sites, significant differences in mean density were noted for four of nine taxa. The ranking of sites with respect to abundance of taxa in the MCF biome were unrelated to the patterns observed for these taxa in the other two biomes. Highest mean densities for taxa that showed significant differences among site lo-

Table 6. Results of the Student-Newman-Keuls multiple comparison tests ($p < 0.05$) used to compare mean densities among river sites in each of three biomes (EDF, GRASS, MCF) for those taxa that were significantly correlated with DF1. River sites are arranged from lowest to highest mean density for the corresponding taxon. Sites linked by lines are not significantly different from one another. Sites are numbered from upstream (site 1) to downstream (site 5).

Taxon	EDF site					GRASS site					MCF site				
Tricladida	5	4	1	3	2	N.S.					N.S.				
Tricorythidae	2	1	3	5	4	N.S.					N.S.				
Leptophlebiidae	4	5	3	2	1	N.S.					N.S.				
Corixidae	5	1	4	3	2	N.S.					N.S.				
Brachycentridae	4	5	3	1	2	N.S.					1	2	5	3	4
Elmidae	5	4	1	2	3	N.S.					2	5	1	3	4
Pulmonata	1	5	4	3	2	5	3	2	4	1	N.S.				
Heptageniidae	2	3	1	4	5	3	1	4	5	2	3	5	2	1	4
Tipulidae	N.S.					2	4	5	3	1	2	1	3	5	4

cation in the MCF (Elmidae, Brachycentridae, Tipulidae, Heptageniidae) occurred at the site 4 location along rivers. Riffle beetles, Elmidae, and the caddisfly, Brachycentridae, exhibited highest benthic densities at mid-river locations (sites 3 and 4). Significant differences in mean density of tipulids occurred among many river site locations.

Distributional patterns along rivers

Although five sample sites were designated along each river, corresponding site numbers among rivers did not always reflect similar distances from site to river source (Fig. 1). For example, site 5 on the Cottonwood River was an equivalent distance downstream to site 2 on the Little Bow River (Fig. 1). In addition, sites were sampled for a greater distance along grassland rivers than along EDF or MCF rivers. Accordingly, regression analyses were performed to examine response curves of given taxa (the 9 taxa that were significantly correlated with DF1; Table 4) along a river using actual river distances rather than site location (number) for each of the three biomes (Table 7).

Most taxa exhibited no significant relationship between mean density and river length within the three biomes. Significant relationships were detected in only four cases (Leptophlebiidae, EDF:

Table 7. Summary of multiple regression analysis to test for the relationship between mean density of taxa and actual river distance for the eastern deciduous forest (EDF), grassland (GRASS) and mountain (MCF) biomes. A, intercept; B, regression coefficient; SE, standard error of the estimate (in parenthesis); Cum R^2, cumulative coefficient of determination. Equations take the form: Ln (density) = $A + B_1$ [Ln (site distance from source)] $+ B_2$ [Ln (site distance from source)^2]. Probability: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Data are presented for only those taxa indicating significant relationships.

Taxon	Biome	A	B_1 (SE)	B_2 (SE)	Cum R^2
Leptophlebiidae	EDF	3.91	− 0.85 (0.32)*		0.35
Pulmonata	GRASS	4.49	− 0.78 (0.26)**		0.41
Tipulidae	GRASS	4.40	− 1.84 (0.35)***	0.20 (0.04)***	0.41
Tipulidae	MCF	− 0.28	0.42 (0.17)*		0.31

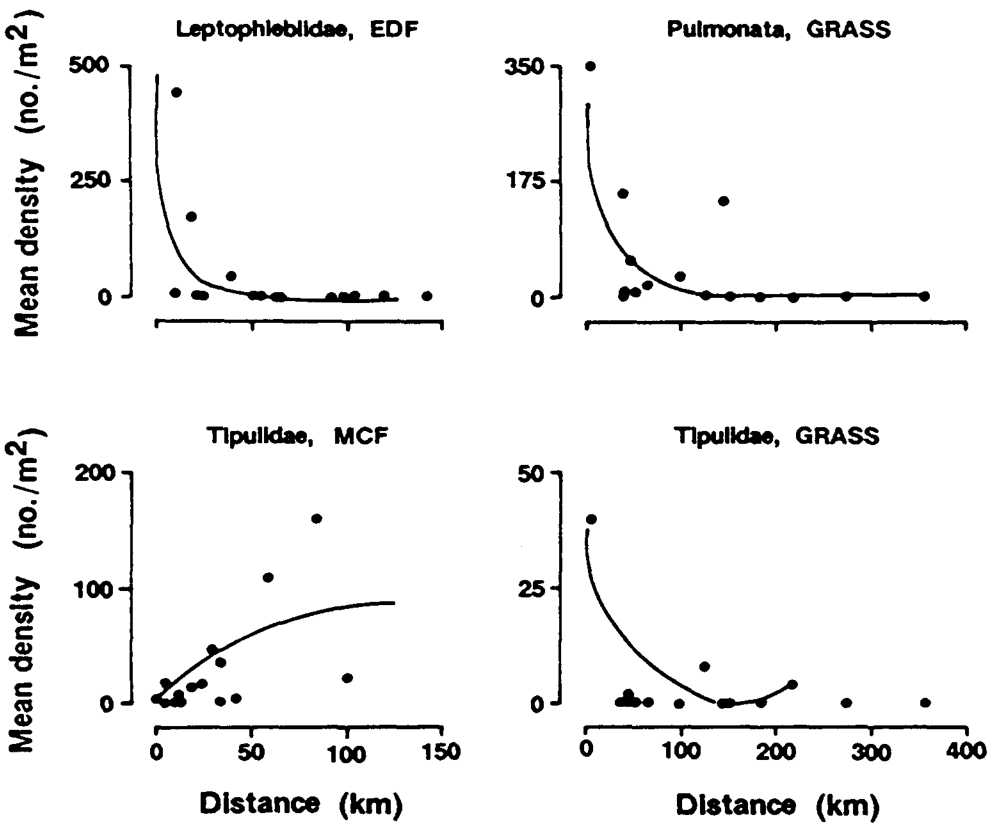

Fig. 3. Significant relationships between mean density and actual river distance for Leptophlebiidae, EDF ($R^2 = 0.35$, $p < 0.05$); Pulmonata, GRASS ($R^2 = 0.41$, $P < 0.01$); Tipuliidae, GRASS ($R^2 = 0.41$, $P < 0.001$) and EDF ($R^2 = 0.31$, $P < 0.05$).

Pulmonata, grasslands; Tipulidae, grasslands and MCF) (Table 7, Fig. 3). The mean density of Leptophlebiidae (EDF) and Pulmonata (grassland) decreased curvilinearly with increasing river distance. A second-order regression model provided the best estimate of relationships between density of tipulids and distance from source in the grasslands with elevated densities upstream and a presence at mid-river reaches. In contrast, mean density of tipulids increased curvilinearly with increasing distance downstream in the mountains. In all four cases, mean benthic densities were low and organisms were frequently absent from samples (Leptophlebiidae larvae were present in 4 of 15 EDF samples; Pulmonata, $^8/_{15}$ grassland samples; Tipulidae, $^4/_{15}$ grassland samples and $^{11}/_{15}$ MCF samples). Accordingly, the relationships described for the density of these taxa and river distance may be spurious because the described association depended on high densities from samples obtained from one or two sites.

Discussion

This study was designed to determine if spatial distributional patterns of macroinvertebrates were more similar at river sites in drainage basins within biomes than among biomes regardless of site location along a river. Vannote *et al.* (1980) predicted a consistent change in the relative abundance of functional feeding groups of macroinvertebrates associated with the energy inputs from outside or within the river system and the downstream transport of organic matter. In contrast, the biome dependency hypothesis (Ross, 1963; Corkum, 1989) suggests that similar assemblages of macroinvertebrates will occur along rivers if the drainage basin occurs within a single biome. In this study, the greatest differences in taxonomic composition occurred among biomes. Total macroinvertebrate densities were equivalent between EDF and grassland sites. However, total density was substantially lower at the montane sites than at sites in the other two biomes.

According to the continuum concept, river ecosystems originate in heterotrophic headwaters where the energy base is dominated by allochthonous inputs from overhanging riparian vegetation. Rivers shift into an autotrophic middle section and end in a heterotrophic region downstream (Vannote *et al.*, 1980). In contrast to the typically viewed EDF drainages, which have forested headwaters and associated autumnal leaf fall (Vannote *et al.*, 1980), the Ausable and Maitland rivers originate in farmland and flow into forested river valleys. The grassland biome sites were all within agricultural areas (cropland and/or pastureland). Within the MCF biome, the steep gradient Cottonwood and Salmo rivers drained hemlock forests; the Salmon River drainage had woodlots scattered throughout farming communities. Of the three biomes, land use patterns were most varied in the EDF.

Significant differences in total benthic density of macroinvertebrates occurred among biomes, among river sites, among rivers within biomes as well as the interaction effect of biome and site location along a river. Although there were no significant differences in total benthic density between EDF and grassland river sites, total benthic density was substantially lower at mountainous river sites than at sites in the other two biomes. One factor that contributed to low total density in the MCF was the flooding of the Cottonwood River when samples were taken. Floods will reduce detrital particle size, disperse particles in the river (Richardson, 1991) and induce catastrophic drift of invertebrates by scouring the streambed (Waters, 1972). However, the low levels of macroinvertebrate density in the other montane rivers suggest that rivers in the MCF are characteristically lower in productivity than rivers in the EDF or GRASS biomes owing to differences in soil type, bedrock, vegetation and climate (Danks, 1979).

The mean annual temperature is similar between the two forested biomes, however the EDF rivers receive more rain than the montane region (Table 1). Coniferous needles of the montane biome fall throughout the year and differ in texture from the autumn leaf fall of deciduous forests. These differences in climate and vegetation as well as variation in altitude, river gradient, and canopy cover contributed to the amount and quality of food resources available to the macroinvertebrate fauna (Wiggins & Mackay, 1978). Thus, differences in total density between the forested biomes were not unexpected.

Although the grassland biome had fewest degree days (above 10 °C) of the three biomes (Table 1), the sunlight and nutrient levels of the unshaded, open rivers flowing through enriched agricultural areas may have contributed to the higher levels of benthic densities in these rivers compared to forested areas in other biomes. The lowest total benthic density in the grasslands was recorded for the downstream sites of the Battle and Rosebud (site 5), where trees and shrubs occurred along stream banks.

Variation in total density also was noted among rivers within biomes. Such variation can be accounted for in the different land use practices. I (Corkum, 1990) showed that lowest and highest mean densities of macroinvertebrates in the EDF occurred in forested (Credit River sites) and farmland areas, respectively; river sites in mixed land use areas (forested river valleys in farmland areas) had intermediate values of benthic densities. Within the grasslands, highest benthic densities were recorded at river sites that flowed through open agricultural areas. The lowest benthic densities in the grasslands were recorded for those river sites with riparian vegetation. In the MCF, high densities were noted at Salmon River sites, which were located in pastureland, and at Salmo River site 5, where pine cones were common in samples.

Density and biomass values of benthic macroinvertebrates are often greater in open, unshaded areas than in forested reaches with overhanging canopies, reflecting potential differences in abundance and production of benthic primary producers. Erman *et al.* (1977, cited in Gregory, 1983) showed a similar relationship in clearcut and forested river sites in California. In an interbiome comparison study, other workers (Minshall *et al.*, 1983; Bott *et al.*, 1985) showed that highest benthic densities occurred in the EDF biome (Michigan river sites) where the surrounding land use was principally urban and agricultural. Others (Woodall & Wallace, 1972; Molles, 1982) also have demonstrated a correspondence between some aspect of the macroinvertebrate community and vegetation type within drainage basins.

My results revealed that the greatest differences in taxonomic composition occurred among biomes, although significant differences also occurred for all other sources of variation examined (Table 3). Despite these faunal differences among biomes, Psephenidae (EDF) was the only taxon examined that was endemic to a biome.

Differences in benthic density of taxa occurred more often along river sites in the EDF than along river sites in the grassland or MCF biomes (Table 6). This trend was probably a function of the different land use areas in drainage basins of the EDF biome. Habitat (substrate) diversity at forested river sites in the EDF also may result in a more patchy (and variable) distribution of macroinvertebrates than at grassland river sites where land use and the riverine substrate is more homogeneous.

There is a strong association between stream characteristics and the surrounding land. For example, farms in the study areas were on flat or more gently rolling hills compared to forested areas on steeper gradients (Fig. 1). Typically, more nutrients are released into receiving waters from farmland than from forested areas (Likens & Borman, 1974). Riparian vegetation controls to a large extent the rates at which sediments and nutrients enter receiving waters (Johnson *et al.*, 1969; Schlosser & Karr, 1981; Peterjohn & Correll, 1984). Thus, the characteristic biome vegetation (and in disturbed areas, the land use) influences the transfer rate of materials and energy to the river and the productivity of the receiving waters. Moreover, land use changes and vegetative succession in a basin also affect the frequency of habitat-disturbing events in rivers (Frissell *et al.*, 1986). Thus, one might anticipate changes in the lotic invertebrate community in response to changes or disturbances in the climax vegetation that characterizes a biome.

Only three taxa (Leptophlebiidae, EDF; Pulmonata, GRASS, Tipulidae, GRASS, MCF) showed significant differences between benthic density and actual river distance. In all cases, mean densities of taxa were low, organisms were absent from many samples, and the variability explained by the regression (R^2) was low (Fig. 3). Often the significance of the relationships depended on elevated densities at one or two sites. The trends observed between benthic density of taxa and actual river distance were not consistent among biomes. For example, the density of Pulmonata (snails) was elevated in headwaters, but decreased with increasing river distance from source only in the grassland biome. Snails were also present in the other biomes, but their density was unrelated to river distance. The relationships described between density of Tipulidae and river distance were reversed between two biomes, grasslands, and MCF (Fig. 3). Thus, empirical relationships developed between density and taxa for one biome were not applicable to another biome. Patterns of taxon-specific abundance, therefore, were biome-dependent.

Macroinvertebrate community composition may be a function of both longitudinal gradients and lateral (vegetation away from the river channel) dimensions (Ward, 1989). I expect that the relative influence of these two components on the lotic macroinvertebrate community will vary with river size and among biomes. Many aspects of the lotic ecosystem have been found to correlate with the spatial distribution of macroinvertebrates. On-site, hydrological features, riparian vegetation, characteristic climax vegetation of biomes as well as land use practices within drainage basins all interact to account for the distributional patterns of lotic macroinvertebrates. My findings suggest that the impact of these features is hierarchical in nature, and that the biome level of organization is the most basic structuring force.

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