PRIMARY RESEARCH PAPER

Environmental variables interact across spatial scales to structure trichopteran assemblages in Ouachita Mountain rivers

Heather S. Galbraith · Caryn C. Vaughn ·
C. Kate Meier

Abstract An important goal in aquatic ecology is to determine the interacting variables that regulate community structure; however, complex biotic and abiotic interactions coupled with the significance of scale have confounded the interpretation of community data. We evaluated stream and riparian habitat features in southeastern Oklahoma, USA at a range of spatial scales from local, in-stream variables to large-scale, regional characteristics to address the following questions: (1) How much variation in trichopteran community composition can be attributed to local, regional, and spatial variables? and (2) What environmental variables are most important in determining trichopteran community structure? We collected data on caddisfly community structure, local and regional environmental variables, and spatial location on the landscape from 25 sites in four rivers. We analyzed these data using canonical correspondence analysis (CCA) and variation partitioning. Our analysis explained approximately 60% of the variation in caddisfly community composition. We found that local and regional environmental variables were near equal in importance in governing caddisfly communities, with each accounting for approximately a quarter of the explained variation. Although pure spatial variables were less important, the amount of variation shared among spatial variables and local and regional variables was substantial, indicating that biogeographic history is also key to understanding caddisfly distributions. We also found a strong influence of human landuse (i.e., percent of land in agriculture, distance to roads) on caddisfly community composition. Our study indicated that communities are influenced by factors across scales, and that bioassessments should focus on not only local habitat conditions, but also incorporate larger-scale factors.

Keywords Caddisfly communities · Trichoptera · Spatial scale · Variation partitioning · Geographic information system (GIS)

Introduction

A primary challenge facing aquatic ecologists is determining the causal factors underlying the distribution and abundance of organisms. This problem arises due to the fact that the processes that regulate stream communities vary across spatial and temporal scales, and range from local biotic interactions to large-scale biogeographic history (Tonn, 1990; Poff, 1997). The role of local, instream environmental variables (e.g., depth, substrate size, current velocity)

H. S. Galbraith (✉) · C. C. Vaughn · C. K. Meier
Oklahoma Biological Survey and Department of Zoology,
University of Oklahoma, 111 East Chesapeake St,
Norman, OK 73019, USA
e-mail: hgalbraith@ou.edu

in structuring stream communities has been well studied (Minshall, 1984; Degani et al., 1993; Voelz et al., 1994; Townsend et al., 1997; Fairchild & Holomuzki, 2002). In recent years, researchers also have begun focusing on how larger scale regional and landscape-scale factors (e.g., annual discharge patterns, watershed area, landuse) influence aquatic communities (Corkum, 1992; Richards et al., 1997; Sandin & Johnson, 2000; Parson et al., 2003; Weigel et al., 2003). Finally, patterns of species distribution and abundance may also be the result of historic events (i.e., past environmental constraints and biotic interactions) and connections among habitats that either facilitate or inhibit dispersal (Borcard et al., 1992; Magnan et al., 1994; Magalhaes et al., 2002; Murphy & Davy-Bowker, 2005). Thus, in some cases the occurrence of an organism at a particular spatial location is not a reflection of local or larger-scale environmental variables, but rather an historical artifact.

It can be very difficult to discriminate between patterns in species distributions caused by local environmental factors, regional-scale factors, and biogeographic history (i.e., location on the landscape). A few studies have examined how local and regional variables simultaneously influence aquatic communities (Levin, 1992; Richards et al., 1996; Palmer et al., 2000; Heino et al., 2003; Weigel et al., 2003), and even fewer have incorporated spatial components (Li et al., 2001; Sponseller et al., 2001; Borcard et al., 2004). However, recently researchers have used statistical variation partitioning techniques to address this issue (Pinel-Alloul et al., 1995; Sandin and Johnson, 2000). This approach partitions the variation in a response matrix (such as the abundance of a group of organisms across a suite of sites) into the variation explained by different matrices of explanatory variables (such as habitat variables, spatial variables, etc.). This approach allows one to examine simultaneously the variation in the distribution and abundance of a group of organisms that are due to factors operating at different spatial scales.

We used the variation partitioning approach to examine factors influencing caddisfly community structure across environmental and spatial scales. Caddisflies (Trichoptera) are a large order of aquatic insects that perform important functions in streams including nutrient cycling (Benke & Wallace, 1980), maintaining streambed stability (Cardinale et al.,

2004), and facilitating colonization by other benthic invertebrates (McCabe & Gotelli, 2003). Caddisflies are significant components of aquatic food webs, serving as a primary food source for many fish and invertebrates (Wiggins, 1996). In addition, because of their diversity and varying sensitivities to aquatic conditions they are often used for biomonitoring and assessing anthropogenic impacts on aquatic ecosystems (Moulton & Stewart, 1996 and references therein, Barbour et al., 1999). Thus, understanding what governs the distributions of caddisflies is both ecologically and economically important.

Numerous studies have examined the role of local biotic interactions in regulating caddisfly community structure (Wallace, 1975; Malas & Wallace 1977; McAuliffe, 1984; Hart, 1985; Cardinale et al., 2002) or have provided detailed descriptions of the ecology of a few common and abundant species, particularly the net-spinning hydropsychid caddisflies (Williams & Hynes, 1973; Hildrew & Edington, 1979; Feminella & Resh, 1990; Voelz et al., 1994). More recently, other studies have examined how regional and landscape-scale factors govern caddisfly distribution (Lancaster et al., 2003; Kilbane & Holomuzki, 2004). Our study is the first to simultaneously examine the influence of local environmental factors, regional factors, and biogeographic history in determining caddisfly community structure. We addressed two questions: (1) How much variability in trichopteran communities can be attributed to local and regional environmental variables and spatial location on the landscape? and (2) Of these variables, which are most important for determining trichopteran community structure?

Materials and methods

Study area

For our study area we chose a biogeographic area known for its relatively pristine rivers and high aquatic biodiversity, the Ouachita Mountains of east-central Oklahoma and west-central Arkansas, USA (Master et al., 1998; Moulton & Stewart, 1996). This area is a center of speciation for both terrestrial and aquatic organisms including fish, crayfish, unionid mussels, and salamanders as well as almost half (13) of the endemic species of caddisflies found in the

Interior Highlands (Mayden, 1985; Moulton & Stewart, 1996). The Kiamichi-Little River basin is one of the major river basins in the Ouachita Mountains region with a drainage area of approximately 15,540 km^2 (United States Department of Agriculture, 1999) that feeds into the Red River. This study was conducted in 4 rivers in the Kiamichi-Little River Basin (Fig. 1), the Kiamichi (272 km long, drainage area of 4,660 km^2), Little (350 km long, drainage area of 10,880 km^2), Mountain Fork (drainage area of 2,240 km^2), and Glover (drainage area of 875 km^2; United States Department of Agriculture, 1999). Landuse in the region is primarily forest with some agriculture and silviculture (Rutherford et al., 1987; United States Department of Agriculture, 1999). The rivers are relatively unimpacted compared to others in the region and globally, due to their location in a remote and rugged area with low human population density (Master et al., 1998).

Caddisfly sampling

Caddisflies were collected between June and September in summer 1997 from 25 riffles across the four
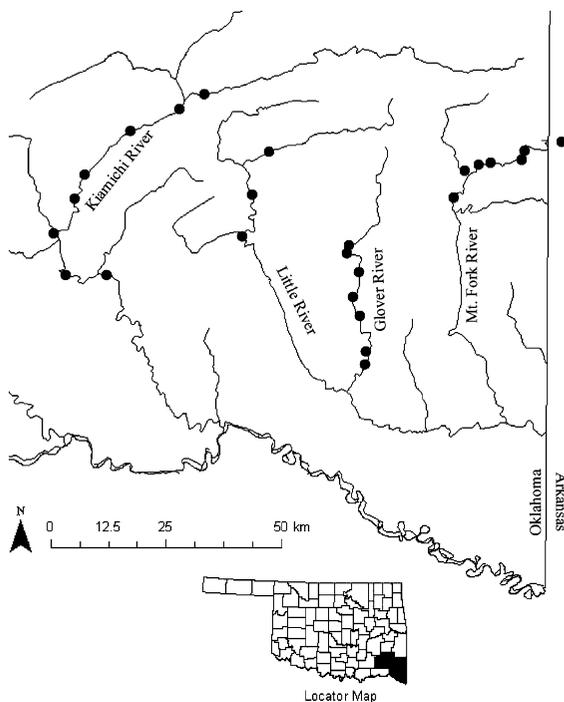
Fig. 1 Sampling sites in four rivers in southeastern Oklahoma, USA

rivers (Fig. 1). A suite of riffles were selected *a priori* to be equally distributed along and among the rivers; however, within this suite we were restricted to sampling riffles that could be accessed by foot or canoe (Fig. 1). Since impoundments are known to change community composition of aquatic organisms (Baxter, 1977), we did not sample below mainstream reservoirs and samples were taken at least 20 km above reservoirs. We collected three, randomly-placed, replicate Surber samples (30 cm × 30 cm) from each riffle. Samples were preserved in 70% ethanol and larval caddisflies were identified to genus. We felt genus was the most biologically relevant taxonomic level for our study: within this region, functional roles and habitat requirements of species within genera are similar. In addition, in many cases identifying caddisflies to species would have required rearing larvae from different riffles to adults, which was beyond the scope of this study.

Local-scale variables

Local-scale environmental variables were measured at each sampling site at the time of caddisfly collection (Table 1). Current velocity and depth were measured at 1-m intervals across the width of each riffle (site) with a Marsh-McBirney digital flow meter and pole. Substrate type and cover were visually estimated within five, 0.25 m^2 quadrats randomly placed within the riffle (Vaughn & Spooner, 2006). Using the Wentworth scale, substrate was categorized as percent boulder, cobble, gravel, sand, and silt. Visual estimates of percent algae, detritus, plant material, and riparian shade cover were estimated in each quadrat (Vaughn & Spooner, 2006).

Regional-scale variables

We measured regional-scale environmental variables believed to be important to invertebrate communities (Table 1; Resh & Rosenberg, 1984). In this study, regional variables were designated as those variables influencing a kilometer or more of river area. Discharge was calculated using the United States Geological Survey (USGS) daily streamflow data from gauging stations on each river for 1997. Other discharge variables, including average discharge

Table 1 Local and regional-scale variables estimated at each sampling site

Variables	Mean	Range
Local-scale		
pH	8.1	7.6–9.2
Conductivity	51.7 μS	36.3–98.7 μS
Water temperature	29.6°C	25.6–34.7°C
Current velocity	0.26 m/s	0.09–0.43 m/s
Depth	11.2 cm	7.4–21.4 cm
Substrate composition[a]		
% Boulder	8.0	0–37.5
% Cobble	51.8	21.9–90.0
% Gravel	33.1	0–68.0
% Sand	2.9	0–21.1
Algal composition[a]		
% Diatoms	30.1	0–68.5
% Detritus	8.7	0–21.9
% Moss	21.1	0–50.2
Shade[a]	15.2	0–90.0
Regional-scale		
Surrounding land use[a]		
% Deciduous forest	55.0	45.8–67.1
% Evergreen forest	26.1	16.4–35.2
% Mixed forest	11.0	0–22.4
% Hay/pasture	5.0	0–19.8
% Row crop	6.6	0–32.5
Watershed area upstream of site	142,634 m^2	30,470–276,808 m^2
Proximity to roads	102.3 m	6.4–419.5 m
Stream gradient	0.0011 m/m	0–0.0027 m/m
Average discharge	20.5 m^3/s	14.1–40.2 m^3/s

[a] values arcsine transformed prior to analysis

across 5 and 10 years, coefficient of variation of discharge across 1, 5, and 10 years, and number of days with flow less than or equal to 0.28 m^3 per second were eliminated from the analysis due to collinearity with the yearlong average discharge.

We used surrounding land use as a gross estimate of large-scale riparian characteristics. Land use was calculated using GIS (ArcGIS 9.0, ESRI Inc. Redlands California) and USGS 30 m × 30 m National Land Cover Data for Oklahoma. Polygon buffers were created 90 m wide (extending 30 m laterally on either side of the 30 m stream) and 1,000 m upstream around each sampling point, and percent land use was calculated within each polygon; forested riparian

buffers narrower than this have been suggested to negatively impact aquatic fauna (Castelle et al., 1994; Harding et al., 1998). Surrounding geology was initially included as a regional variable, but was eliminated due to limited variation among the sampling sites (i.e., all sites fell within similar geologic formations).

The incidence and proximity of roads has been shown to be a strong predictor of anthropogenic stress (Brown & Laband, 2006). We measured the distance of each sampling point to the nearest road using ArcGIS 9.0 and 1:100,000 scale road maps from the Digital Atlas of Oklahoma (Rea & Becker, 1997) and the digital database GeoStor (http://www.cast.uark.edu/cast/geostor/). Watershed area upstream of each sampling site was calculated using the hydrology extension in ArcGIS 9.0, a 1:100,000 digital elevation map (DEM) with 60 m × 60 m cells, and a flow direction map of the state of Oklahoma. Stream gradient also was obtained using GIS and the same DEM as above. Elevation was measured every 100 m for 1,000 m upstream of each sampling site. Distance upstream of each sampling site was plotted against the corresponding elevation and stream gradient was estimated by the slope of the regression line fitted to the points.

Spatial variables

We used two categories of spatial variables in our analyses: geographic location on the landscape and relative position in a stream network. A matrix of geographic coordinates was obtained with a cubic trend surface polynomial to estimate the parameters of a trend surface regression equation,

$$Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3,$$

where X and Y are orthogonal coordinates representing latitude and longitude, and Z is caddisfly distribution and abundance information in the form of ordination scores (Borcard et al., 1992; Magnan et al., 1994; Vaughn & Taylor, 2000; Vaughn & Spooner, 2006). This equation is a representation of how caddisfly communities vary over the array of X and Y coordinates. The trend surface analysis allows for the investigation of linear relationships among

sites, but also allows for more complex patterns to be represented by the quadratic and cubic terms structure (Legendre & Legendre, 1998).

We used a hierarchical network analysis as an estimate of river interconnectivity and potential dispersal pathways among rivers. We created a tree representing the connectivity of all of the streams in the study back to a common root river (the Red River), and each stream in the tree received a unique node number. We scored the relative position of each site in a stream network by the sequence of nodes taken from the direct path between a given sampling site and the root of the hydrographic tree; we then used this information to construct a locality-by-nodes matrix (Magnan et al., 1994; Vaughn & Taylor, 2000; Vaughn & Spooner, 2006). The spatial matrix used in our analyses consisted of the terms from the cubic trend regression model and the locality-by-nodes information.

Variation partitioning

Densities of all caddisfly genera were log transformed $(y(' = \ln(y + 1))$ (Sokal & Rohlf, 1995). Percent substrate type, algal cover, percent shade, and land use were arcsine transformed to reduce the effects of outliers (Sokal & Rohlf, 1995). Rare species (fewer than five individuals in the dataset) were removed from the analysis (Table 2). We acknowledge the debate over removing rare species from data analyses (Cao et al., 1998; Marchant, 1999); however only eight total individuals were removed from our dataset, and we feel that this number is small enough to have minimally impacted our results.

We examined the variation in caddisfly assemblage structure associated with local, regional, and spatial variables, and shared variation among these components, using variation partitioning (Borcard et al., 1992). Our data were grouped into four

Table 2 Caddisfly densities (#/m^2) in each of four rivers considered in this study

Genera	Glover		Kiamichi		Little		Mountain Fork	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Brachycentridae *Brachycentrus*[a]	0	0	0.4	0.4	0	0	0	0
Glossosomatidae early instars	125.6	119.1	93.3	50.8	1.2	1.2	3.1	2.0
Glossosomatidae *Protoptila*	103.5	96.5	105.8	33.8	2.4	2.4	2.6	1.7
Helicopsychidae *Helicopsyche*	185.6	86.8	10.3	3.0	93.3	25.1	390.1	250.8
Hydropsychidae *Cheumatopsyche*	514.1	364.9	429.7	274.8	52.6	13.3	286.5	109.5
Hydropsychidae early instars	418.3	254.4	558.4	232.8	15.5	8.6	239.4	133.3
Hydropsychidae *Hydropsyche*	633.6	392.9	636.0	309.0	16.7	9.6	310.1	158.0
Hydropsychidae *Macrostemum*	5.6	4.5	885.4	366.6	4.8	3.2	84.1	44.1
Hydroptilidae early instars[a]	0.5	0.5	0	0	0	0	0	0
Hydroptilidae *Hydroptila*	26.7	13.6	283.5	134.7	4.8	2.4	47.7	16.2
Hydroptilidae *Mayatrichia*[a]	0	0	0	0	0	0	0.5	0.5
Hydroptilidae *Metrichia*[a]	0	0	0.4	0.4	0	0	0	0
Hydroptilidae *Oxyethira*[a]	0	0	0	0	1.2	1.2	1.0	0.7
Lepidostomatidae *Lepidostoma*	0	0	0	0	0	0	41.5	25.7
Leptoceridae *Ceraclea*	1.5	1.5	4.5	3.0	0	0	11.8	9.5
Leptoceridae early instars	9.7	5.8	3.6	1.4	0	0	0.5	0.5
Leptoceridae *Nectopsyche*	0.5	0.5	3.6	2.1	0	0	24.6	16.8
Leptoceridae *Oecetis*	92.3	34.2	76.7	33.1	1.2	1.2	95.9	56.6
Philopotamidae *Chimarra*	704.8	459.9	734.2	350.8	106.4	38.3	600.7	250.4
Philopotamidae early instars	94.3	76.5	40.8	20.0	0	0	35.9	11.1
Polycentropodidae *Neureclipsis*	0.5	0.5	4.0	1.4	1.2	1.2	0	0
Polycentropodidae *Polycentropus*[a]	0	0	0	0	0	0	0.5	0.5

[a] Rare species excluded from analyses

matrices, representing the densities of each caddisfly genus by sample site (response matrix), and local environmental variables, regional environmental variables, and spatial variables by sample site (predictor matrices). Variation partitioning was then used to separate out the "pure" effects of each of the three predictor matrices (local, regional, and spatial) and the amount overlapping, or shared variation among the predictor matrices (Borcard et al., 1992; Legendre & Legendre, 1998).

We first ran a correspondence analysis (CA) using CANOCO (ter Braak & Simlauer, 1998) on the response matrix to obtain an estimate of total inertia or variation explained in the caddisfly abundance matrix. We then ran three separate canonical correspondence analyses (CCA) where the response matrix (caddisfly densities) was constrained by one of the three predictor matrices (local variables, regional variables, and spatial variables). To avoid artificial increase in the explained variation due to chance (Borcard et al., 1992), we reduced the number of variables in the predictor matrices with forward selection. Forward selection eliminates co-linear variables and retains a subset of variables that best explain variation in the response (caddisfly density) matrix. In CANOCO, forward selection is a stepwise procedure that adds single variables one at a time until adding additional variables no longer explains a significant amount of the variation in community composition (http://www.ordination.okstate.edu/). Those variables that contributed most to explaining variation in caddisfly density ($\alpha \leq 0.05$, with 9999

Monte Carlo permutations) were retained in a separate matrix. Next a series of nine partial CCAs were run on the constrained models using the forward selected variables in the two remaining matrices individually as covariables, and then removing the combined effects of the two matrices. These analyses enabled us to separate out the pure effects of the local, regional, and spatial matrices as a percentage after dividing by the total inertia from the CA and multiplying by 100 (Borcard et al., 1992; Anderson & Gribble 1998; Legendre & Legendre 1998; Vaughn & Taylor 2000; Vaughn & Spooner 2006).

Results

We found 17 genera of caddisflies, as well as early instars that could not accurately be identified beyond family (Table 2). We were concerned that differences in caddisfly densities among the four rivers might be influenced by sampling date. There was an association between sampling date and river ($r = 0.931$, $P < 0.001$). Despite this relationship, there were no significant associations between caddisfly density and time of year for abundant genera (*Cheumatopsyche*: $r = -0.082$, $P = 0.144$; *Hydropsyche*: $r = -0.089$, $P = 0.671$; *Chimarra*: $r = -0.082$, $P = 0.695$; *Nectopsyche*: $r = -0.365$, $P = 0.081$; *Oecetis*: $r = -0.208$, $P = 0.318$; *Hydroptila*: $r = -0.005$, $P = 0.979$), suggesting that community composition was not dependent on sampling date. When the variation in caddisfly community structure was partitioned,

Fig. 2 Results of variation partitioning. (**a**) Local, regional, and spatial variables explained a total of 59.5% of the variation in caddisfly community structure. (**b**) Percentage of the explained variation accounted for by local, regional, and spatial variables, and shared variation among these components
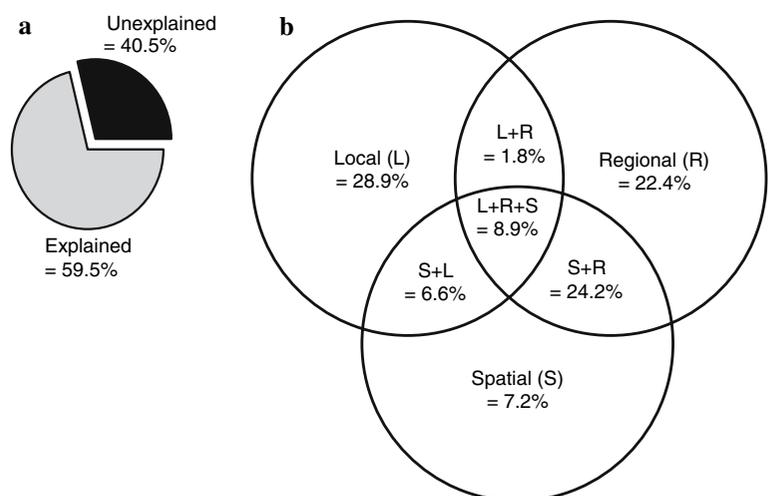
59.5% of the variation was explained by our environmental variables (Fig. 2a; variables listed below). Of this explained variation, 28.9% was explained by "pure" (non-shared) local variables, 22.4% by regional variables, and 7.2% by spatial variables (Fig. 2b). There was approximately 41.5% of the explained variation that could not be partitioned into pure effects, with the largest portion of this variation distributed in the overlap of spatial and regional variables (24.2%). The overlap between spatial, regional, and local variables explained 8.9% of the variation, 6.6% by the overlap between local and spatial variables, and 1.8% by the overlap between local and regional variables.

CCA with forward selection identified three local, three regional, and two spatial variables as those contributing most to the overall explained variation in caddisfly assemblage structure. The local variables retained were pH, depth and bank slope (Fig. 3). The first canonical axis was statistically significant (eigenvalue = 0.055, $F = 2.999$, $P = 0.0311$) and all four axes were significant as well (sum of all canonical eigenvalues = 0.120, $F = 2.648$, $P = 0.0002$). Depth had a strong positive correlation with axis 1, while pH and bank slope were positively correlated with axis 2, and slightly negatively correlated with axis 1. Several
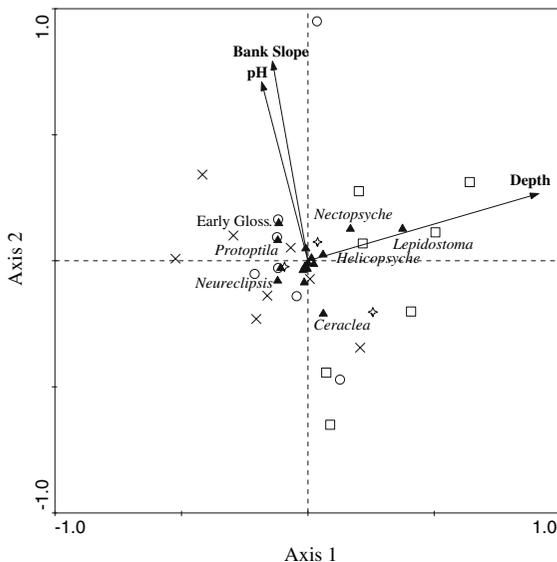
Fig. 3 Canonical correspondence analysis (CCA) biplot of the first two axes showing the relationship between caddisfly taxa (▲), sites (Glover ◯, Kiamichi ✕, Little ✦, Mountain Fork ☐), and retained local variables (arrows)

of these variables were closely associated with specific genera: *Nectopsyche* and *Lepidostoma* were associated with deeper water, while *Protoptila,* and other early Glossomatidae were associated with the axis 2 variables.

The regional variables most important to community structure were distance to the nearest road, average flow in 1997, and % row crops in the riparian area (Fig. 4). The first canonical axis (eigenvalue = 0.100, $F = 6.263$, $P = 0.0001$) and all canonical axes (sum of all canonical eigenvalues = 0.149, $F = 3.630$, $P = 0.0001$) were significant in this analysis. Distance to the nearest road was positively correlated with both axes 1 and 2. Percent row crop was negatively correlated with axis 1 and slightly positively correlated with axis 2, while average yearlong flow was negatively correlated with axis 1 and positively with axis 2. A biplot of genera and regional variables (Fig. 4) showed differences in densities of certain species in association with these regional variables. *Lepidostoma*, *Ceraclea*, and *Nectopsyche* were found in greater density with increasing distance from roads. Several taxa including *Macrostemum*, *Neureclipsis*, *Protoptila* and early glossosomatids were associated with yearlong flow and % riparian row crop.

Forward selection retained two spatial variables, X^2 and node 2. The X^2 term indicates that importance of patchy or complex patterns on the landscape in explaining community composition, while node 2 of the hierarchical network analysis represents the Little River watershed (including the Little, Glover, and Mt. Fork Rivers). The first axis (eigenvalue = 0.074, $F = 4.481$, $P = 0.0003$) and all canonical axes (sum of all canonical eigenvalues = 0.122, $F = 4.249$, $P = 0.0001$) were significant for this analysis.

Discussion

Our findings support the idea that communities are influenced by factors existing across a range of spatial scales that may interact in complex ways to regulate local community composition. We found that "pure" local and regional environmental variables were near equal in importance in governing caddisfly communities, with each accounting for approximately a quarter of the explained variation. Although pure spatial variables were less important, the amount of variation shared among spatial variables and local
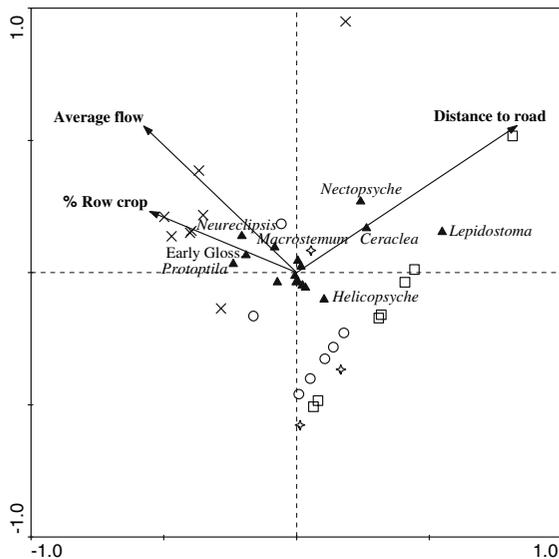
Fig. 4 Canonical correspondence analysis (CCA) biplot of the first two axes showing the relationship between caddisfly taxa (▲), sites (Glover ○, Kiamichi ×, Little ✧, Mountain Fork □), and retained regional variables (arrows)

and regional variables was substantial, indicating that biogeographic history is also key to understanding caddisfly distributions.

We expected local environmental variables to be important. Poff (1997) and Tonn (1990) suggested that local species pools are a result of regional species pools that were 'filtered' out (i.e., reduced) due to interactions between the environment and species traits. Based on this supposition, it follows that local communities should be a reflection of the finest grained filter through which they passed. This makes sense since local habitat variables are the ones that individual organisms experience directly (Johnson & Goedkoop, 2000). Like other studies that have examined caddisfly community structure and local environmental variables, we found measures that quantify stream reach characteristics (i.e., depth and bank slope, water chemistry) to be important (Minshall 1984; Degani et al., 1993; Voelz et al., 1994; Townsend et al., 1997). We also found evidence of habitat preferences among certain genera based on these environmental variables. For example, *Nectopsyche* and *Lepidostoma* were associated with deeper riffles, while *Neureclipsis* and *Macrostemum* appeared to prefer particular flow regimes. The mechanisms behind these apparent preferences are unclear, but present opportunities for further research.

We found that regional factors were approximately equal in importance to local factors in determining caddisfly distribution. Regional variables that were important included measures that described overall river characteristics (average discharge) and landuse and disturbance (% of row crops, distance to the nearest road). Examination of the CCA plots (Figs. 3 and 4) shows separation of sites among rivers and between drainages. Sites located within the Little River drainage tend to be deeper on average than those in the Kiamichi drainage, and contain a distinctive set of taxa (*Helicopsyche* and *Lepidostoma*). Sites in the Kiamichi drainage have higher average flows and a greater percentage of surrounding agricultural land.

A disturbing result of our regional analysis was the importance of stream modification, particularly agriculture and road construction, on caddisfly community composition. Wooded riparian buffers serve to filter sediments and pollutants from runoff, regulate stream temperature, and are important sources of organic matter for stream food webs. Loss of this critical riparian habitat has been found to influence community composition and taxonomic richness of both benthic macroinvertebrate and fish communities (Castelle et al., 1994; Harding et al., 1998; Wooster and DeBano, 2006). Further studies have shown that road construction can have significant impacts on channel morphology and sediment load kilometers downstream while facilitating human access to rivers and potentially the introduction of a variety of invasive species, all of which might alter caddisfly habitat (Trombulak and Frissell, 2000). The importance of road distance to each sampling site and % row crop in regulating community structure suggests that anthropogenic effects are replacing natural environmental variables in the regulation of community structure, even in the few remaining "pristine" parts of the world.

In this study, the amount of pure spatial variation in caddisfly community composition likely reflects dispersal pathways and connectivity among habitat patches. Caddisflies can disperse via two mechanisms: short distances within rivers as drifting larvae, and longer distances both within and between rivers as winged adults (Ross 1967; Hershey et al., 1993; Holomuzki et al., 1999; Jackson et al., 1999). However, most trichoptera are weak fliers (Resh & Sorg, 1978; Statzner, 1978; Waringer, 1991). The X^2

term, indicating patchy distributions of caddisflies along a longitudinal gradient, could be a reflection of assemblage differences among rivers, which are also oriented along a longitudinal gradient (Fig. 1). Given that these rivers are separated by regions of high elevation (particularly in the headwaters), the significance of this term may signify dispersal limitations as a major factor influencing differences in community composition.

Correspondingly, the significance of node 2 implies that community composition is more similar in the Little River drainage than in the Kiamichi drainage; this watershed effect could again reflect dispersal limitation among the Kiamichi and Little River watersheds, but could also reflect dispersal pathways of larvae within the rivers or flight patterns of adults along the rivers.

Variation partitioning is useful in separating out the variation among subsets of variables, but also allows examination of shared variation or overlap among variables. Such shared variation is expected in ecological data because of the hierarchical nature of ecological systems, the complicated nature of the environment, and because rarely is one able to measure all of the variables that may be important to an organism (Menge & Olson, 1990; Vaughn & Taylor, 2000). In this study, local and regional variables and spatial location on the landscape each contributed to the variability in caddisfly community structure across the biogeographic region; however, shared variation among these components was substantial. This shared variation represents underlying spatial autocorrelation among measured variables, unmeasured environmental, historical, or biotic variables, and hierarchial connections among variables (Borcard et al.,1992; Legendre & Legendre, 1998). For example surrounding landuse, a regional variable, influences sediment organic matter and nutrient inputs, thus influencing local variables such as substrate, algal composition, temperature regimes, and water chemistry (Vannote et al., 1980; Richards et al., 1996; Harding et al., 1998). Shared variation between spatial and environmental variables likely represents caddisfly colonization history and available species pools, unmeasured environmental variables that are autocorrelated with the landscape, and past local biotic interactions and processes that have led to nonrandom distribution patterns (Caley & Schluter, 1997)

Understanding the factors influencing community composition is becoming increasingly important for both scientists and managers in light of the dramatic loss of global biodiversity and the shift in conservation efforts toward preserving entire communities, not just individual species. In this study, we found approximately equal importance of local, regional, and spatial variables, and their interactions, in structuring caddisfly communities within one biogeographic region. Many studies of aquatic invertebrates have focused solely on the importance of environmental variables at a single scale to their distribution and abundance; fewer look across scales and therefore probably overemphasize the importance of local conditions and processes to aquatic communities. This has implications for our understanding of community structure as well as practical implications for how biological assessments are conducted and interpreted. For example, this study showed that caddisfly distributions were influenced just as strongly by landscape-scale processes as they were by the local factors that are traditionally measured in bioassessments. We recommend that both biologists and managers incorporate larger scale factors into their studies of aquatic communities.

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