ASSOCIATIONS OF WATERSHED AND INSTREAM ENVIRONMENTAL FACTORS WITH AQUATIC MACROFAUNA IN TRIBUTARIES OF THE PEDERNALES RIVER, TEXAS

A Thesis

by

JENNY S. BIRNBAUM

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2005

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Kirk O. Winemiller
(Chair of Committee)

Frances I. Gelwick
(Member)

Bradford P. Wilcox
(Member)

John C. Abbott
(Member)

Robert D. Brown
(Head of Department)

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ABSTRACT

Associations of Watershed and Instream Environmental Factors with Aquatic
Macrofauna in Tributaries of the Pedernales River, Texas. (May 2005)
Jenny S. Birnbaum, B.S., The University of Texas at Austin
Chair of Advisory Committee: Dr. Kirk O. Winemiller

Intermittent headwater streams serve important functions in semi-arid rangelands, both for humans and wildlife. However, few studies have assessed species-environment relationships for fish and benthic macroinvertebrate assemblages in these systems. Additionally, no published studies could be found that addressed the influence of juniper coverage in watersheds on assemblage structure of these taxa. Increased juniper coverage in recent decades is believed to be associated with decreased water yields in central Texas streams. During summer 2003 and spring 2004, I examined potential effects of juniper cover on aquatic ecology. Fishes, benthic macroinvertebrates, and the physicochemical habitat were investigated in spring-fed headwater tributaries of the Pedernales River. My objectives were to: 1) describe the typical fish and benthic macroinvertebrate assemblages in headwater creeks of the Pedernales River basin; 2) compare seasonal variability of fish and benthic macroinvertebrate assemblages; 3) identify species-environment relationships in this river basin; and 4) evaluate the influence of juniper coverage in the watershed, relative to local and landscape-level environmental factors, on the structure of fish and benthic macroinvertebrate assemblages.

A total of 4,181 individual fish were collected in summer 2003 samples, 551 fish were collected in spring 2004, 59,555 macroinvertebrates were captured in summer 2003 samples, and 51,500 macroinvertebrates were collected in spring 2004. Assemblages were typical for the area and habitat conditions. Faunal richness was lower in spring than in summer, possibly due to a combination of sampling after a relatively dry period in the spring, and lack of winter refugia in the form of deep pools. Fish assemblages may structure based principally on abiotic factors in spring, the harsher season (less available water), whereas predation pressure may influence structure in summer. Another important environmental gradient for both fish and invertebrate assemblages contrasts pool and run mesohabitats. In general, juniper cover was weakly associated with fish and invertebrate assemblages, although it tended to be associated with relatively high quality habitat for sensitive taxa (flowing runs with coarse substrate; deep, connected pools). In these intermittent streams, local-scale environmental factors probably are the dominant influences on fish and benthic macroinvertebrate assemblages. Implications for future studies are discussed.

DEDICATION

In memory of my mother, Cynthia Birnbaum

you continue to be a major influence in who I am today; I would not be here without you

To my dad

for always being there when I need you

To Jorge

for your support, love, and encouragement, despite the distance

To Josei

you know you have a good friend when she tells you what you need to hear,
even if you don't want to hear it

and To Annie

for making me smile every day over the last year and
helping me to remember the simple things in life!

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Well, it’s finally coming to a close and this thesis could not have been completed without the help of numerous people, so I will try to thank as many as I can here… My thesis was part of a large project funded by the Army Corps of Engineers (Ft. Worth District). Additional funding was provided by Texas A&M University (Merit Fellowship), several academic scholarships from the Department of Wildlife and Fisheries Sciences, and a Texas Water Resources Institute Mills Scholarship.

My field helpers logged countless hours in the field and this project would be non-existent without them. I would like to mention in particular, Li Shen, who accompanied me on nearly every trip – I could not have done it without you; your patience, hard work, and memory for exact locations where we had previously sampled were exceptional! Rosana Lopez went out in the field with me during all the summer trips and helped out in the lab. Thanks for all the hard work and great conversations; I wish you luck in whatever you end up doing. I would also like to thank the following people, many of whom went out just for fun and/or to help me out: Rachel Butzler, Jorge Chaves, Scott Gardener, Elizabeth Hebert, David Hoeinghaus, John Kirk, Dave LaFever, Ray Li, Hernán Lopez, Monty Mitchell, Jake Philley, Clint Robertson, Virginia Shervette, Stuart Willis, and Steve Zeug.

I want to thank my committee chair, Kirk Winemiller, for his guidance and support throughout this project, and willingness to chat whenever I needed help. John Abbott, Fran Gelwick, and Brad Wilcox taught me through several classes, and provided advice throughout the project, in particular improving this thesis. Thanks especially to

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INTRODUCTION

Background

As the human population increases, putting a strain on global freshwater resources (Yevjevich 1992), quality and allocation of water become increasingly important issues. In semi-arid landscapes, classified as having 25 to 50 cm of rainfall per year, water is commonly in short supply. Nonetheless, semi-arid rangelands in many regions of the world provide water for grazing livestock, agriculture, and human population centers. Since water is such an important resource in semi-arid regions, people continually seek new water sources and strategies that increase the efficiency of its use.

One strategy for increasing the water supply is watershed management of encroaching brush. It is thought that removal of deep-rooted woody species, such as mesquite (*Prosopis glandulosa*) and ashe juniper (*Juniperus ashei*), in areas where annual precipitation exceeds 450 mm may considerably increase groundwater recharge of reservoirs and streams (Hibbert 1983, Wu et al. 2001). A review of 94 time-trend catchment experiments (Bosch and Hewlett 1982) from a wide range of study areas and vegetation types concluded that both the direction and magnitude of water yield changes can be predicted. As further examples of the relationship between woody vegetation and water yields, Stednick (1996), in his review of paired catchment studies in different regions of the U.S, suggested that a measurable increase in annual water yield could be

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This thesis follows the style and format of Ecological Applications.

attained through a 20% harvest, while Trimble et al. (1987) observed decreased water yields with reforestation of the southern Piedmont in the southeastern U.S.

The few studies that have been done in Texas rangelands have yielded conflicting interpretations. For example, a study (Dugas et al. 1998) of juniper removal in the Seco Creek watershed showed no significant difference between evapotranspiration (ET) in the untreated area and ET in a treated area. In contrast, a study on mechanical removal of mixed woody vegetation in an Edwards Plateau watershed (Richardson et al. 1979) produced an approximately 20 percent decrease in surface runoff. Given the shallow soils and fractured limestone substratum of the Edwards Plateau, much of the stored runoff was thought to have percolated to groundwater.

Given these conflicting studies, when is brush management likely to increase water yields? Wilcox (2002) proposed a set of criteria for successful brush control. First, average annual precipitation should be above 450 mm/year. In order to reduce the soil water deficit, the ratio of precipitation to potential evapotranspiration must be greater. Second, there should be a greater effect on streamflow when a high-density patch of woody vegetation is cleared compared to when a low-density patch is cleared. Third, in a region such as the Edwards Plateau, where there is little Horton overland flow (runoff that occurs when rainfall intensity exceeds the infiltration capacity of the soil) and groundwater recharge is rapid, successful brush management is more likely. Fourth and last, an area with large amounts of juniper, as opposed to mesquite, is a better candidate for brush management because juniper should intercept more precipitation, as it is an evergreen, has dense needles, and has high litter production.

Aquatic macrofauna as environmental indicators

Aquatic macrofauna, such as benthic macroinvertebrates and fishes, are sensitive environmental indicators in streams and rivers (Karr 1991, Harding et al. 1998, Chessman 1999) because both human and natural environmental factors influence aquatic macrofauna communities in these systems. Here I focus principally on abiotic factors, which can be human influenced. An important hypothesis regarding the structuring of fish and macroinvertebrate communities in streams and rivers is the River Continuum Concept (Vannote et al. 1980). This model postulates that species in stream communities are replaced longitudinally, from headwaters to mouth. The longitudinal gradient also spans different P/R (photosynthesis/respiration) ratios, energy inputs (allochthonous versus autochthonous), and physical features such as depth, width, velocity, temperature, and entropy gain. Multiple studies have documented longitudinal changes in assemblages, including changes in life history, body size, and species diversity and composition, in downstream versus upstream reaches (Sheldon 1968, Horwitz 1978, Schlosser 1990, Heino et al. 2004).

Additionally, the Intermediate Disturbance Hypothesis postulates that biotic diversity is high where there are intermediate levels of disturbance and low where disturbances are intense and/or frequent, or where disturbances are small and/or infrequent (Connell 1978). Although the Intermediate Disturbance Hypothesis was originally applied to sessile organisms such as trees and corals, Ward and Stanford (1983) suggest that the high diversity in natural streams may be explained by the non-equilibrium conditions in these systems. For example, richness of organisms living in a spring (fairly constant environment) or an intermittent stream (fairly high disturbance) might be lower than for organisms living in the middle reaches of a river, where there are moderate amounts of disturbance (Ward and Stanford 1983).

Expanding on this, Schlosser (1987) described a conceptual framework for understanding fish community organization in small warmwater streams. He postulated that species richness, density, and fish density are low in areas with poorly developed pools, shallow depths, and low habitat volume because these do not provide suitable habitat for older (larger) age classes and pool species. Furthermore, he suggests that the lowest fish densities occur in the spring because of the large degree of emigration/ mortality during the winter of fish without large pool refugia. In contrast, the effects of periods of cold or drying are more likely to be mediated in invertebrates, such as many crayfish species, that can survive by burrowing in wet mud and aestivating (Taylor 1983, Jordan et al. 2000).

Many studies have found that physicochemical factors impart major influences on the biota of streams and rivers. The role of longitudinal position in structuring fish and benthic macroinvertebrate communities was discussed above; a surrogate for this would be stream order. Many studies have identified differences in communities and age classes within a single species among stream mesohabitats such as riffles, runs, and pools (Schlosser and Ebel 1989, Muhlfeld et al. 2001, Eros et al. 2003). Such habitats are characterized by differences in depth, water velocity, and turbulence. Dominant substrate, which may be a correlate of mesohabitat type, is highly correlated with fishes and macroinvertebrates in some studies (Chipps et al. 1994, Lammert and Allan 1999). Additionally, species or communities can even differ between microhabitats (Chipps et al. 1994, Bouckaert and Davis 1998, Vadas, Jr. and Orth 2000). Other studies have established the influence of environmental factors such as oxygen, pH, conductivity, and temperature in structuring fish and invertebrate assemblages (Matthews et al. 1992, Kilgour and Barton 1999, Ostrand and Wilde 2002). Lastly, complex habitats can support more diverse fish communities and provide refugia from harsh environmental conditions and predators (Gorman and Karr 1978, Schlosser 1995, Jordan et al. 2000).

The issue of scale, both spatial and temporal, pervades the study of ecology (Wiens 1989), particularly the ecology of stream organisms. Seasonal, annual, and historical environmental fluctuations may affect species diversity (Harding et al. 1998, Winemiller and Jepsen 1998), life history attributes (Schlosser 1990), and colonization dynamics (Lohr and Fausch 1997). Habitat selection of young may change over time due to ontogenetic shifts (Everest and Chapman 1972, Reichard et al. 2002). Regarding spatial scale, scientists have long called for studies that assess how local community structure is regulated (Ricklefs 1987, Cornell 1993). Multi-scale studies are extremely important because there are many instances when results of a study conducted at one scale were found to be inapplicable when a similar study was conducted at a different spatial scale (Wiens 1989). Multi-scale studies allow us to gain a deeper understanding of the factors influencing community structure. Historically, many studies focused on local biotic (predation, competition) and abiotic (hydrologic cycle, disturbance) processes as the principal regulators of local community diversity (Reice 1983, Schlosser and Ebel 1989, Grossman and Sostoa 1994, Poff and Allan 1995). More recently, focus has been on regional environmental factors and diversity as the primary regulators of local community structure (Hugueny and Paugy 1995, Griffiths 1997, Marsh-Matthew and Matthews 2000). A more realistic explanation is probably a hierarchical system of environmental filters, with regional factors having dominant effects on assemblages at broad spatial scales, and local factors playing a greater role at smaller spatial scales (Jackson and Harvey 1989, Tonn et al. 1990, Jackson et al. 2001).

Introduction and objectives of this study

One example of a multi-scale environmental influence on fish and invertebrate communities, as implied by the beginning of this introduction, is the vegetation cover on the landscape. At the local scale, vegetation at the water's edge may provide shade, which in turn regulates water temperature and therefore dissolved oxygen concentrations. Woody debris from dead trees, or parts of trees (such as leaf litter) that fall in the water body can provide important habitat for fishes, food for invertebrates, and refugia from predators and high flows, to name a few roles (Wallace et al. 1997, Fairchild and Holomuzki 2002, Neumann and Wildman 2002). At a larger scale, riparian and watershed vegetation influence siltation rates in streams, rates of pesticide/fertilizer runoff, and even the amount of water available to the water body.

These and other processes can impact aquatic macrofaunal communities (Cooper 1993, Stednick 1996, Jones III et al. 1999, Whiles et al. 2000).

Given the link between fish and macroinvertebrate communities, and the physical environment, these fauna should be useful to assess the influence of vegetation composition and density on the instream physical environment. This study was part of a larger multi-disciplinary project to assess the ecological effects of ashe juniper management in headwater tributaries of the Pedernales River basin of central Texas. Sampling occurred in summer 2003 and spring 2004. If the null hypothesis that juniper removal has no influence on water yields is false, I would expect increased discharge and therefore increased richness of aquatic macrofauna in streams where juniper in the watershed is managed, as opposed to streams where juniper is not managed (Schlosser 1987, Schlosser and Ebel 1989). The key assumption here is that increase in discharge (and species richness) is directly proportional to decrease in juniper coverage.

With this in mind, the objectives of this study were to 1) describe the typical fish and benthic macroinvertebrate assemblages in headwater creeks of the Pedernales River basin; 2) compare seasonal variability of fish and benthic macroinvertebrate assemblages; 3) identify species-environment relationships in this river basin; and 4) evaluate the influence that juniper coverage in the watershed, relative to local and landscape-level environmental factors, has in structuring fish and benthic macroinvertebrate assemblages. I expected that 1) richness of fish and benthic macroinvertebrates would be lower in the summer sampling season when water levels were more likely to be low, as opposed to the spring sampling season when water levels were more likely to be higher; 2) fish assemblage structure would be highly correlated with water depth, while (based on preliminary field surveys) macroinvertebrate assemblage structure would be highly correlated with local environmental factors, such as percent coverage of instream vegetation or canopy cover of riparian vegetation over the stream; and 3) in watersheds with less juniper cover, fish and benthic macroinvertebrate assemblages would be richer due to increased discharge.

METHODS

Study area

The Pedernales River basin of central Texas was chosen for this study. This region satisfies Wilcox's (2002) criteria for successful brush management. Annual precipitation is over 450 mm/year. Ashe juniper commonly occurs through the area and has increased in density in the last 50 years (Fuhlendorf and Smeins 1997). Since the soils are shallow and are underlain by fractured parent rock formations, water can quickly percolate beyond the root zone to groundwater sources, minimizing overland runoff (B. Wilcox, *personal communication*). The presence of springs further indicates a good surface to sub-surface connection. Any influence of brush management on water yield and subsequently on macrofauna should be local in nature because recharge to streams, reservoirs, and aquifers in the area tends to occur extremely quickly during large, infrequent rain events (B. Wilcox, *personal communication*). Therefore, the sampling sites were located on spring-fed, headwater tributaries of the Pedernales River.

The Pedernales River flows West to East into the Colorado River, just West of Lake Travis, in western Travis County. The headwaters occur in Kimble and Kerr Counties, and the river primarily flows through Gillespie (western county) and Blanco (eastern county) Counties. These counties are generally rural, with small population centers such as Fredericksburg, Gillespie County (about 10,000 people) and Johnson City, Blanco County (about 1,200 people). Much of the basin is used as agricultural or grazing lands. Vegetation is generally rangeland, with juniper and oak as the dominant woody vegetation on the landscape. The basin occurs in the Edwards Plateau ecoregion, which is characterized by limestone geology, and is home to many endemic plant and animal species, and the famous Edwards Aquifer, which supplies drinking water to San Antonio and many of the surrounding towns. Many tributaries of the Pedernales River are at least partially spring-fed. Average annual precipitation is approximately 75-86 cm (depending on location in the watershed) with peaks in the early spring and fall. Average high temperatures in August and January are approximately 35˚ C and 16˚ C, respectively (LCRA 2000).

Selection of sampling sites

Spring-fed headwater streams for which landowner access was granted were sampled (B. Hayes, *personal communication*). A further condition for the spring locations was that they occur close to or on the geologic interface between the Edwards and the Upper Glen Rose Formation or between the Lower Glen Rose and the Hensell Formations (Fig. 1, TAES 2004) to ensure consistency in geological features associated with spring outflow. Also, a wide range of springs with varying amounts of juniper cover was desired. Sampling sites for aquatic biota were selected at locations as far upstream in the spring watershed as landowner access permitted, and in general were chosen to maximize diversity of mesohabitat types (eg., runs, pools, riffles). The goal was to sample four sites for each spring. However, due to the ephemeral nature of many of the streams, the actual number of sites sampled per spring ranged from one to six sites. Sites were sampled once from June to September 2003 (summer 2003), and once from March to April 2004 (spring 2004). A total of 92 sites associated with 31 springs

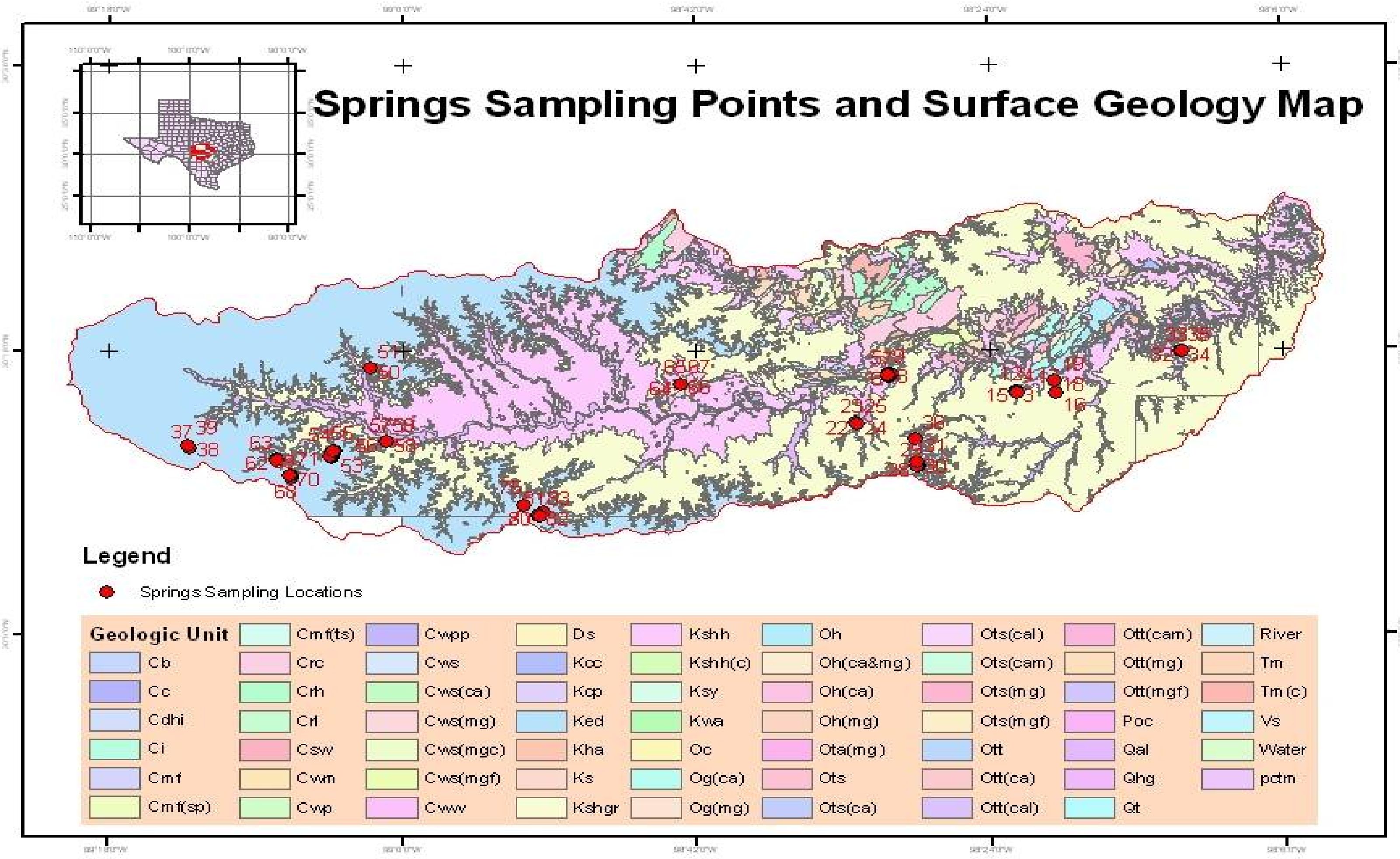

FIG. 1. Surface geology of the Pedernales River basin with spring sampling locations shown as red dots. The dominant geological formations are Glen Rose Limestone (Kshgr), Edwards Limestone (Ked), Hensell Sand (Kshh), and Comanche Peak Limestone (Kcp) (TAES 2004).

were sampled during summer 2003, and 96 sites on 33 springs were sampled during spring 2004. These sites included several creeks that were dry during the summer, but were sampled during the spring, and vice versa. An additional four sites on one spring were sampled in both seasons but were not used in analyses, because it was determined they did not fit the geological criteria of the study.

Physicochemical characterization of sites

All sites were characterized using common qualitative and quantitative methods. At each site, the date, time of day, general weather conditions, and general land-use characteristics were recorded, as well as Global Positioning System (GPS) coordinates and length of each sample reach. In order to standardize estimates, percent canopy cover, percent coverage of woody debris, and percent coverage of aquatic vegetation were qualitatively estimated by myself at each site. Three lateral transects were identified at each site, with one in the middle of the site and one located near the upstream and downstream limit of the survey reach. The wetted width (m) of the stream was measured at each transect. Water depth (m) and velocity (using a Marsh-McBirney digital flowmeter, m/s) were measured at five points on each transect: nearbank (the right-hand bank when facing upstream), 1/4 width (one-quarter across the wetted width from the nearbank side), 1/2 width (halfway across the wetted width), 3/4 width (three-quarters across the wetted width from the nearbank side), and farbank (opposite bank). Physicochemical parameters measured *in situ* included dissolved oxygen (DO, mg/L), water temperature (°C), and conductivity (µs), which were measured with a YSI Model 85 multiparameter meter and probe, and pH, which was measured with an Oaklon digital pH meter. Each of these parameters were measured at two to three locations on the middle transect, dependent on depth. The parameters were measured once at the nearbank position, and at the 1/2 width position. At the 1/2 width position, the parameters were measured in the middle of the water column and also at the surface (when depth permitted). Substrate composition was visually estimated at each position where a benthic macroinvertebrate sample was collected (see below for methodology). Percent coverage of five substrate types was identified according to a modified Wentworth scale, as follows. The silt/clay category consisted of particles less than 0.062 mm in size, sand ranged from 0.062-2 mm, gravel was 2-63.5 mm in size, cobble ranged from 63.5-254 mm, and boulder was anything greater than 254 mm. Additional categories were detritus and bedrock.

Environmental variables provided by other team members

This work was part of a multi-discipline study commissioned by the Army Corps of Engineers. Thus, I used several variables in my analyses that were provided by other team members. Discharge values were calculated from a width measurement across a narrow part of the stream at the upstream or downstream boundary of the site, three depth measurements at this location, and three velocity measurements at this location. Additionally, land coverage values for cropland, rangeland, juniper (*Juniperus ashei*), and oak (mainly *Quercus viginiana* and other woody vegetation) were determined for each stream watershed. Replicate reference areas were used to classify pixels of Landsat images taken in 1999 and 2003. From these classifications, coverage values were generated, and the difference in coverage for each classification between 1999 and 2003 was calculated. Classifications were ground-truthed in May 2004. I calculated land coverage percent of total woody vegetation in each basin from the juniper and oak (and other woody vegetation) variables which were provided to me. Surface basin area was also calculated for each stream watershed. Paper copies of geologic maps for the Pedernales River basin were digitized into digital elevation models (DEMs). Stream shape files from the USGS National Hydrography Dataset and spring GPS coordinates were overlain on top of the DEMs, and surface basin area was delineated using software from the U.S. Environmental Protection Agency (EPA). For more detailed methods describing how these variables were derived, see TAES 2004.

Biotic characterization of sites

Fish and crayfish were collected by seining (3.66 m x 1.83 m with 4.76 mm mesh). A second seine was used to block the downstream portion of the stream segment being sampled to prevent fishes escaping the sampling area. Since these headwater streams have low species diversity and/or total abundance, I focused on obtaining an accurate representation of total abundance as opposed to species richness. Thus, seine hauls were repeated until a haul captured ten percent or less of the number of individuals of the dominant taxon in the initial haul. Seining was conducted by performing long mid-pool sweeps, followed by efforts in which vegetation along the bank was surrounded on one side by the seine, and kicked to dislodge organisms. In some instances, fishes were identified, counted, and released alive. All other specimens from a given site were preserved in 15% formalin in the field, transferred to 70% ethanol in the laboratory, then sorted by species and counted. Fishes were identified according to Hubbs et al. (1991) and Page and Burr (1991). For the summer 2003 seine data, ninety-one sites were included in analyses, because one site was not sampled adequately due to heavy vegetation. All ninety-six sites were included in analyses for spring 2004 seine data. Crayfish were grouped with fish in most statistical analyses (except for analyses involving species/taxa richness) because they were captured by seining as opposed to kick-netting. Additionally, since crayfish individuals typically have a large biomass, they should have a disproportionately large role in the streams as compared to the other macroinvertebrates.

Three benthic macroinvertebrate samples were collected at each site to maximize taxa richness by sampling in different types of microhabitats (middle of channel, edge of channel, aquatic vegetation, no aquatic vegetation, silt bottom, leaf litter, etc.). Samples were collected using a 30.5-cm diameter, D-frame kick net (500 μm mesh) by kicking and sweeping the substrate three to four times downstream into the net. In order to standardize procedures and reduce subjective bias, I (as opposed to field helpers) collected each benthic macroinvertebrate sample. Samples were preserved in a solution of Rose Bengal plus 70% ethanol in the field, and returned to the laboratory to be sorted, identified, and counted. Insects were identified to family and other invertebrates were identified to class or order according to Merritt and Cummins (1996), McCafferty

(1983), and Pennak (1978). In the rare case that an insect could not be identified to family because it was too small or key body parts were missing, it was noted in an unidentified category for that order. These insects were not used in analyses, except unidentified odonates, because the whole order is predaceous (Merritt and Cummins 1996). Additionally, pupae were only identified to order, and were thus not included in analyses. A single site sample was obtained by adding data from all three benthic macroinvertebrate samples for that site. For summer 2003 data, ninety sites were included in analyses because the samples for two sites were mislabeled. All ninety-six sites were included in analyses of spring 2004 data. However, in a few instances one of the three samples was improperly preserved and biota could not be identified. In that case, I averaged the abundances for the other two samples and added the averages to the original values to obtain the single site sample.

Data analysis

Representation of variables

In statistical analyses, water depth was represented as average depth, maximum depth, and coefficient of variation (CV) of depth, where CV = (SD/mean)*100. Velocity was represented as maximum and average velocity. A coefficient of variation for velocity could not be calculated since many of the values were zero. Average channel width and CV of channel width were calculated for each site. For each site, the average and CV of DO, water temperature, conductivity, and pH also were calculated. The percent coverage for each substrate category was averaged among sample estimates for a given site, and the dominant substrate category (other than bedrock, which was the parent substrate of all streams) was determined. Substrate variables were converted into binary categorical values, with a value of one indicating that the category was dominant at the site, and a value of zero assigned to all other categories that were not dominant at that site. Because they were difficult to distinguish in the field, the categories fine particulate detritus and silt/clay were combined. GPS coordinates were recorded in decimal degrees. The variables length, percent canopy cover, percent woody debris, and percent aquatic vegetation were represented as described above.

Correspondence analysis and canonical correspondence analysis

Correspondence analysis (CA) was performed in order to investigate species (or taxon) assemblage relationships to site characteristics without the influence of environmental variables. CA is a multivariate ordination technique that uses reciprocal averaging in an iterative process to discover the underlying environmental gradient behind species abundances at sites. Its main assumption is that species abundance distributions are unimodal and reflect an approximately normal distribution in response to the environmental gradient (Gotelli and Ellison 2004). CA was performed using the software CANOCO (ter Braak and Smilauer 1998) separately for the summer 2003 and spring 2004 seine data (fish and crayfish), and the benthic macroinvertebrate data for each season. In order to reduce bias from rare species in the dataset, I excluded from the analysis those fish species that were not collected from at least two of the total sites surveyed. I excluded from CA those macroinvertebrate taxa that did not occur in at least four of the total sites surveyed.

Canonical correspondence analysis (CCA) is a direct gradient ordination technique that chooses the linear combination of environmental variables that maximally explains variation of the species scores. This procedure produces the first CCA axis. Subsequent axes are calculated in a similar fashion, but are constrained by being uncorrelated with previous CCA axes (Jongman et al. 1995). CCA was used to investigate environmental gradients that could be determining species (taxa) assemblages. Two CCA's, one containing environmental variables from the local scale and one containing landscape scale variables, were performed using the software CANOCO (ter Braak and Smilauer 1998) for the seine and benthic datasets in each season. A third CCA analysis incorporating the combined environmental variable sets was also run on each of the four datasets. The CCA's presented are those in which redundant environmental variables were removed from the analyses. In the first run of each analysis, variables with variance inflation factor (VIF) scores greater than 20 were noted and removed for the final CCA analysis. VIF scores greater than 20 indicate multicollinearity among the variables (ter Braak and Smilauer 1998). The criteria for frequency of occurrence at sites used in CA were also used to exclude rare species from CCA.

Regression analyses

Since fish were not collected at many of the sites (52 out of 91 sites in summer 2003 and 70 out of 96 sites in spring 2004), fishless sites were effectively excluded by CANOCO (ter Braak and Smilauer 1998) from the CA and CCA analyses. It was desirable to determine what environmental variables might predict the fishless condition. In a logistic regression, environmental variables are used to create a model that predicts the probability of a categorical dependent variable (Gotelli and Ellison 2004). In this case, the dependent variable was binary, with one indicating a site with fish and zero indicating a fishless site. Independent variables tested were chosen from non-redundant variables in the local and landscape scale CCA's. The program SPSS (SPSS Inc. 2002) was used to perform separate logistic regressions for the summer 2003 and spring 2004 fish datasets.

Linear regressions were performed using Microsoft Excel (Microsoft Inc. 2001) to further examine the relationship between CA axis scores and percent juniper coverage or change in percent juniper coverage (1999-2003). Additionally, I determined the influence of certain key environmental variables (percent juniper cover, change in percent juniper cover, percent total woody cover, basin area, and discharge) on species/taxa richness. A bivariate linear regression was performed between species/taxa richness and each of the key environmental variables for summer 2003 fish, spring 2004 fish, and benthic macroinvertebrates from each year. A multiple regression was performed to model the simultaneous influence of these environmental variables. A multiple regression is similar to a linear regression, but it may contain two or more predictor variables. Since a multiple regression assumes normality of variables and my variables were not normal, all variables were log transformed as log(x+20). These analyses were also performed using SPSS (SPSS Inc. 2002).

RESULTS

Description of typical aquatic macrofauna assemblages and seasonal differences

Summed over all study sites, a total of 4,181 individual fish were collected in summer 2003 samples and 551 fish were collected in spring 2004 samples. A total of 59,555 macroinvertebrates were captured in the summer 2003 samples and 51,500 macroinvertebrates were collected in spring 2004. More information about species/taxa collected can be obtained from TAES (2004). During summer 2003, the streams associated with three springs (springs 35, 36, and 37) were completely dry and thus were not sampled. These streams contained water during the spring 2004 surveys. During spring 2004, the stream associated with one spring (spring 11) was completely dry and not sampled.

Fifty-two out of 91 sites contained water but no fish during summer 2003; 70 out of 96 sites contained water but no fish during spring 2004. Macroinvertebrates were collected at every site containing water during summer 2003 and spring 2004.

Species-environment relationships

Summer 2003 seine data–CA analysis of species assemblages

CA ordination of seine collections (fishes + crayfish) from the summer 2003 survey revealed a principal gradient (modeling 25% of variation) that contrasted species assemblages containing crayfish (Cambaridae), Mexican tetras (*Astyanax mexicanus*), green sunfish (*Lepomis cyanellus*), and central stoneroller (*Campostoma anomalum*) with species assemblages containing mosquitofish (*Gambusia affinis*) and longear sunfish (*Lepomis megalotis*) (Table 1, Fig. 2). The second axis (modeling an additional 21.9% of variation) contrasted species assemblages with abundant crayfish and tetras with those having larger numbers of plains killifish and the four minnow species.

TABLE 1. Species loadings from CA of summer 2003 seine data.

Species	**Axis 1**	**Axis 2**
Eigenvalue	0.883	0.776
Cumulative % variance of species data	25.0	46.9
Astyanax mexicanus	4.462	1.405
Campostoma anomalum	1.962	-2.750
Cyprinella lutrensis	2.252	-3.421
Cyprinella venusta	1.716	-3.047
Dionda episcopa	0.477	-3.048
Fundulus zebrinus	1.848	-3.481
Gambusia affinis	-2.744	0.878
Lepomis cyanellus	3.300	0.705
Lepomis megalotis	-1.493	-0.140
Cambaridae	5.045	3.241

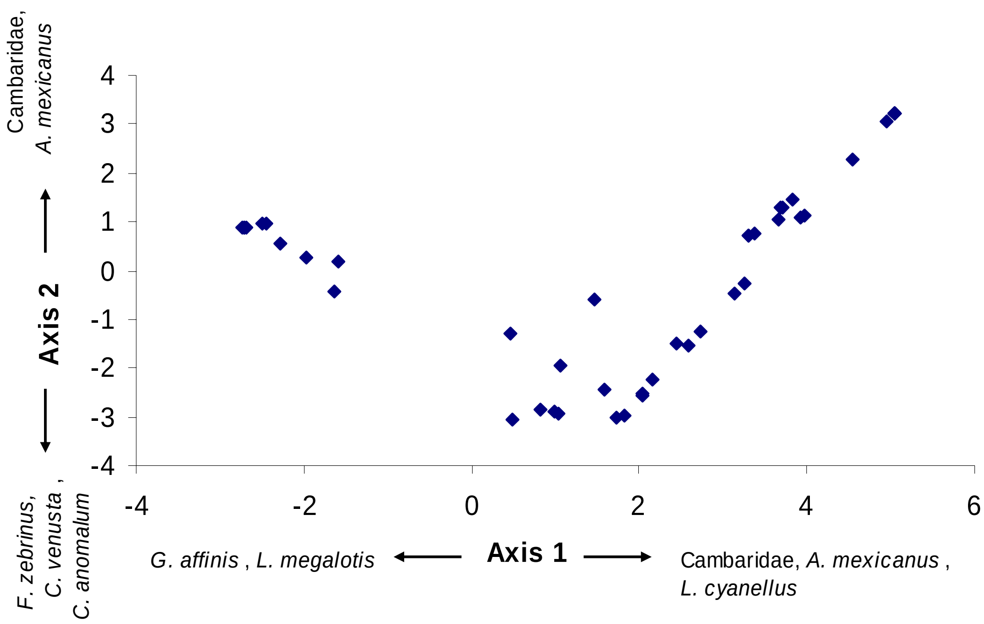

FIG. 2. Plot of site scores from CA of summer 2003 seine data.

Summer 2003 seine data–CCA with local environmental variables

CCA for summer 2003 performed with species abundance and local environmental variables yielded a principal gradient (modeling 22% of species variation and 31.3% of environmental variation) that associated high abundance of mosquitofish and longear sunfish (large negative axis 1 loadings) with higher densities of aquatic vegetation (high negative loading), lower average dissolved oxygen concentrations (high positive loading), shorter stream segments (high positive loading), and lower water discharge (high positive loading) (Table 2). The opposite suite of environmental conditions was associated with higher abundances of all other fish species and crayfish. In other words, local conditions associated with greater stream discharge and better water quality tended to be associated with higher abundances of most species, and relatively lower abundances of two tolerant species (mosquitofish and longear sunfish). The second CCA axis (modeling 16% of species variation, 22.7% of environmental variation) contrasted sites with relatively large abundance of tetras, green sunfish, and crayfish (high positive axis 2 loadings) with those tending to have higher abundances of the other fish species (negative loadings) (Table 2, Fig. 3). Highest positive environmental loadings on axis 2 were for average water velocity and CV of channel width, and highest negative environmental loadings were for average dissolved oxygen and discharge.

TABLE 2. Species and local environment loadings from CCA of summer 2003 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.777	0.565
Species-environment correlations	0.955	0.875
Cumulative % variance: species data	22.0	38.0
Cumulative % variance: species-environment relation	31.3	54.0
Astyanax mexicanus	2.933	6.102
Campostoma anomalum	2.438	-0.878
Cyprinella lutrensis	2.237	-0.615
Cyprinella venusta	2.055	-0.530
Dionda episcopa	2.073	-2.611
Fundulus zebrinus	3.043	-1.079
Gambusia affinis	-2.171	-0.069
Lepomis cyanellus	2.283	3.245
Lepomis megalotis	-0.513	0.402
Cambaridae	1.418	1.874
Time of day	0.209	0.079
Length of site	0.223	0.114
% Canopy cover	0.150	-0.086
% Woody debris	0.068	0.062
% Aquatic vegetation	-0.189	0.114
Discharge	0.210	-0.151
Depth (avg)	0.035	0.137

TABLE 2. Continued

Species/Environment	Axis 1	Axis 2
Depth (CV)	0.065	0.083
Velocity (max)	0.183	0.118
Velocity (avg)	0.154	0.208
Width (avg)	-0.000	-0.098
DO (avg)	0.285	-0.195
Water temperature (avg)	0.167	-0.036
pH (avg)	0.143	0.018
Width (CV)	0.063	0.180
DO (CV)	-0.070	0.080
Conductivity (CV)	0.036	-0.026
pH (CV)	-0.069	0.034
Silt/clay/detritus	-0.045	-0.023
Mud	-0.127	0.134
Sand	-0.047	0.088
Gravel	0.202	-0.084
Cobble	0.147	-0.122

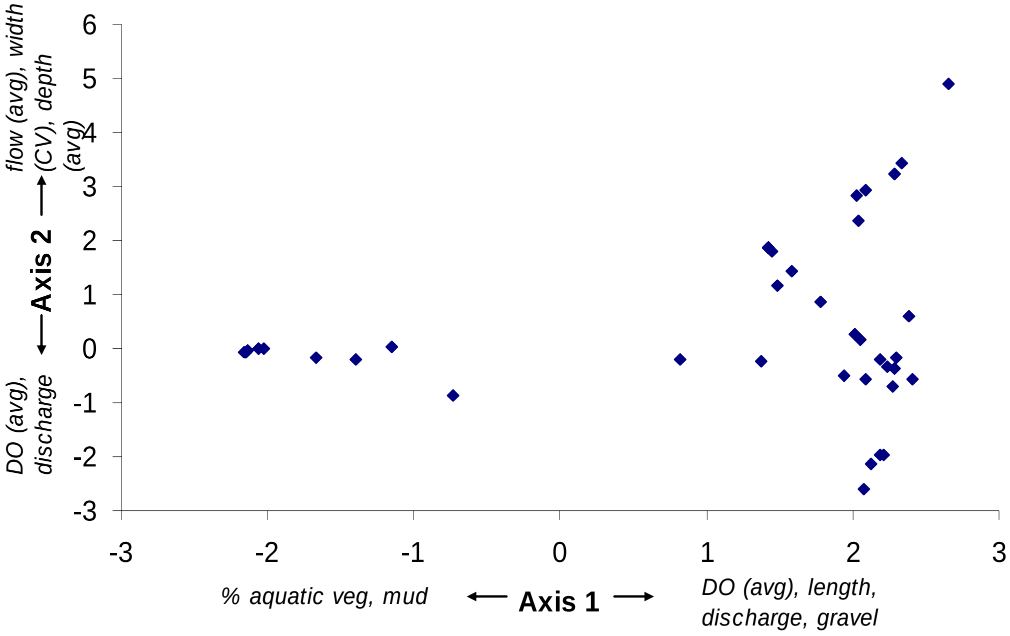

FIG. 3. Plot of site scores from CCA of summer 2003 seine data and local environmental variables.

Summer 2003 seine data–CCA with landscape environmental variables

CCA for summer 2003 performed with species abundance and landscape environmental variables yielded a principal gradient (modeling 15.4% of species variation, 40% of environmental variation) that associated high abundance of green sunfish, crayfish, and three of the four minnow species (large positive axis 1 loadings) with higher coverage of juniper in the watershed (high positive loading), increased juniper coverage in the watershed in 2003 images as opposed to 1999 images (high positive loading), and decreased oak coverage in the watershed in 2003 as compared to 1999 (high negative loading) (Table 3). The opposite suite of landscape attributes was associated with higher abundances of longear sunfish, mosquitofish, and plains killifish. This dominant axis from CCA indicates that, more juniper and increase in juniper coverage in watersheds was associated with greater relative abundances of five of the ten taxa collected in seines, including sensitive minnow species and tolerant green sunfish. The second CCA axis (modeling 11.7% of species variation, 30.5% of environment variation) contrasted sites with relatively large abundance of crayfish and *Dionda episcopa* (high negative axis 2 loadings) with those tending to have higher abundances of many of the other fish species (positive loadings) (Table 3, Fig. 4). Highest positive environmental loadings on axis 2 were for latitude and temporal change in coverage of oak in watersheds, and the highest negative environmental loadings were for oak coverage and longitude.

TABLE 3. Species and landscape environment loadings from CCA of summer 2003 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.545	0.415
Species-environment correlations	0.813	0.783
Cumulative % variance: species data	15.4	27.1
Cumulative % variance: species-environment relation	40.0	70.5
Astyanax mexicanus	-0.661	3.774
Campostoma anomalum	1.177	1.298
Cyprinella lutrensis	1.712	3.260
Cyprinella venusta	1.097	3.483
Dionda episcopa	-0.128	-0.450
Fundulus zebrinus	-1.363	3.787
Gambusia affinis	-1.322	-0.090
Lepomis cyanellus	3.156	0.329
Lepomis megalotis	-1.419	-0.168
Cambaridae	1.737	-2.311
Latitude	0.041	0.269
Longitude	-0.101	-0.117
Basin area	-0.022	-0.070
% Juniper	0.286	0.139
% Oak	-0.072	-0.118
% Cropland	-0.210	0.044
% Change juniper	0.254	-0.046
% Change oak	-0.238	0.194
% Change rangeland	-0.125	0.096

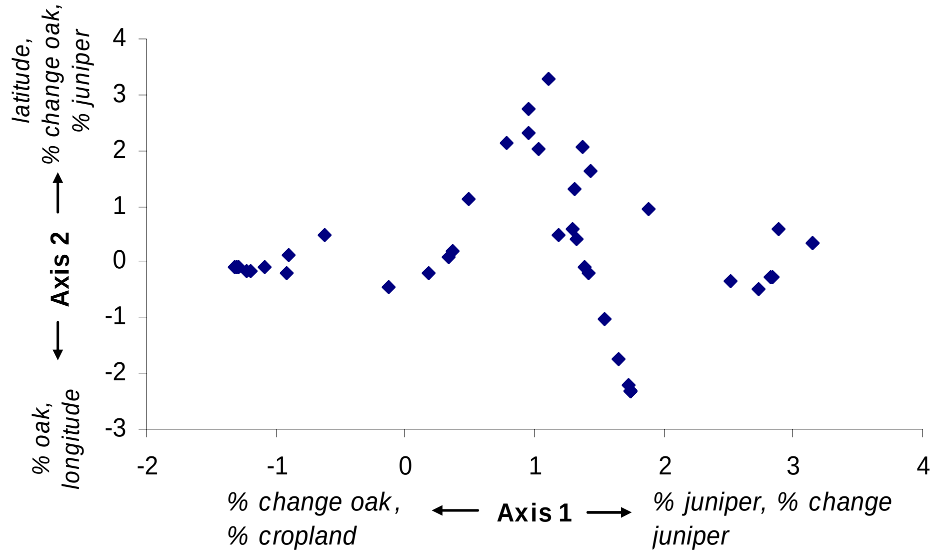

FIG. 4. Plot of site scores from CCA of summer 2003 seine data and landscape environmental variables.

Summer 2003 seine data–CCA with combined local and landscape environmental variables

CCA for summer 2003 performed with species abundance and combined local and landscape environmental variables yielded a principal gradient (modeling 22.5% of species variation, 29.7% of environment variation) that associated high abundance of eight of ten seine sample taxa (large positive axis 1 loadings) with longer stream segments, later time of day, higher discharge, gravel as the dominant substrate over the bedrock bottom, higher maximum water velocity, higher water temperature, greater riparian canopy cover over the stream (high positive loadings), and low coverage of aquatic vegetation (negative loading) (Table 4). The opposite suite of landscape attributes was associated with higher abundances of mosquitofish and longear sunfish. This dominant axis from CCA seems to reveal associations between stream discharge, stream size, riparian canopy cover, and water temperature with greater relative abundances of 8 of 10 taxa, including crayfish, sensitive minnow species, and tolerant green sunfish. The positive end of this axis was also positively associated with the coverage of juniper in local watersheds. The second CCA axis (modeling 16.7% of species variation, 22% of environment variation) yielded a species gradient that was similar to the second axis from CCA performed with local environmental variables. The most influential environmental variables for CCA axis 2 were change in oak coverage (negative loading), average water temperature (negative loading), and CV of channel width (positive loading) (Table 4, Fig. 5).

TABLE 4. Species and combined environmental loadings from CCA of summer 2003 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.796	0.590
Species-environment correlations	0.960	0.878
Cumulative % variance: species data	22.5	39.2
Cumulative % variance: species-environment relation	29.7	51.7
Astyanax mexicanus	3.725	2.958
Campostoma anomalum	2.286	-1.704
Cyprinella lutrensis	2.447	-2.980
Cyprinella venusta	1.757	-2.734
Dionda episcopa	1.788	-1.470
Fundulus zebrinus	1.738	-4.286
Gambusia affinis	-2.275	0.077
Lepomis cyanellus	2.698	2.106
Lepomis megalotis	-0.582	0.513
Cambaridae	2.099	2.750
Time of day	0.204	0.008
Length of site	0.221	0.089
% Canopy cover	0.144	0.002

TABLE 4. Continued.

Species/Environment	Axis 1	Axis 2
% Woody debris	0.065	-0.028
% Aquatic vegetation	-0.175	0.077
Discharge	0.188	-0.113
Depth (avg)	0.045	0.139
Depth (CV)	0.070	0.046
Velocity (max)	0.181	0.066
Width (avg)	-0.007	-0.050
Water temperature (avg)	0.145	-0.195
pH (avg)	0.137	-0.026
Width (CV)	0.079	0.160
DO (CV)	-0.061	0.059
Water temperature (CV)	-0.106	-0.010
Conductivity (CV)	0.030	-0.058
Silt/clay/detritus	-0.048	-0.047
Mud	-0.113	0.109
Sand	-0.031	0.134
Gravel	0.185	-0.109
Cobble	0.135	-0.060
Longitude	-0.043	0.007
Basin area	-0.039	0.109
% Juniper	0.129	0.066
% Oak	0.002	-0.038
% Change oak	-0.109	-0.249

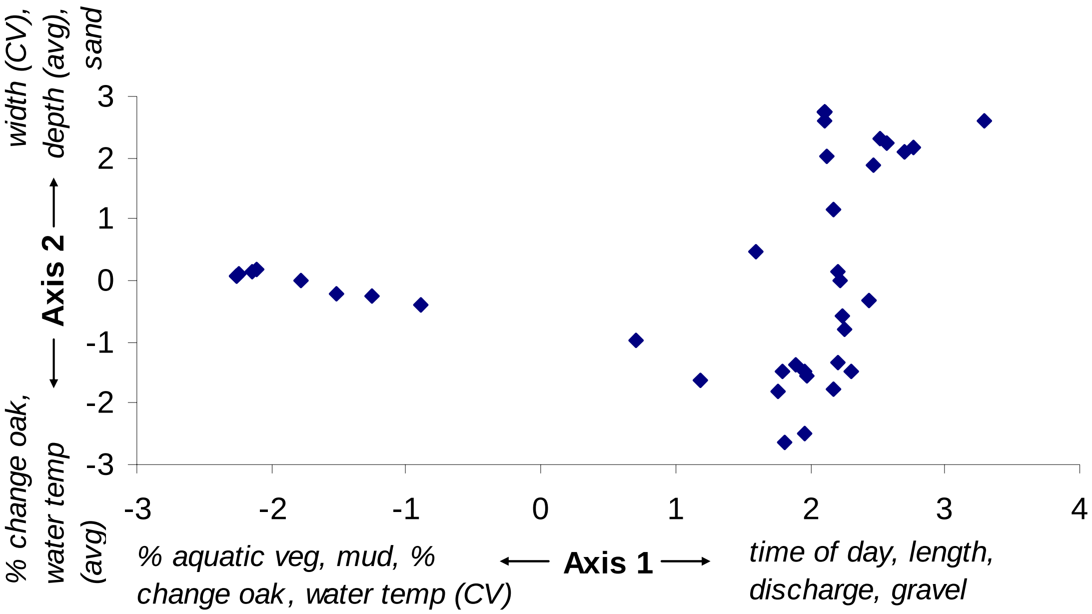

FIG. 5. Plot of site scores from CCA of summer 2003 seine data and combined environmental variables.

Spring 2004 seine data–CA analysis of species assemblages

CA ordination of seine collections from the spring 2004 survey revealed a principal gradient (modeling 40.6% of variation) that was similar in some ways to the principal species gradient obtained during the summer. Axis 1 was still dominated by crayfish (Cambaridae) and stonerollers (*Campostoma anomalum*) at one end of the gradient (negative loadings), but the other end of the gradient described assemblages dominated by five other species with large positive loadings that included the two sunfish species (*Lepomis* spp.), mosquitofish (*Gambusia affinis*), a minnow (*Dionda episcopa*), and the greenthroat darter (*Etheostoma lepidum*) (Table 5, Fig. 6). The plains killifish (*Fundulus zebrinus*) and both shiner species (*Cyprinella* spp.) were not captured or rarely captured at the same sites during spring 2004. The second axis (modeling 23.8% of variation) contrasted species assemblages with abundant green sunfish, minnows and darters (positive loadings) with those having larger numbers of mosquitofish (negative loading).

TABLE 5. Species loadings from CA of spring 2004 seine data.

Species	**Axis 1**	**Axis 2**
Eigenvalue	0.818	0.480
Cumulative % variance: species data	40.6	64.4
Campostoma anomalum	-0.812	3.190
Dionda episcopa	6.901	2.544
Etheostoma lepidum	6.853	2.978
Gambusia affinis	6.890	-1.249
Lepomis cyanellus	3.134	6.617
Lepomis megalotis	7.426	0.825
Cambaridae	-0.847	-0.327

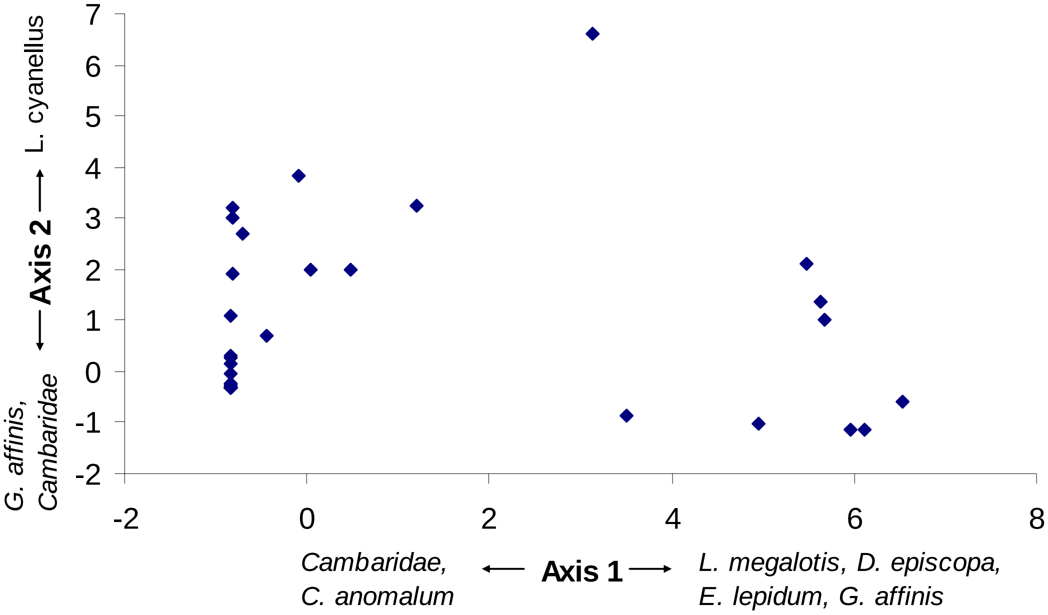

FIG. 6. Plot of site scores from CA of spring 2004 seine data.

Spring 2004 seine data–CCA with local environmental variables

CCA for spring 2004 performed with species abundance and local environmental variables yielded a principal gradient (modeling 34.5% of species variation, 48.8 % of environment variation) that associated high abundance of all six fish species (positive axis 1 loadings) with higher average conductivity, average width, and densities of aquatic vegetation (all with high positive loadings) plus lower CV of depth and average pH (high negative loadings) (Table 6, Fig. 7). The opposite suite of environmental conditions tended to be associated with higher abundances of crayfish. The second CCA axis (modeling 17.4% of species variation, 24.6% of environment variation) contrasted sites with relatively large abundances of five fish species (high positive axis 2 loadings) and those tending to have higher abundances of mosquitofish and crayfish (negative loadings) (Table 6). Highest positive environmental loadings on axis 2 were for aquatic vegetation coverage, average pH and average dissolved oxygen concentration, and highest negative environmental loadings were for coverage of submerged woody debris and percent canopy coverage over the stream (Table 6).

TABLE 6. Species and local environment loadings from CCA of spring 2004 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.695	0.351
Species-environment correlations	0.931	0.858
Cumulative % variance: species data	34.5	51.9
Cumulative % variance: species-environment relation	48.8	73.4
Campostoma anomalum	0.677	2.112
Dionda episcopa	4.316	2.765
Etheostoma lepidum	3.998	2.934
Gambusia affinis	5.422	-1.306
Lepomis cyanellus	1.715	6.607

TABLE 6. Continued.

Species/Environment	**Axis 1**	**Axis 2**
Lepomis megalotis	5.680	0.504
Cambaridae	-0.728	-0.240
Time of day	-0.055	-0.019
Length of site	0.025	-0.020
% Canopy cover	-0.002	-0.118
% Woody debris	0.062	-0.146
% Aquatic vegetation	0.282	0.181
Discharge	0.113	-0.054
Depth (max)	-0.002	-0.021
Depth (CV)	-0.165	-0.009
Velocity (max)	0.045	0.060
Velocity (avg)	0.145	-0.045
Width (avg)	0.172	0.100
DO (avg)	0.097	0.148
Water temperature (avg)	-0.056	-0.011
Conductivity (avg)	0.173	-0.060
pH (avg)	-0.163	0.159
Width (CV)	-0.098	0.018
DO (CV)	-0.039	-0.032
Water temperature (CV)	-0.021	0.031
Conductivity (CV)	-0.039	0.066
pH (CV)	0.059	-0.027
Silt/clay/detritus	0.077	-0.030
Mud	-0.025	-0.018
Sand	-0.021	-0.057
Gravel	0.016	0.116
Cobble	-0.058	-0.020

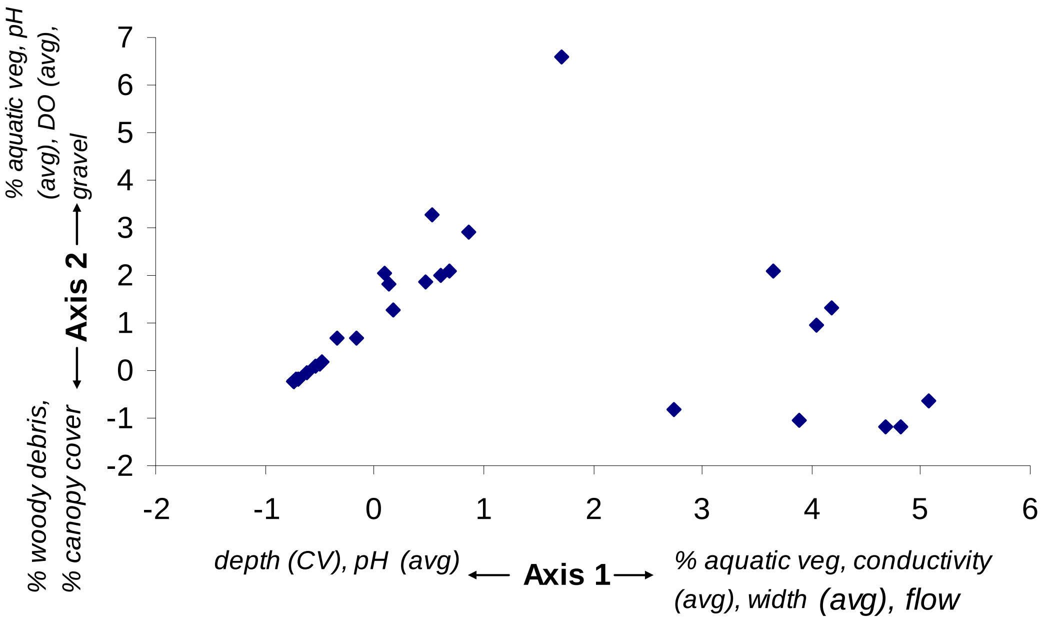

FIG. 7. Plot of site scores from CCA of spring 2004 seine data and local environmental variables.

Spring 2004 seine data–CCA with landscape environmental variables

CCA for spring 2004 performed with species abundance and landscape environmental variables yielded a principal gradient (modeling 21.2% of species variation, 47.1% of environment variation) that associated high abundance of five of the six fish species, especially *Dionda episcopa* and *Etheostoma lepidum* (large positive axis 1 loadings), with higher coverage of rangeland in the watershed (moderate positive loading), recent reduction in rangeland coverage in the watershed (moderate negative loading for percent change between 1999 and 2003), and smaller watershed area (moderate negative loading) (Table 7). The opposite suite of landscape attributes was weakly associated with higher abundances of stonerollers and crayfish (low negative loadings). This dominant axis from CCA was influenced very little by juniper and changes in oak and cropland coverage in watersheds. The second CCA axis (modeling 16.1% of species variation, 35.6% of environment variation) contrasted sites with relatively large abundances of five fish species (high positive loadings) with sites weakly dominated by crayfish and mosquitofish (moderate negative axis-2 loadings) (Table 7, Fig. 8). Highest positive environmental loadings on axis 2 were for latitude and percent coverage of juniper in watersheds, and the highest negative environmental loading was for increased oak coverage in watersheds between 1999 and 2003.

TABLE 7. Species and landscape environment loadings from CCA of spring 2004 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.428	0.323
Species-environment correlations	0.832	0.838
Cumulative % variance: species data	21.2	37.3
Cumulative % variance: species-environment relation	47.1	82.7
Campostoma anomalum	-0.895	4.483
Dionda episcopa	10.653	0.778
Etheostoma lepidum	10.653	0.778
Gambusia affinis	1.987	-0.319
Lepomis cyanellus	2.241	2.261
Lepomis megalotis	5.803	0.080
Cambaridae	-0.342	-0.374
Latitude	-0.010	0.303
Longitude	0.081	0.039
Basin area	-0.165	-0.079
% Juniper	-0.021	0.419
% Rangeland	0.185	0.035
% Change oak	-0.029	-0.252
% Change cropland	-0.052	-0.024
% Change rangeland	-0.216	0.009

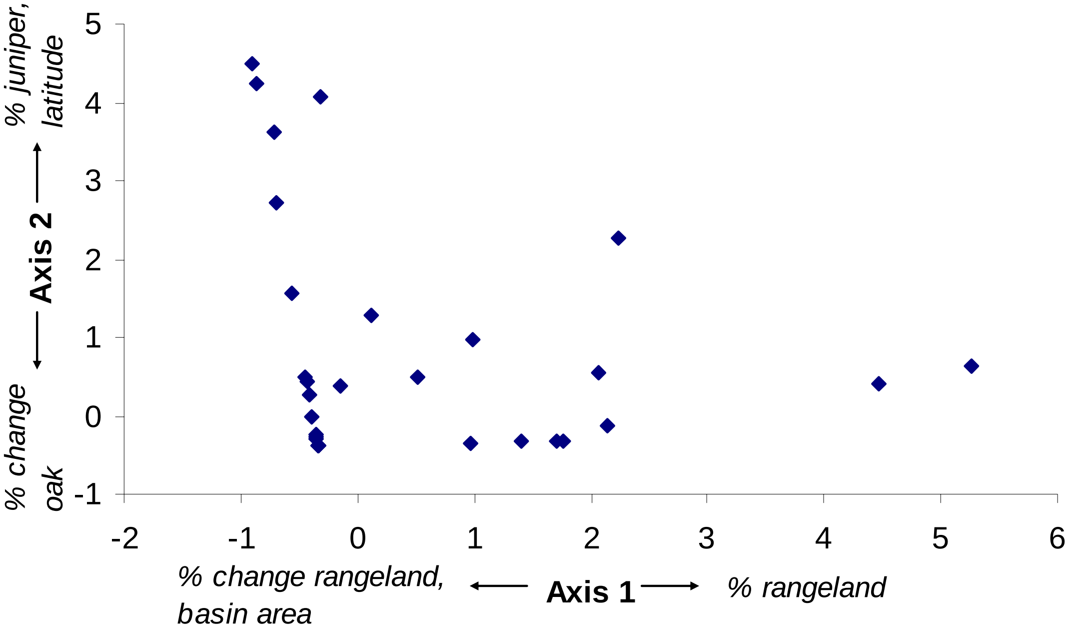

FIG. 8. Plot of site scores from CCA of spring 2004 seine data and landscape environmental variables.

Spring 2004 seine data–CCA with combined local and landscape environmental variables

CCA for spring 2004 performed with species abundance and combined local and landscape environmental variables yielded a principal gradient (modeling 37.2% of species variation, 45% of environment variation) that associated high abundance of five of seven seine sample taxa (high positive axis 1 loadings) with more aquatic vegetation, greater average width, higher average conductivity, greater average water velocity (high positive loadings), and lower depth variation, watershed basin area, and decrease in the coverage of rangeland between 1999 and 2003 (negative loading) (Table 8, Fig. 9). The opposite suite of landscape attributes was associated with higher abundances of stonerollers and crayfish. This species assemblage gradient was virtually the same as that obtained from CCA using only local environmental variables. Vegetation cover did not appear to have a significant association with local environmental variables and fishes and crayfishes. The second CCA axis (modeling 19.6% of species variation, 23.6% of environment variation) yielded a species gradient that also was similar to the second axis from CCA performed with local environmental variables. The most influential environmental variables for CCA axis 2 were percent coverage of juniper in the watershed (high positive loading) and change in oak coverage between 1999 and 2003 (high negative loading) (Table 8).

TABLE 8. Species and combined environmental loadings from CCA of spring 2004 seine data.

Species/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.750	0.395
Species-environment correlations	0.959	0.918
Cumulative % variance: species data	37.2	56.8
Cumulative % variance: species-environment relation	45.0	68.6
Campostoma anomalum	-0.192	4.480
Dionda episcopa	6.811	0.933
Etheostoma lepidum	6.781	0.791
Gambusia affinis	5.718	-0.877
Lepomis cyanellus	2.813	3.329
Lepomis megalotis	6.965	0.006
Cambaridae	-0.759	-0.345
Time of day	-0.053	-0.031
Length of site	0.033	-0.049
% Canopy cover	-0.010	-0.078
% Woody debris	0.049	-0.115
% Aquatic vegetation	0.257	0.175
Discharge	0.092	-0.011
Depth (max)	0.011	-0.074
Depth (CV)	-0.142	-0.073
Velocity (avg)	0.124	-0.021
Width (avg)	0.164	0.071

TABLE 8. Continued.

Species/Environment	Axis 1	Axis 2
DO (avg)	0.081	0.158
Conductivity (avg)	0.143	-0.025
Width (CV)	-0.082	-0.024
DO (CV)	-0.026	-0.090
Water temperature (CV)	-0.014	-0.019
Conductivity (CV)	-0.035	0.045
pH (CV)	0.058	-0.047
Silt/clay/detritus	0.074	-0.042
Mud	-0.022	-0.024
Sand	-0.022	-0.038
Gravel	0.005	0.158
Cobble	-0.057	0.009
Longitude	0.056	0.019
Basin area	-0.149	-0.048
% Juniper	0.009	0.399
% Rangeland	0.055	0.037
% Change oak	-0.056	-0.241
% Change cropland	-0.038	-0.016
% Change rangeland	-0.126	0.019

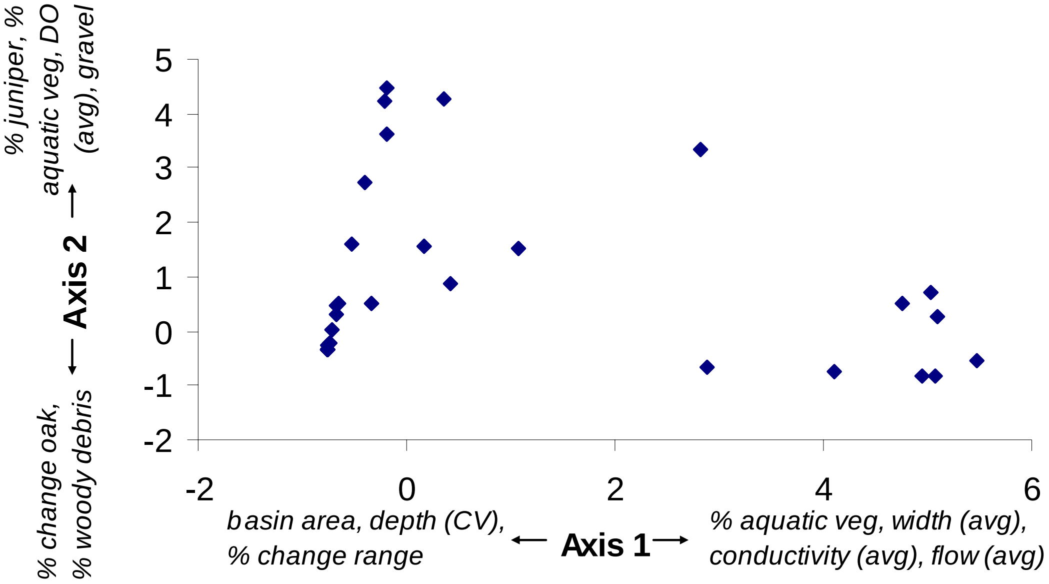

FIG. 9. Plot of site scores from CCA of spring 2004 seine data and combined environmental variables.

Summer 2003 macroinvertebrate data–CA analysis of taxa assemblages

CA ordination of macroinvertebrate collections from the summer 2003 survey revealed a principal gradient (modeling 20.7% of variation) that contrasted taxa assemblages dominated by Amphipoda, Simuliidae (Diptera), Elmidae (Coleoptera), and Polycentropodidae (Trichoptera) (all with high positive loadings) with taxa assemblages dominated by unidentified Odonata nymphs, Hydroptilidae (Trichoptera), and Pyralidae (Lepidoptera) (high negative loadings) (Table 9, Fig. 10). The second axis (modeling 14.5% of variation) contrasted taxa assemblages with abundant Hydroptilidae (Trichoptera), Ceratopogonidae (Diptera), Elmidae (Coleoptera), and Gerridae (Hemiptera) (high positive loadings) with those sites having larger numbers of Notonectidae (Hemiptera), aquatic Oligochaeta, and leeches of the class Hirudinea.

TABLE 9. Taxa loadings from CA of summer 2003 benthic macroinvertebrate data.

Taxa	**Axis 1**	**Axis 2**
Eigenvalue	0.359	0.251
Cumulative % variance: taxa data	20.7	35.2
Annelida Hirudinea	0.581	-0.963
Turbellaria	0.320	0.375
Oligochaeta	-0.758	-1.14
Crustacea Amphipoda	2.481	-0.717
Crustacea Isopoda	0.212	1.222
Pelecypoda	0.874	-0.261
Gastropoda	-0.215	-0.45
Arachnoidea	-0.016	1.169
Collembola	1.054	0.797
Coleoptera Dytiscidae	-0.482	-0.909
Coleoptera Elmidae	1.542	1.398
Coleoptera Haliplidae	-1.010	-0.718
Coleoptera Hydrophilidae	-0.710	0.415
Diptera Ceratopogonidae	-0.591	1.975
Diptera Chironomidae	-0.983	-0.928

TABLE 9. Continued.

Taxa	**Axis 1**	**Axis 2**
Diptera Culicidae	0.071	-0.154
Diptera Simuliidae	1.633	0.441
Diptera Stratiomyidae	-0.959	1.000
Diptera Tabanidae	-0.341	-0.240
Diptera Tipulidae	-0.218	1.199
Ephemeroptera Baetidae	0.269	0.268
Ephemeroptera Caenidae	1.136	0.977
Ephemeroptera Ephemeridae	1.373	-0.479
Ephemeroptera Heptageniidae	1.221	0.738
Hemiptera Gerridae	0.67	1.347
Hemiptera Belostomatidae	1.018	-0.537
Hemiptera Corixidae	0.905	-0.392
Hemiptera Notonectidae	0.796	-1.789
Hemiptera Veliidae	-0.364	0.486
Hemiptera Naucoridae	-0.116	0.204
Lepidoptera Pyralidae	-1.022	0.564
Odonata Aeshnidae	-0.943	-0.537
Odonata Coenagrionidae	-0.226	0.186
Odonata Gomphidae	0.940	0.757
Odonata Lestidae	0.446	-0.589
Odonata Libellulidae	-1.017	-0.245
Odonata unidentified	-1.700	0.111
Trichoptera Calamoceratidae	1.406	0.761
Trichoptera Hydroptilidae	-1.195	2.831
Trichoptera Odontoceridae	0.694	1.185
Trichoptera Polycentropodidae	1.508	0.968

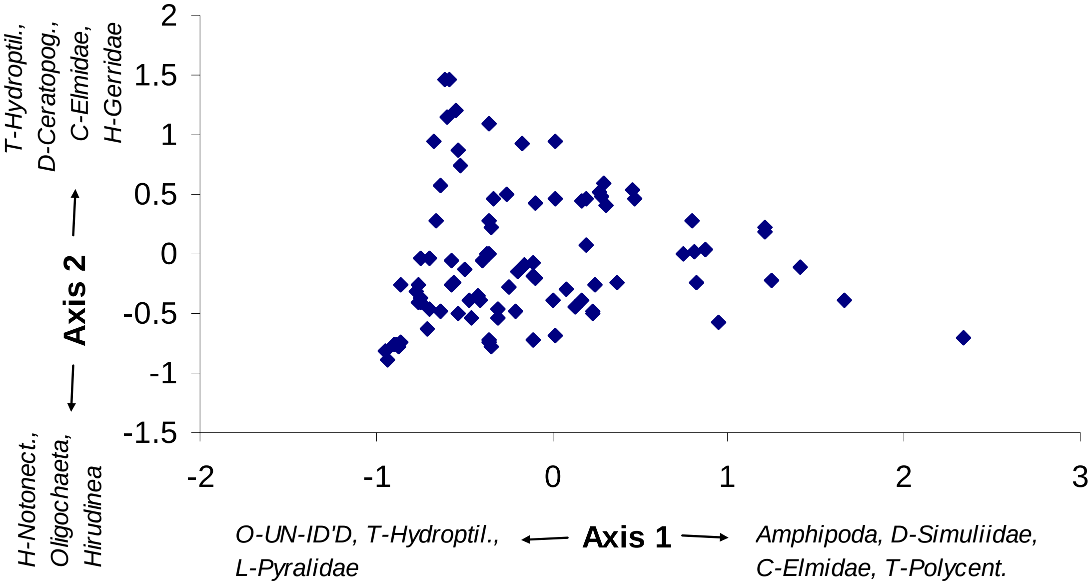

FIG. 10. Plot of site scores from CA of summer 2003 benthic macroinvertebrate data.

Summer 2003 macroinvertebrate data–CCA with local environmental variables

CCA for summer 2003 performed with taxa abundance and local environmental variables yielded a principal gradient (modeling 10.4% of species variation, 26.2% of environment variation) that associated high abundance of Gerridae (Hemiptera), Elmidae (Coleoptera), Amphipoda, and Ephemeridae (Ephemeroptera) (large positive axis 1 loadings) with greater riparian canopy cover over the stream, more variable water temperature, gravel substrate, greater ranges of depth within the site, and higher average dissolved oxygen (all with high positive loadings). In contrast, unidentified Odonata, Oligochaeta, Haliplidae (Coleoptera), and Aeshnidae (Odonata) tended to associate with silt/clay/detritus substrate, greater average stream width, higher average water temperature, and higher average water velocity (all with high negative loadings) (Table 10, Fig. 11). The second CCA axis (modeling 7.7% of species variation, 19.4% of environment variation) contrasted sites tending to have higher abundances of Notonectidae (Hemiptera), Oligochaeta, and Dytiscidae (Coleoptera) (high positive axis 2 loadings) with those tending to have relatively large abundances of Hydroptilidae, Odontoceridae and Polycentropodidae (Trichoptera), as well as Ceratopogonidae (Diptera) and Gomphidae (Odonata) (high negative loadings) (Table 10). Highest positive environmental loadings on axis 2 were for average pH, variation in dissolved oxygen concentration, and mud substrate, while highest negative loadings were for average dissolved oxygen concentration, discharge, and cobble substrate (Table 10).

TABLE 10. Taxa and local environment loadings from CCA of summer 2003 benthic macroinvertebrate data.

Taxa/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.180	0.134
Taxa-environment correlations	0.737	0.737
Cumulative % variance: taxa data	10.4	18.1
Cumulative % variance: taxa-environment relation	26.2	45.6
Annelida Hirudinea	-0.150	1.012
Turbellaria	0.074	-0.997
Oligochaeta	-1.956	1.458
Crustacea Amphipoda	1.887	0.389
Crustacea Isopoda	1.301	-0.045
Pelecypoda	0.872	-0.832
Gastropoda	-0.311	0.113
Arachnoidea	-0.824	-0.896
Collembola	0.734	0.721
Coleoptera Dytiscidae	-0.507	1.443
Coleoptera Elmidae	2.197	-0.538
Coleoptera Haliplidae	-1.249	0.540
Coleoptera Hydrophilidae	-0.314	-0.461
Diptera Ceratopogonidae	-0.998	-1.679
Diptera Chironomidae	-0.444	0.919

TABLE 10. Continued.

Taxa/Environment	Axis 1	Axis 2
Diptera Culicidae	0.616	-0.311
Diptera Simuliidae	1.571	1.131
Diptera Stratiomyidae	-0.462	-0.010
Diptera Tabanidae	-1.180	0.453
Diptera Tipulidae	0.399	-0.906
Ephemeroptera Baetidae	0.197	-0.759
Ephemeroptera Caenidae	1.362	-0.906
Ephemeroptera Ephemeridae	1.805	-0.165
Ephemeroptera Heptageniidae	1.541	-0.413
Hemiptera Gerridae	2.738	-0.674
Hemiptera Belostomatidae	0.397	0.911
Hemiptera Corixidae	1.506	-0.994
Hemiptera Notonectidae	0.005	3.125
Hemiptera Veliidae	-0.567	-0.650
Hemiptera Naucoridae	-0.708	-0.282
Lepidoptera Pyralidae	-0.640	0.049
Odonata Aeshnidae	-1.240	0.752
Odonata Coenagrionidae	-0.240	0.038
Odonata Gomphidae	0.542	-1.643
Odonata Lestidae	0.744	-0.206
Odonata Libellulidae	-0.938	0.310
Odonata unidentified	-2.311	-0.787
Trichoptera Calamoceratidae	1.601	-1.117
Trichoptera Hydroptilidae	-1.086	-3.253
Trichoptera Odontoceridae	0.947	-1.828
Trichoptera Polycentropodidae	1.212	-1.740
Time of day	-0.041	-0.027
Length of site	-0.058	0.024
% Canopy cover	0.176	0.013
% Woody debris	0.090	0.036
% Aquatic vegetation	0.004	0.046
Discharge	-0.001	-0.090
Depth (max)	-0.054	-0.023
Depth (avg)	-0.097	0.013
Depth (CV)	0.119	0.039
Velocity (max)	-0.058	-0.040
Velocity (avg)	-0.124	-0.006
Width (avg)	-0.141	0.026
DO (avg)	0.119	-0.135
Water temperature (avg)	-0.136	0.051
Conductivity (avg)	-0.105	-0.044

TABLE 10. Continued.

Taxa/Environment	Axis 1	Axis 2
pH (avg)	0.023	0.179
Width (CV)	0.107	0.018
DO (CV)	-0.001	0.130
Water temperature (CV)	0.167	0.003
Conductivity (CV)	-0.0512	0.063
pH (CV)	-0.037	0.061
Silt/clay/detritus	-0.143	-0.023
Mud	0.022	0.086
Sand	-0.025	0.041
Gravel	0.120	0.033
Cobble	0.091	-0.089

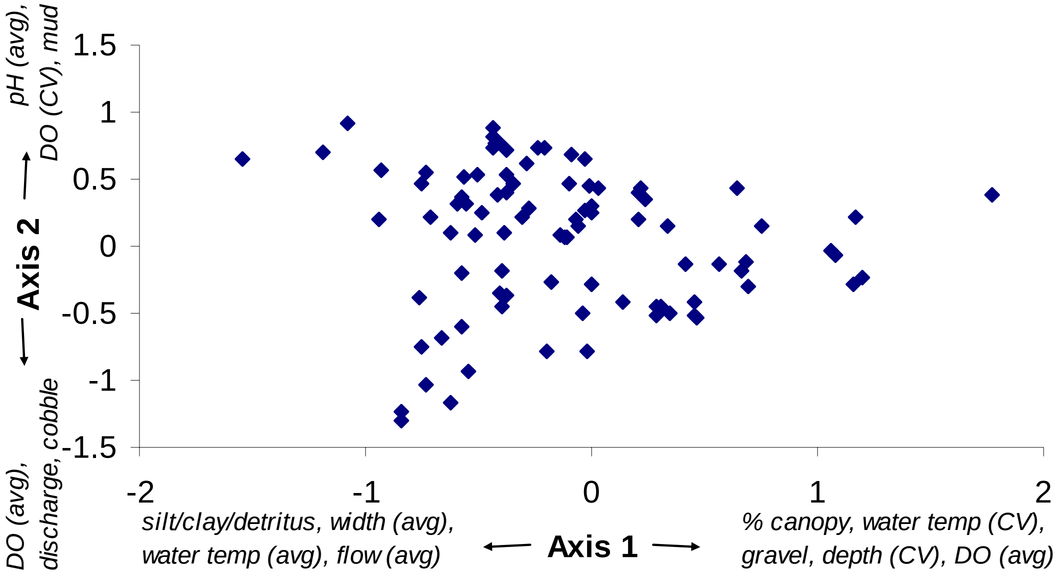

FIG. 11. Plot of site scores from CCA of summer 2003 benthic macroinvertebrate data and local environmental variables.

Summer 2003 macroinvertebrate data–CCA with landscape environmental variables

CCA for summer 2003 performed with taxa abundance and landscape environmental variables yielded a principal gradient (modeling 12.8% of species variation, 43.6% of environment variation) that associated high abundance of unidentified Odonata, Haliplidae (Coleoptera), Pyralidae (Lepidoptera), Libellulidae (Odonata), and Oligochaeta (largest positive axis 1 loadings) with greater latitude, higher percent coverage of cropland in the watershed, increase in cropland coverage in the watershed between 1999 and 2003, and increase in oak coverage in the watershed (Table 11). In contrast, higher abundances of Simuliidae (Diptera), Amphipoda, Notonectidae (Hemiptera), and Calamoceratidae (Trichoptera) were associated with increases in percent coverage of juniper between 1999 and 2003 (largest negative loadings). The second CCA axis (modeling 5.5% of species variation, 18.7% of environment variation) contrasted sites with relatively large abundances of Gerridae (Hemiptera), Collembola, Isopoda, and Simuliidae (Diptera) (high positive loadings) with sites containing leeches of the class Hirudinea, Aeshnidae (Odonata), Notonectidae (Hemiptera), and Amphipoda (largest negative loadings on axis 2) (Table 11, Fig. 12). The highest positive environmental loadings on axis 2 were for the percent coverage of rangeland in the watershed, high latitudes, and large basin areas, and the highest negative environmental loading was for percent of oak in watersheds.

TABLE 11. Taxa and landscape environment loadings from CCA of summer 2003 benthic macroinvertebrate data.

Taxa/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.222	0.095
Taxa-environment correlations	0.797	0.668
Cumulative % variance: taxa data	12.8	18.3
Cumulative % variance: taxa-environment relation	43.6	62.3
Annelida Hirudinea	-0.102	-2.246
Turbellaria	-0.374	-0.619
Oligochaeta	1.306	-0.139
Crustacea Amphipoda	-2.007	-1.424
Crustacea Isopoda	-1.326	7.684
Pelecypoda	-0.205	-0.416
Gastropoda	0.456	-0.511
Arachnoidea	-0.539	2.351
Collembola	-1.798	7.861
Coleoptera Dytiscidae	0.990	-1.011
Coleoptera Elmidae	-1.638	1.429
Coleoptera Haliplidae	1.986	-0.368
Coleoptera Hydrophilidae	0.776	0.397
Diptera Ceratopogonidae	0.233	0.964
Diptera Chironomidae	0.934	-0.482
Diptera Culicidae	-0.383	0.780
Diptera Simuliidae	-2.032	5.423
Diptera Stratiomyidae	0.893	0.104
Diptera Tabanidae	1.083	-0.784
Diptera Tipulidae	-0.756	2.102
Ephemeroptera Baetidae	-0.633	-0.129
Ephemeroptera Caenidae	-1.291	1.890
Ephemeroptera Ephemeridae	-1.734	0.049
Ephemeroptera Heptageniidae	-1.460	3.119
Hemiptera Gerridae	-0.976	8.295
Hemiptera Belostomatidae	-0.694	-0.580
Hemiptera Corixidae	-0.992	3.299
Hemiptera Notonectidae	-1.934	-1.942
Hemiptera Veliidae	-0.695	0.522
Hemiptera Naucoridae	0.432	-0.344
Lepidoptera Pyralidae	1.867	0.690
Odonata Aeshnidae	0.333	-2.158
Odonata Coenagrionidae	0.510	0.153
Odonata Gomphidae	-1.377	2.057
Odonata Lestidae	-0.446	1.231

TABLE 11. Continued.

Taxa/Environment	Axis 1	Axis 2
Odonata Libellulidae	1.563	0.330
Odonata unidentified	2.967	0.299
Trichoptera Calamoceratidae	-1.923	1.743
Trichoptera Hydroptilidae	0.596	0.861
Trichoptera Odontoceridae	-0.321	-0.537
Trichoptera Polycentropodidae	-1.365	1.441
Latitude	0.222	0.107
Longitude	0.072	-0.025
Basin area	-0.025	0.073
% Juniper	-0.001	0.029
% Oak	0.044	-0.139
% Cropland	0.201	0.026
% Rangeland	0.034	0.115
% Change juniper	-0.215	-0.023
% Change oak	0.183	0.057
% Change cropland	0.185	0.059
% Change rangeland	0.071	-0.032

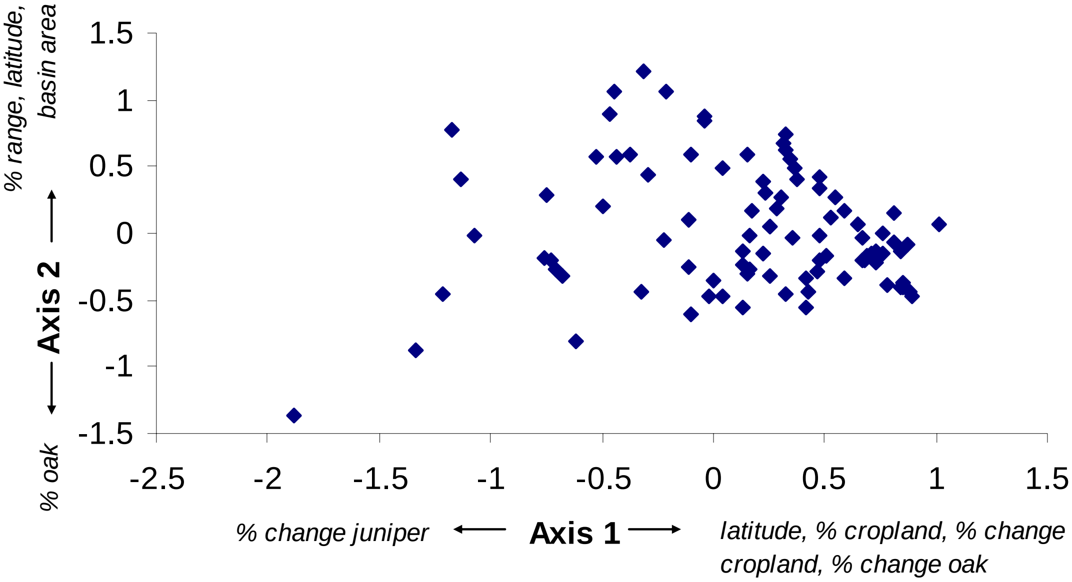

FIG. 12. Plot of site scores from CCA of summer 2003 benthic macroinvertebrate data and landscape environmental variables.

Summer 2003 macroinvertebrate data–CCA with combined local and landscape environmental variables

CCA for summer 2003 performed with taxa abundance and combined local and landscape environmental variables yielded a principal gradient (modeling 16.7% of species variation, 29.4% of environment variation) that associated high abundance of Elmidae (Coleoptera), Amphipoda, Simuliidae (Diptera), Heptageniidae (Ephemeroptera), and Calamoceratidae (Trichoptera) (high positive axis 1 loadings) with increased juniper coverage between 1999 and 2003, increased variation in water temperature, greater canopy coverage, increased range in depth, and higher average dissolved oxygen (high positive loadings) (Table 12, Fig. 13). Higher abundances of unidentified and Libellulidae Odonata, Haliplidae (Coleoptera), Pyralidae (Lepidoptera), and Oligochaeta were associated with greater latitudes, higher cropland coverage, increased oak in the watershed between 1999 and 2003, and silt/clay/detritus substrates (high negative loadings on axis 1). The second CCA axis (modeling 9.1% of species variation, 16.2% of environment variation) contrasted sites with relatively large abundances of Gerridae Hemiptera, Hydroptilidae (Trichoptera), Isopoda, and Collembola (high positive loadings) with sites more dominated by Notonectidae (Hemiptera), and Dytiscidae (Coleoptera) (largest negative loadings on axis 2) (Table 12). The highest positive environmental loadings on axis 2 were for basin area, average dissolved oxygen, discharge, latitude, and percent coverage of rangeland in the watershed; the highest negative environmental loadings were for average pH and variation in dissolved oxygen concentration (Fig. 13).

TABLE 12. Taxa and combined local and landscape environmental variable loadings from CCA of summer 2003 benthic macroinvertebrate data.

Taxa/Environment	Axis 1	Axis 2
Eigenvalue	0.289	0.159
Taxa-environment correlations	0.901	0.805
Cumulative % variance: taxa data	16.7	25.8
Cumulative % variance: taxa-environment relation	29.4	45.6
Annelida Hirudinea	0.404	-0.856
Turbellaria	0.079	0.470
Oligochaeta	-1.153	-0.551
Crustacea Amphipoda	2.257	-0.896
Crustacea Isopoda	0.795	2.469
Pelecypoda	0.530	0.493
Gastropoda	-0.520	-0.447
Arachnoidea	0.115	1.526
Collembola	1.198	2.381
Coleoptera Dytiscidae	-0.507	-1.375
Coleoptera Elmidae	2.302	-0.249
Coleoptera Haliplidae	-1.294	-0.136
Coleoptera Hydrophilidae	-0.550	0.641
Diptera Ceratopogonidae	-0.545	1.724
Diptera Chironomidae	-0.892	-0.895
Diptera Culicidae	0.291	0.498
Diptera Simuliidae	2.030	1.479
Diptera Stratiomyidae	-0.862	0.398
Diptera Tabanidae	-0.797	-0.266
Diptera Tipulidae	0.345	1.250
Ephemeroptera Baetidae	0.479	0.624
Ephemeroptera Caenidae	1.201	1.063
Ephemeroptera Ephemeridae	1.601	-0.085
Ephemeroptera Heptageniidae	1.841	0.825
Hemiptera Gerridae	0.924	2.896
Hemiptera Belostomatidae	0.931	-0.562
Hemiptera Corixidae	1.270	1.525
Hemiptera Notonectidae	0.246	-2.599
Hemiptera Veliidae	0.025	0.566
Hemiptera Naucoridae	-0.140	0.727
Lepidoptera Pyralidae	-1.187	1.398
Odonata Aeshnidae	-0.822	-1.130
Odonata Coenagrionidae	-0.264	0.187
Odonata Gomphidae	1.269	1.470
Odonata Lestidae	0.075	0.135
Odonata Libellulidae	-1.718	-0.252

TABLE 12. Continued.

Taxa/Environment	**Axis 1**	**Axis 2**
Odonata unidentified	-2.261	0.937
Trichoptera Calamoceratidae	1.703	1.397
Trichoptera Hydroptilidae	-0.871	2.749
Trichoptera Odontoceridae	0.902	1.349
Trichoptera Polycentropodidae	1.062	1.347
Time of day	-0.022	0.027
Length of site	-0.046	-0.015
% Canopy cover	0.137	-0.027
% Woody debris	0.051	-0.025
% Aquatic vegetation	0.011	-0.040
Discharge	0.017	0.096
Depth (max)	-0.021	0.030
Depth (avg)	-0.075	0.014
Depth (CV)	0.120	-0.076
Velocity (max)	-0.019	0.064
Velocity (avg)	-0.089	0.037
Width (avg)	-0.115	0.000
DO (avg)	0.109	0.107
Water temperature (avg)	-0.114	-0.029
Conductivity (avg)	-0.060	0.073
pH (avg)	-0.010	-0.184
Width (CV)	0.084	-0.033
DO (CV)	0.002	-0.123
Water temperature (CV)	0.162	-0.047
Conductivity (CV)	-0.066	-0.076
pH (CV)	-0.055	-0.070
Silt/clay/detritus	-0.121	0.036
Mud	0.004	-0.066
Sand	-0.020	-0.025
Gravel	0.093	-0.051
Cobble	0.101	0.061
Latitude	-0.222	0.089
Longitude	-0.068	-0.034
Basin area	0.010	0.129
% Juniper	-0.009	0.043
% Cropland	-0.195	0.009
% Rangeland	-0.039	0.085
% Change juniper	0.200	0.034
% Change oak	-0.170	-0.016
% Change rangeland	-0.065	-0.008

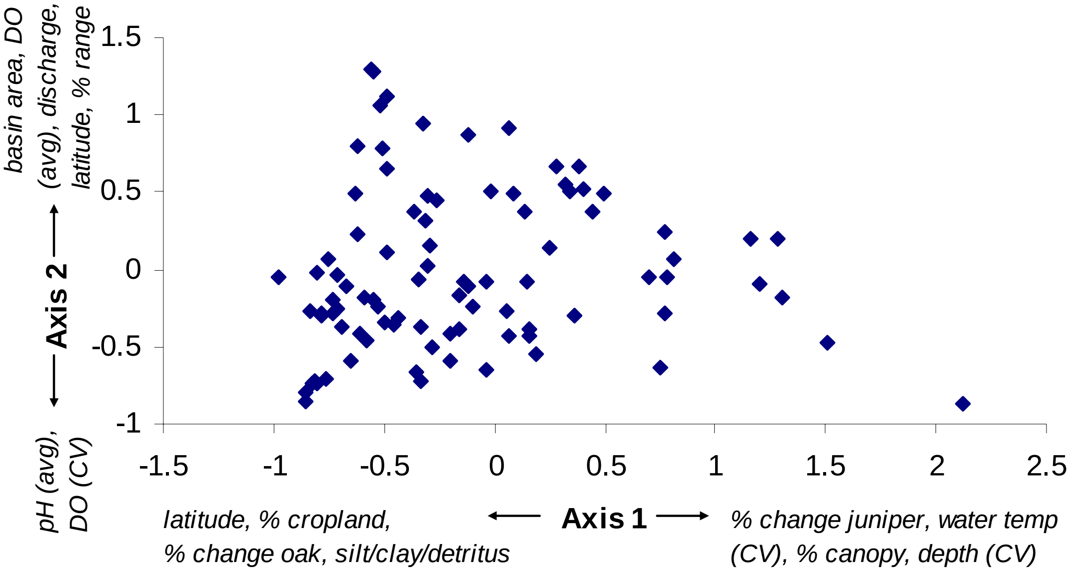

FIG. 13. Plot of site scores from CCA of summer 2003 benthic macroinvertebrate data and combined environmental variables.

Spring 2004 macroinvertebrate data–CA analysis of taxa assemblages

CA ordination of macroinvertebrate collections from the spring 2004 survey revealed a principal gradient (modeling 15.4% of variation) that contrasted taxa assemblages dominated by Culicidae (Diptera) and to a lesser degree Hydrophilidae (Coleoptera) (both with high positive loadings) with taxa assemblages dominated by Amphipoda, leeches of class Hirudinea, Pelecypoda, and Caenidae (Ephemeroptera) (high negative loadings) (Table 13, Fig. 14). The second axis (modeling 13.5% of variation) contrasted taxa assemblages with abundant leeches of class Hirudinea, Amphipoda, Notonectidae (Hemiptera), Gomphidae (Odonata), and Naucoridae (Hemiptera) (high positive loadings) with those sites having larger numbers of Dixidae

(Diptera), Caenidae, Ephemeridae, and Heptageniidae (Ephemeroptera), as well as Polycentropodidae (Trichoptera) (high negative loadings on axis 2) (Table 13).

TABLE 13. Taxa loadings from CA of spring 2004 benthic macroinvertebrate data.

Taxa	**Axis 1**	**Axis 2**
Eigenvalue	0.367	0.323
Cumulative % variance: taxa data	15.4	28.9
Annelida Hirudinea	-1.377	2.224
Turbellaria	-0.519	0.977
Oligochaeta	1.436	-0.149
Crustacea Amphipoda	-1.674	2.105
Pelecypoda	-1.278	0.484
Gastropoda	0.296	-0.038
Arachnoidea	0.168	-1.039
Collembola	-0.300	-1.566
Coleoptera Dytiscidae	1.443	0.670
Coleoptera Elmidae	0.240	-0.581
Coleoptera Haliplidae	0.062	0.106
Coleoptera Hydrophilidae	2.421	0.412
Diptera Ceratopogonidae	1.225	-0.160
Diptera Chironomidae	0.253	0.330
Diptera Culicidae	6.581	0.930
Diptera Dixidae	-0.784	-2.520
Diptera Simuliidae	-0.340	-1.212
Diptera Stratiomyidae	0.797	0.530
Diptera Tabanidae	0.402	1.403
Diptera Tipulidae	0.865	-0.757
Ephemeroptera Baetidae	-0.797	0.363
Ephemeroptera Caenidae	-1.233	-2.195
Ephemeroptera Ephemeridae	-0.562	-2.163
Ephemeroptera Heptageniidae	-0.694	-2.001
Hemiptera Corixidae	0.151	-1.194
Hemiptera Notonectidae	-1.020	1.775
Hemiptera Naucoridae	-1.091	1.715
Odonata Coenagrionidae	-0.079	-0.322
Odonata Gomphidae	-0.361	1.772
Odonata Lestidae	-0.574	0.791
Odonata Libellulidae	1.075	0.683
Odonata unidentified	0.251	1.448
Trichoptera Calamoceratidae	-0.648	-0.580

TABLE 13. Continued.

Taxa	Axis 1	Axis 2
Trichoptera Hydroptilidae	-0.649	-0.646
Trichoptera Odontoceridae	-0.573	-0.658
Trichoptera Polycentropodidae	-0.794	-1.944

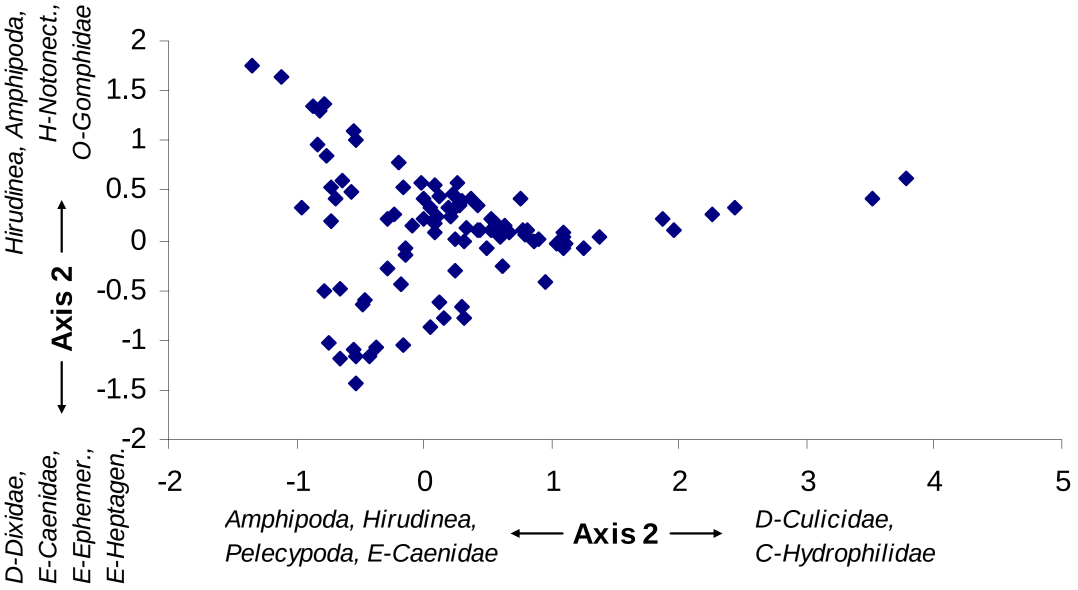

FIG. 14. Plot of site scores from CA of spring 2004 benthic macroinvertebrate data.

Spring 2004 macroinvertebrate data–CCA with local environmental variables

CCA for spring 2004 performed with taxa abundance and local environmental variables yielded a principal gradient (modeling 8.8% of species variation, 24.2% of environment variation) that associated high abundances of Hydrophilidae (Coleoptera), Stratiomyidae and Culicidae (Diptera), as well as Gomphidae (Odonata) and Ceratopogonidae (Diptera) (large positive axis 1 loadings) with higher average water temperature, greater average stream width, and greater maximum depth (all with high positive loadings). In contrast, Calamoceratidae (Trichoptera), Caenidae (Ephemeroptera), Collembola, and Polycentropodidae (Trichoptera) tended to associate with cobble substrate, greater riparian canopy cover over the stream, and more woody debris in the stream (all with high negative loadings) (Table 14, Fig. 15). The second CCA axis (modeling 5.9% of species variation, 16.5% of environment variation) contrasted sites tending to have higher abundances of Culicidae (Diptera), Polycentropodidae (Trichoptera), Dixidae (Diptera), and Elmidae (Coleoptera) (high positive axis 2 loadings) with those tending to have relatively large abundances of Notonectidae (Hemiptera), unidentified Odonata, Lestidae (Odonata), and Amphipoda (high negative loadings) (Table 14). Highest positive environmental loadings on axis 2 were for variation in stream width, time of day, maximum water velocity, and average velocity, while highest negative loadings were for silt/clay/detritus substrate and variation in pH (Table 14).

TABLE 14. Taxa and local environment loadings from CCA of spring 2004 benthic macroinvertebrate data.

Taxa/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.209	0.141
Taxa-environment correlations	0.800	0.690
Cumulative % variance: taxa data	8.8	14.7
Cumulative % variance: taxa-environment relation	24.2	40.7
Annelida Hirudinea	-1.027	-1.302
Turbellaria	-0.081	-0.681
Oligochaeta	0.760	0.578
Crustacea Amphipoda	-0.689	-1.785
Pelecypoda	-1.039	-0.444
Gastropoda	-0.762	-0.387
Arachnoidea	0.818	-0.141

TABLE 14. Continued.

Taxa/Environment	Axis 1	Axis 2
Collembola	-1.800	2.219
Coleoptera Dytiscidae	1.203	0.121
Coleoptera Elmidae	0.742	2.253
Coleoptera Haliplidae	0.724	-0.271
Coleoptera Hydrophilidae	3.216	1.023
Diptera Ceratopogonidae	1.395	0.986
Diptera Chironomidae	0.536	-0.623
Diptera Culicidae	2.134	3.076
Diptera Dixidae	-1.079	2.397
Diptera Simuliidae	-1.180	1.630
Diptera Stratiomyidae	2.681	1.429
Diptera Tabanidae	0.939	-0.102
Diptera Tipulidae	-0.079	0.745
Ephemeroptera Baetidae	-0.736	-0.187
Ephemeroptera Caenidae	-1.923	1.436
Ephemeroptera Ephemeridae	-0.534	0.485
Ephemeroptera Heptageniidae	0.088	-1.115
Hemiptera Corixidae	-0.896	0.133
Hemiptera Notonectidae	-0.601	-3.004
Hemiptera Naucoridae	0.607	-1.144
Odonata Coenagrionidae	-0.545	-0.538
Odonata Gomphidae	1.893	0.930
Odonata Lestidae	-0.438	-1.821
Odonata Libellulidae	0.631	-0.070
Odonata unidentified	-1.086	-2.286
Trichoptera Calamoceratidae	-2.139	-0.245
Trichoptera Hydroptilidae	0.623	0.381
Trichoptera Odontoceridae	-0.124	2.187
Trichoptera Polycentropodidae	-1.611	2.705
Time of day	0.026	0.121
Length of site	0.035	-0.028
% Canopy cover	-0.133	-0.061
% Woody debris	-0.128	0.026
% Aquatic vegetation	0.033	-0.044
Discharge	0.131	0.058
Depth (max)	0.177	0.019
Depth (CV)	0.060	-0.077
Velocity (max)	-0.089	0.111
Velocity (avg)	-0.063	0.107
Width (avg)	0.191	-0.055
DO (avg)	0.085	0.087

TABLE 14. Continued.

Taxa/Environment	Axis 1	Axis 2
Water temperature (avg)	0.212	0.039
Conductivity (avg)	0.143	0.017
pH (avg)	0.152	0.036
Width (CV)	0.005	0.134
DO (CV)	0.074	-0.032
Water temperature (CV)	-0.020	0.029
Conductivity (CV)	0.054	-0.056
pH (CV)	0.040	-0.119
Silt/clay/detritus	0.119	-0.150
Mud	0.088	-0.001
Sand	0.065	0.058
Gravel	-0.021	0.068
Cobble	-0.216	0.042

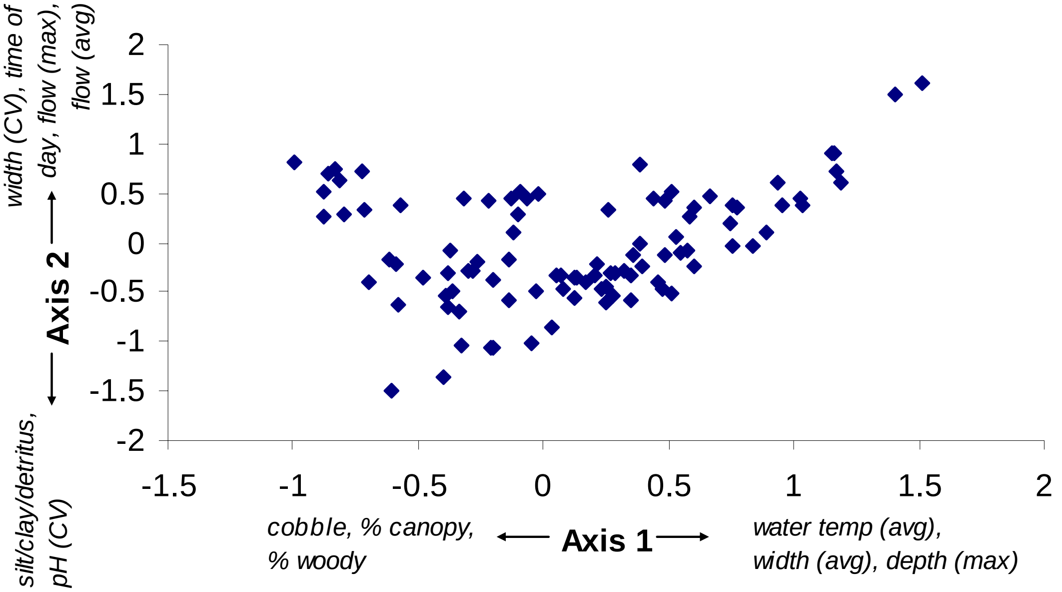

FIG. 15. Plot of site scores from CCA of spring 2004 benthic macroinvertebrate data and local environmental variables.

Spring 2004 macroinvertebrate data–CCA with landscape environmental variables

CCA for spring 2004 performed with taxa abundance and landscape environmental variables yielded a principal gradient (modeling 10.0% of species variation, 36.3% of environment variation) that associated high abundance of Culicidae (Diptera), Hydrophilidae and Dytiscidae (Coleoptera), and Ceratopogonidae (Diptera) (largest positive axis 1 loadings) with greater latitude, higher percent coverage of cropland in the watershed, and larger basin area (Table 15). In contrast, higher abundances of Caenidae (Ephemeroptera), Lestidae (Odonata), Collembola, Pelecypoda, and Calamoceratidae (Trichoptera) were associated with increases in percent coverage of juniper between 1999 and 2003 (largest negative loadings). The second CCA axis (modeling 5.9% of species variation, 21.2% of environment variation) contrasted sites with relatively large abundances of Ephemeridae and Heptageniidae (Ephemeroptera), Dixidae (Diptera), and Corixidae (Hemiptera) (high positive loadings) with sites more dominated by leeches of class Hirudinea, Gomphidae (Odonata), Pelecypoda, Turbellaria, and Amphipoda (largest negative loadings on axis 2) (Table 15, Fig. 16). The highest positive environmental loading on axis 2 was for increase in juniper coverage between 1999 and 2003, and the highest negative environmental loadings were for percent of oak in watersheds and increase in rangeland coverage in watersheds.

TABLE 15. Taxa and landscape environment loadings from CCA of spring 2004 benthic macroinvertebrate data.

Taxa/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.239	0.140
Taxa-environment correlations	0.828	0.685
Cumulative % variance: taxa data	10.0	15.9
Cumulative % variance: taxa-environment relation	36.3	57.5
Annelida Hirudinea	-0.789	-3.071
Turbellaria	-0.351	-1.792
Oligochaeta	1.088	0.750
Crustacea Amphipoda	-0.918	-1.624
Pelecypoda	-1.342	-1.841
Gastropoda	-0.282	0.631
Arachnoidea	0.140	0.425
Collembola	-1.463	2.157
Coleoptera Dytiscidae	2.025	0.383
Coleoptera Elmidae	0.641	-0.440
Coleoptera Haliplidae	-0.060	-0.459
Coleoptera Hydrophilidae	3.016	-0.185
Diptera Ceratopogonidae	1.594	-0.030
Diptera Chironomidae	0.201	-0.121
Diptera Culicidae	4.028	0.365
Diptera Dixidae	0.465	2.298
Diptera Simuliidae	-0.446	0.238
Diptera Stratiomyidae	1.325	-1.514
Diptera Tabanidae	1.032	-1.311
Diptera Tipulidae	1.246	1.644
Ephemeroptera Baetidae	-1.047	-1.187
Ephemeroptera Caenidae	-1.535	1.468
Ephemeroptera Ephemeridae	-1.128	2.777
Ephemeroptera Heptageniidae	-0.501	2.332
Hemiptera Corixidae	-0.979	2.281
Hemiptera Notonectidae	-0.912	-1.042
Hemiptera Naucoridae	0.311	-0.927
Odonata Coenagrionidae	-0.036	0.729
Odonata Gomphidae	-0.223	-2.207
Odonata Lestidae	-1.524	0.476
Odonata Libellulidae	1.158	-0.145
Odonata unidentified	-0.318	0.599
Trichoptera Calamoceratidae	-1.220	2.070
Trichoptera Hydroptilidae	-0.944	-0.706
Trichoptera Odontoceridae	-0.113	-0.930
Trichoptera Polycentropodidae	-1.003	1.198

TABLE 15. Continued.

Taxa/Environment	Axis 1	Axis 2
Latitude	0.316	0.096
Longitude	-0.081	0.049
Basin area	0.196	-0.024
% Juniper	-0.049	0.089
% Oak	-0.027	-0.184
% Cropland	0.203	-0.026
% Rangeland	0.070	0.003
% Change juniper	-0.161	0.162
% Change oak	0.163	-0.119
% Change cropland	0.147	-0.048
% Change rangeland	0.091	-0.148

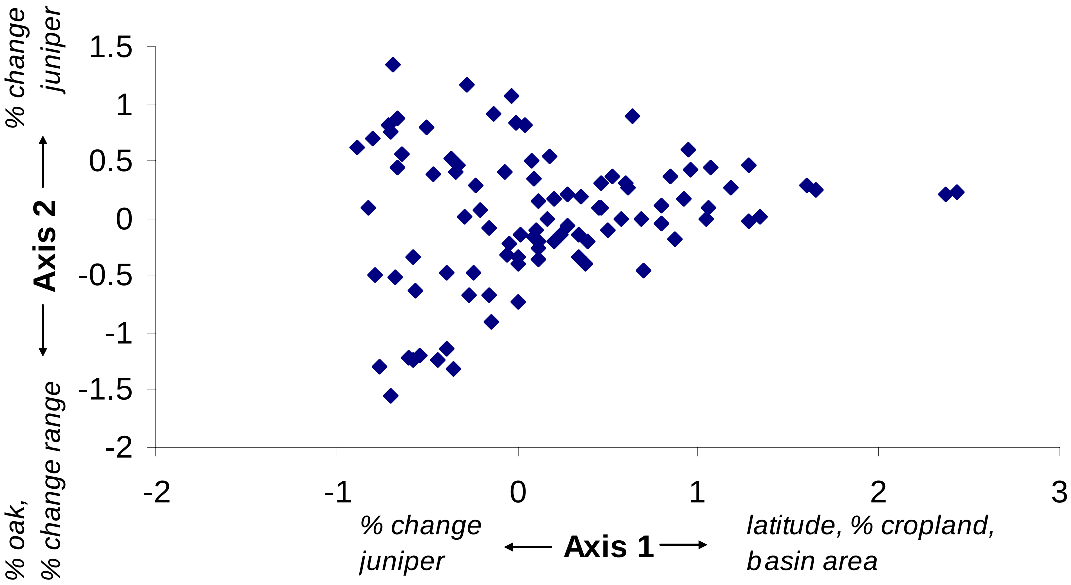

FIG. 16. Plot of site scores from CCA of spring 2004 benthic macroinvertebrate data and landscape environmental variables.

Spring 2004 macroinvertebrate data–CCA with combined local and landscape environmental variables

CCA for spring 2004 performed with taxa abundance and combined local and landscape environmental variables yielded a principal gradient (modeling 11.9% of species variation, 21.9% of environment variation) that associated high abundances of Culicidae (Diptera), and Hydrophilidae and Dytiscidae (Coleoptera) (high positive axis 1 loadings) with higher latitude, greater maximum depth, larger basin area, and higher average water temperature (high positive loadings) (Table 16, Fig. 17). Higher abundances of Pelecypoda, Hydroptilidae (Trichoptera), Caenidae (Ephemeroptera), and Amphipoda were associated with substrate cobble, increased juniper coverage in the watershed between 1999 and 2003, and greater canopy cover of the riparian vegetation over the stream (high negative loadings on axis 1). The second CCA axis (modeling 9.2% of species variation, 16.8% of environment variation) contrasted sites with relatively large abundances of Dixidae (Diptera), Collembola, Ephemeridae (Ephemeroptera), and Polycentropodidae (Trichoptera) (high positive loadings) with sites containing leeches of class Hirudinea, Tabanidae (Diptera), Amphipoda, as well as Notonectidae and Naucoridae (Hemiptera) (largest negative loadings on axis 2) (Table 16). The highest positive environmental loadings on axis 2 were for increase in juniper coverage between 1999 and 2003, percent woody debris in the stream, maximum velocity, and cobble substrate; the highest negative environmental loadings were for silt/clay/detritus substrate, increase in rangeland coverage between 1999 and 2003, and oak coverage in the watershed (Fig. 17).

TABLE 16. Taxa and combined local and landscape environmental variable loadings from CCA of spring 2004 benthic macroinvertebrate data.

Taxa/Environment	**Axis 1**	**Axis 2**
Eigenvalue	0.285	0.219
Taxa-environment correlations	0.894	0.834
Cumulative % variance: taxa data	11.9	21.1
Cumulative % variance: taxa-environment relation	21.9	38.7
Annelida Hirudinea	-1.153	-2.393
Turbellaria	-0.391	-1.221
Oligochaeta	1.414	0.552
Crustacea Amphipoda	-1.314	-1.800
Pelecypoda	-1.523	-1.046
Gastropoda	0.057	0.232
Arachnoidea	0.238	0.142
Collembola	-0.816	2.628
Coleoptera Dytiscidae	1.682	-0.444
Coleoptera Elmidae	0.283	-0.125
Coleoptera Haliplidae	-0.183	-0.587
Coleoptera Hydrophilidae	2.760	-0.958
Diptera Ceratopogonidae	1.416	-0.196
Diptera Chironomidae	0.187	-0.289
Diptera Culicidae	4.767	0.615
Diptera Dixidae	-0.546	3.026
Diptera Simuliidae	-0.413	1.092
Diptera Stratiomyidae	1.344	0.390
Diptera Tabanidae	0.857	-1.878
Diptera Tipulidae	1.174	1.232
Ephemeroptera Baetidae	-1.242	-0.386
Ephemeroptera Caenidae	-1.334	1.982
Ephemeroptera Ephemeridae	-0.195	2.284
Ephemeroptera Heptageniidae	0.318	1.947
Hemiptera Corixidae	-0.179	1.765
Hemiptera Notonectidae	-0.802	-1.537
Hemiptera Naucoridae	-0.204	-1.488
Odonata Coenagrionidae	-0.194	0.059
Odonata Gomphidae	0.375	-1.043
Odonata Lestidae	-0.919	0.025
Odonata Libellulidae	0.896	-0.213
Odonata unidentified	-1.018	-0.952
Trichoptera Calamoceratidae	-0.881	1.679
Trichoptera Hydroptilidae	-1.427	0.325
Trichoptera Odontoceridae	-0.227	0.661
Trichoptera Polycentropodidae	-0.841	2.133

TABLE 16. Continued.

Taxa/Environment	Axis 1	Axis 2
Time of day	0.045	0.050
Length of site	0.020	-0.021
% Canopy cover	-0.114	0.045
% Woody debris	-0.082	0.114
% Aquatic vegetation	-0.015	-0.052
Discharge	0.100	-0.025
Depth (max)	0.180	-0.034
Depth (CV)	0.021	-0.056
Velocity (max)	-0.064	0.106
Velocity (avg)	-0.051	0.077
Width (avg)	0.149	-0.075
DO (avg)	0.055	0.040
Water temperature (avg)	0.173	-0.061
Conductivity (avg)	0.145	-0.010
pH (avg)	0.123	0.004
Width (CV)	0.032	0.068
DO (CV)	0.080	-0.030
Water temperature (CV)	-0.006	0.011
Conductivity (CV)	0.025	-0.048
pH (CV)	0.010	-0.103
Silt/clay/detritus	0.024	-0.157
Mud	0.096	-0.043
Sand	0.082	0.043
Gravel	0.021	0.049
Cobble	-0.179	0.104
Latitude	0.309	0.016
Longitude	-0.056	0.078
Basin area	0.176	-0.057
% Juniper	-0.042	0.069
% Oak	-0.041	-0.143
% Rangeland	0.058	-0.006
% Change juniper	-0.131	0.168
% Change oak	0.144	-0.130
% Change cropland	0.135	-0.057
% Change rangeland	0.050	-0.148

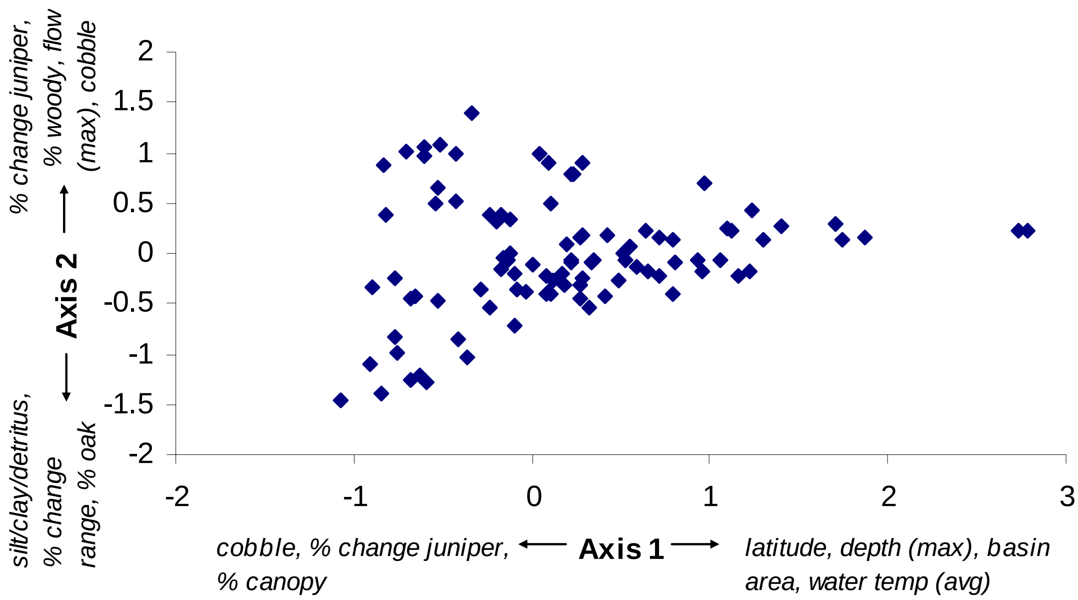

FIG. 17. Plot of site scores from CCA of spring 2004 benthic macroinvertebrate data and combined environmental variables.

Logistic regression model predicting fish presence

Logistic regression was performed to create models predicting the presence or absence of fish depending on environmental variables at the local and landscape levels (Tables 17, 18, and 19). Separate analyses were performed for summer 2003 and spring 2004 data. Both analyses yielded highly significant models that successfully predicted over 85 percent of observations (Table 17).

In the summer 2003 analysis, the largest positive coefficient was for average water velocity (Table 18), meaning that velocity was a strong determinant of the presence of fish at survey sites (i.e., more velocity resulting in a higher likelihood of fish being present). Average depth also was positively associated with the presence of fish. Latitude was strongly negatively associated with the presence of fish (Table 18). This pattern probably results from the fact that most streams we surveyed flow from south to north, and many show reduction in aquatic habitats in reaches located farther from springs and headwaters. The presence of fish was weakly and negatively associated with the percent coverage of oak and the percent change in juniper (1999-2003) in watersheds, and weakly and positively associated with the percentage of cropland (Table 18). Thus, findings from logistic regression are consistent with multivariate analyses that show extremely weak relationships between land-cover variables and fish assemblages. However it should be noted that the weak negative association between percent change in juniper and fish presence/absence indicates a weak signal revealing reductions in juniper increase the probability of encountering fish in stream habitats.

TABLE 17. Results of logistic regression models predicting fish presence and absence.

Analysis	Overall percentage of sites predicted correctly in final step	Significance of model coefficients in final step	-2 Log Likelihood in final step	Cox & Snell R^2 in final step	Nagelkerke R^2 in final step
Summer-2003	85.2	<0.0001	48.15	0.560	0.751
Spring-2004	91.7	<0.0001	23.91	0.601	0.872

TABLE 18. Variables included in logistic regression model predicting fish presence and absence for summer 2003 data (df = 1 for each independent variable).

Variable	B	S.E.	Wald	Signif.
Time of day	-0.006	0.002	7.441	0.006
Length of site	0.328	0.170	3.745	0.053
% Aquatic vegetation	-0.045	0.022	4.183	0.041
Depth (avg)	23.995	6.200	14.977	<0.0001
Velocity (avg)	147.315	51.479	8.189	0.004
Water temperature (avg)	1.018	0.322	10.016	0.002
DO (CV)	-0.138	0.054	6.528	0.011
Silt/clay/detritus	-5.631	1.963	8.225	0.004
Sand	-4.869	1.927	6.384	0.012
Cobble	-2.494	1.272	3.842	0.050
Latitude	-41.692	14.758	7.981	0.005
% Oak	-0.312	0.102	9.303	0.002
% Cropland	1.110	0.514	4.659	0.031
% Change juniper	-0.522	0.163	10.283	0.001

In the spring 2004 analysis, the largest positive coefficient was for maximum water depth (Table 19), meaning that the probability of fish presence was higher at a site with greater maximum depth. Average pH also was positively associated with the presence of fish. Mud was the strongest negative correlate (and the strongest overall correlate) with the presence of fish (Table 19), indicating that sites with mud as the dominant substrate were less likely to contain fish. In weak relationships, the presence of fish was less likely where oak coverage had increased between 1999 and 2003, and more likely where the amount of cropland had recently increased (Table 19). These findings are similar to those from the summer 2003 logistic regression, in that relationships between land-cover variables and fish assemblages are extremely weak. In this analysis, there was no significant relationship between juniper coverage in the watershed and fish presence/absence.

TABLE 19. Variables included in logistic regression model predicting fish presence and absence for spring 2004 data (df= 1 for each independent variable).

Variable	B	S.E.	Wald	Sig.
Time of day	-0.020	0.007	7.473	0.006
% Canopy cover	0.083	0.035	5.714	0.017
% Aquatic vegetation	0.129	0.049	7.005	0.008
Discharge	0.706	0.260	7.353	0.007
Depth (max)	24.849	8.849	7.886	0.005
Depth (CV)	-0.183	0.084	4.720	0.030
Conductivity (avg)	0.062	0.022	7.671	0.006
pH (avg)	15.262	5.885	6.727	0.009
Water temperature (CV)	-4.378	1.728	6.421	0.011
Mud	-27.854	11611.677	0.000	0.998
Basin area	0.018	0.007	6.827	0.009
% Change oak	-0.394	0.153	6.660	0.010
% Change cropland	2.826	1.211	5.444	0.020

Relative importance of juniper cover

Relationship between juniper cover and CA axis scores

To examine further the potential relationships between juniper cover and aquatic faunal composition, I performed linear regressions of CA axis 1 and 2 site scores versus percent juniper cover and the percent change in juniper cover (1999-2003) for summer 2003 seine samples, spring 2004 seine samples, and macroinvertebrate samples summed by site for both seasons. For summer 2003 seine samples, the only significant and strong coefficient of variation ($R^2 > 0.10$) values were obtained for percent change in juniper cover (1999-2003) versus CA axis 1 and CA axis 2 (Table 20). Thus, changes in juniper cover seem to be weakly associated with the species gradients derived from summer surveys of fishes and crayfish.

TABLE 20. Linear regressions of percent juniper cover or change in percent juniper cover versus CA axis 1 and axis 2 scores for summer 2003 seine data.

Analysis: X, Y	Coefficient of X	R^2	p-value
CA: % juniper, Axis 1	-0.053	0.035	0.157
CA: % juniper, Axis 2	-0.062	0.069	0.045
CA: % change juniper, Axis 1	0.157	0.167	0.001
CA: % change juniper, Axis 2	0.132	0.168	0.001

None of the regressions from spring 2004 seine samples were significant (Table 21). Thus, juniper cover variables seem to have little relationship with species gradients involving seine specimens collected during spring.

TABLE 21. Linear regressions of percent juniper cover or change in percent juniper cover versus CA axis 1 and axis 2 scores for spring 2004 seine data.

Analysis: X, Y	Coefficient of X	R^2	p-value
CA: % juniper, Axis 1	0.0573	0.061	0.074
CA: % juniper, Axis 2	-0.025	0.029	0.221
CA: % change juniper, Axis 1	-0.062	0.059	0.079
CA: % change juniper, Axis 2	-0.043	0.071	0.054

From summer 2003 macroinvertebrate samples, the regression of percent change in juniper cover (1999-2003) versus CA axis 1 yielded a significant coefficient of variation > 0.10 (Table 22). Thus, change in juniper cover in watersheds seems to have a weak relationship with taxa gradients associated with macroinvertebrates during summer.

TABLE 22. Linear regressions of percent juniper cover or change in percent juniper cover versus CA axis 1 and axis 2 scores for summer 2003 benthic data.

Analysis: X, Y	Coefficient of X	R^2	p-value
CA: % juniper, Axis 1	-0.004	0.004	0.533
CA: % juniper, Axis 2	0.004	0.007	0.437
CA: % change juniper, Axis 1	0.029	0.160	<0.001
CA: % change juniper, Axis 2	0.005	0.006	0.467

None of the regressions from spring 2004 macroinvertebrate samples were significant (Table 23). Thus, juniper cover seems to have little relationship with taxa gradients involving macroinvertebrates during spring.

TABLE 23. Linear regressions of percent juniper cover or change in percent juniper cover versus CA axis 1 and axis 2 scores for spring 2004 benthic data.

Analysis: X, Y	Coefficient of X	R^2	p-value
CA: % juniper, Axis 1	0.002	0.001	0.810
CA: % juniper, Axis 2	-0.003	0.003	0.568
CA: % change juniper, Axis 1	-0.015	0.021	0.162
CA: % change juniper, Axis 2	-0.010	0.019	0.179

Relationship between species (taxa) richness and key environmental variables

I performed bivariate linear regressions between fish species richness and several key environmental variables of interest (percent juniper cover, change in percent juniper cover, percent total woody cover, basin area, and discharge). Watershed basin area was the only one of these variables that accounted for a large amount of the variation in species richness (Table 24). Plots of fish species richness versus basin area reveal that two survey sites from the largest watershed are disproportionately responsible for the regression relationship (Fig. 18). These sites were located on a relatively large stream with low water velocity and a dry stream bed upstream from the survey reaches. During summer, one site had *Campostoma anomalum*, *Dionda episcopa*, *Lepomis megalotis*, and mosquitofish, whereas the other site had all of these species plus *Lepomis cyanellus*. During spring, both sites supported the same species plus *Etheostoma lepidum*, except that the second site lacked *Campostoma anomalum*. The relationship between fish species richness and watershed basin area was much weaker in summer 2003 ($R^2 = 0.21$) and very weak ($R^2 < 0.10$) in spring 2004 when the two sites from the largest watershed were excluded.

TABLE 24. Linear regressions of percent juniper cover, change in percent juniper cover, percent woody cover, basin area, or discharge versus species richness of fish.

Analysis: X, Y	**Coefficient of X**	**R^2**	**p-value**
Summer 2003: % juniper, species richness	0.041	0.087	0.005
Summer 2003: % change juniper, species richness	-0.033	0.040	0.057
Summer 2003: % woody cover, species richness	0.013	0.007	0.425
Summer 2003: basin area, species richness	0.006	0.316	<0.0001
Summer 2003: discharge, species richness	0.023	0.005	0.513
Spring 2004: % juniper, species richness	0.006	0.004	0.528
Spring 2004: % change juniper, species richness	-0.013	0.012	0.292
Spring 2004: % woody cover, species richness	-0.010	0.010	0.341
Spring 2004: basin area, species richness	0.004	0.335	<0.0001
Spring 2004: discharge, species richness	0.009	0.003	0.596

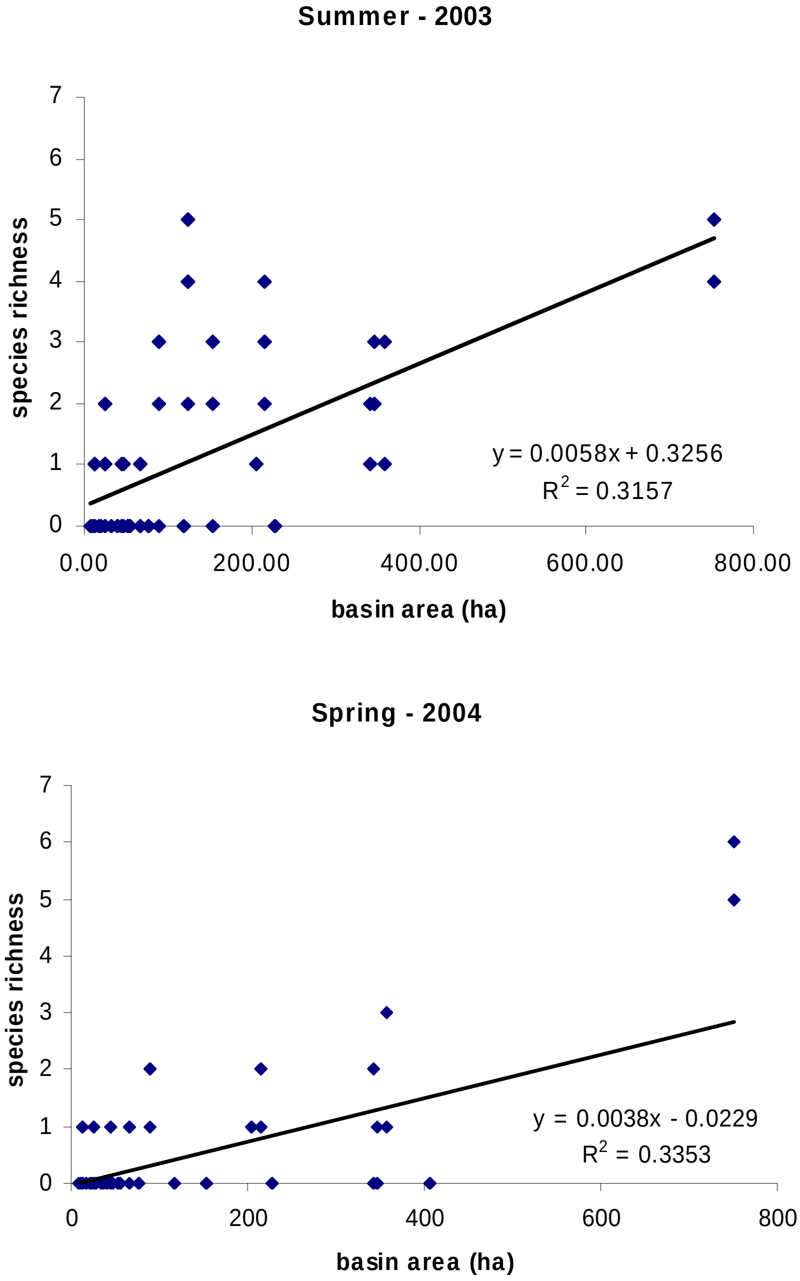

FIG. 18. Linear regression of basin area versus fish species richness in summer 2003 and spring 2004.

To further test for significant associations between key landscape variables and fish species richness, multiple regression was performed on seine data from summer 2003 and spring 2004. Independent variables were selected for retention in the regression model in a step-wise manner that identified those variables with large significant effects first, then included others sequentially based on the amount of residual variation modeled. Only those independent variables with significant coefficients are reported in Table 25. For summer 2003, basin area, percent juniper cover in watersheds, and percent change in juniper in watersheds (1999-2003) were the only significant variables. Coefficients were positive for basin area and juniper coverage, meaning that larger watersheds with more juniper cover tended to be associated with more fish species at sites. The coefficient for percent change in juniper cover was negative, which indicates that sites associated with recent declines in juniper cover tended to have more fish species during summer 2003. For spring 2004, watershed basin area was the only key landscape variable that was significant (Table 25).

TABLE 25. Multiple regressions with fish species richness as the dependant variable. Independent variables were basin area, percent juniper cover, change in percent juniper cover, percent total woody cover, and discharge. Dependant and independent variables were log transformed as log(x+20).

Analysis	Variables retained in model	Coefficient of X	model R^2	df	F statistic	p-value
Summer 2003			0.412	3	20.317	<0.001
	basin area	0.038				
	% juniper	0.075				
	% change juniper	-0.038				
Spring 2004			0.181	1	20.749	<0.001
	basin area	0.022				

The suite of linear regression and multiple regression tests was repeated for taxa richness of benthic macroinvertebrates collected in both seasons. In bivariate linear regressions performed between taxa richness and key environmental variables, only regressions including percent juniper cover and discharge were significant in summer 2003 (Table 26). However, the relationships were extremely weak, with percent juniper cover having a negative effect on taxa richness (lower juniper cover associated with increased taxa richness) and discharge having a positive relationship with taxa richness (increased discharge linked with increased taxa richness). For spring 2004 collections, there were no significant relationships between taxa richness and key environmental variables (Table 26).

TABLE 26. Linear regressions of percent juniper cover, change in percent juniper cover, percent woody cover, basin area, or discharge versus taxa richness of benthic macroinvertebrates.

Analysis: X, Y	**Coefficient of X**	**R^2**	**p-value**
Summer 2003: % juniper, taxa richness	-0.118	0.086	0.005
Summer 2003: % change juniper, taxa richness	-0.049	0.011	0.328
Summer 2003: % woody cover, taxa richness	-0.081	0.037	0.070
Summer 2003: basin area, taxa richness	-0.005	0.024	0.142
Summer 2003: discharge, taxa richness	0.234	0.061	0.019
Spring 2004: % juniper, taxa richness	-0.060	0.025	0.126
Spring 2004: % change juniper, taxa richness	0.003	<0.001	0.953
Spring 2004: % woody cover, taxa richness	0.040	0.009	0.355
Spring 2004: basin area, taxa richness	-0.002	0.005	0.511
Spring 2004: discharge, taxa richness	0.124	0.037	0.060

In the multiple regression performed on benthic macroinvertebrate taxa richness and all five key environmental variables, percent juniper cover and discharge were the only significant variables in the final model for macroinvertebrates collected in summer 2003 (Table 27). The coefficient for percent juniper cover was negative, meaning that taxa richness was higher where juniper cover was smaller. The coefficient for discharge was positive, meaning that higher taxa richness was associated with higher discharge. For spring 2004 the only significant variable was discharge, which was positively associated with taxa richness of benthic macroinvertebrates (Table 27).

TABLE 27. Multiple regression with benthic macroinvertebrate taxa richness as the dependant variable. Independent variables were basin area, percent juniper cover, change in percent juniper cover, percent total woody cover, and discharge. Dependant and independent variables were log transformed as log(x+20).

Analysis	Variables retained in model	Coefficient of X	model R^2	df	F statistic	p-value
Summer 2003			0.137	2	6.920	0.002
	% juniper	-0.114				
	discharge	0.191				
Spring 2004			0.045	1	4.437	0.038
	discharge	0.147				

DISCUSSION

Description of typical aquatic macrofauna assemblages and seasonal differences

Fish (and crayfish) assemblages

In summer 2003 4,181 fish were collected at 39 out of 91 sites. The ichthyofauna in headwater tributaries of the Pedernales River contained few species. Twelve species were collected over the summer, and the overall average species richness was 0.99 species per site, while the average species richness at those sites containing fish was 2.31. The maximum species richness was five, and approximately 36% of the sites contained just one species. The most frequently collected species was the central stoneroller (*Campostoma anomalum*), collected at 25 sites, followed closely by the green sunfish (*Lepomis cyanellus*) which was collected at 24 sites. Mosquitofish (*Gambusia affinis*) were the most numerically dominant in summer collections. Other fairly common species included blacktail shiners (*Cyprinella venusta*) and roundnose minnows (*Dionda episcopa*). During spring 2004, species richness, total number of individuals collected, and percentage of sites containing fish were even lower than summer 2003. In spring 2004, 551 fish were collected at only 26 out of 96 sites. Seven species were collected, and overall species richness was 0.45 species per site, whereas the average species richness for only the sites containing fish was 1.65. The maximum species richness was six but approximately 65% of the sites contained only one species. The most frequently collected species was again the central stoneroller, collected at 16 sites, with green sunfish and mosquitofish ranking second and third, respectively. The mosquitofish again was the most numerically dominant species in my collections.

Crayfish (Cambaridae) were collected at 36 sites (636 individuals) in summer 2003 and 49 sites (2,405 individuals) in spring 2004. This was the only common taxon that substantially *increased* both in abundance and frequency of occurrence in the spring. Crayfish seemed able to tolerate harsher physical conditions; they were often collected at sites with low dissolved oxygen concentrations and where no fishes were present. Seiler and Turner (2004) found higher densities of crayfish and lower densities of fish in streams affected by acidification. Some crayfish can survive in drying pools by burrowing in wet sediments (Jordan et al. 2000). Crayfish may recolonize sites more quickly than fishes, and since they are omnivores, serve as the main predator of invertebrates until competitive pressure or predation from fishes lowers their numbers. Other studies have documented lower invertebrate densities in the presence of crayfish (Usio 2000, Usio and Townsend 2002), and the effects of predation by fish on crayfish (Garvey et al. 1994).

Given the ephemeral nature of most of the streams that were sampled, low species richness of fishes was expected. During the two collecting periods and a third visit to the sites in May 2004, I observed differences in connectedness of pools of water at many of the streams. These were harsh environments for fishes, with stretches of the stream bed filling with water and emptying at various times of the year. The most abundant species in my collections, the mosquitofish, fits Winemiller and Rose's (1992) description of the colonizing, opportunistic life-history strategy, characterized by small body size with early maturation, frequent reproduction, and small eggs in small clutches. Although green sunfish were fairly common in collections and would be classified on the gradient between equilibrium and periodic strategists (Winemiller and Rose 1992), most individuals were juveniles.

Although I had expected to collect fewer fish during the summer when conditions tend to be drier, my collections revealed an opposite trend. This could be due to a combination of two reasons. First, according to TAES (2004), the summer collection was actually made after a relatively wet period, and the spring collection was made after a relatively dry period (and right before a large spring rain event). Second, according to Schlosser's (1987) findings for a second-order stream in Illinois, fish density is lowest in spring because age 0 to age 1 fish have likely not survived the harsh conditions of the previous winter. Schlosser (1987) formulated a conceptual framework for understanding fish community organization in small warmwater streams. He stated that species richness, density, and fish density are low in areas with poorly developed pools, shallow depths, and low habitat volume "because of the absence of deeper habitats needed by older age classes and pool species" (Schlosser 1987). He goes on to say that the lowest fish densities occur in the spring because of the large degree of emigration/mortality during the winter of fish without refugia in the form of large pools. Schlosser (1995) states that temperatures between 0 and 4º C can be stressful to small fishes, and winter air temperatures in central Texas typically reach this range at night during December and January (LCRA 2000). Given the lack of deep pools and relatively low winter temperatures at the study streams, it is understandable that the spring collections made up a fraction of the summer collections, and that species richness and fish density were so low.

A third possibility explaining why spring collections were so much smaller than summer collections is that the collections made in summer 2003 depleted the fauna, leading to decreased abundances in spring 2004. Ideally, I should have revisited the sites, or a sub-sample of the sites, a month or two after sampling to establish that there was no depletion. Although this was not done, it is highly improbable that summer sampling led to decreased abundances in spring. It is quite possible that the pools actually sampled, or at least areas connecting pools, dried up and re-filled several times between the two sampling periods. Additionally, colonization happens very quickly in these ephemeral streams. For example, one site contained fish in summer 2003 and no fish during the spring 2004 sampling period. However, when we returned to all the sites in early June 2004 (approximately three months later) to collect discharge measurements, I observed fish in the pool. In a more extreme example, fish were collected at the sites associated with a particular spring in summer 2003, but the stream was dry during the spring 2004 sampling. In June 2004, just three months later, I was able to observe fish from its confluence with a larger stream all the way to the most upstream sampling location. Because of these observations, it seems unlikely that summer 2003 sampling had a significant effect on fish abundance in spring 2004 samples.

Benthic macroinvertebrate assemblages

The benthic macroinvertebrate fauna collected in the study was taxonomically diverse. In summer 2003, 59,555 macroinvertebrates were collected at the 90 sites sampled (three samples per site). This included 52 taxonomic groups that were collected over the summer. The average taxa richness was 14.57 taxonomic groups per site, the maximum taxa richness was 26, and the minimum was five. The most frequently collected groups were chironomid (90 sites) and ceratopogonid Diptera (89 sites), followed by oligochaetes (79 sites), baetid mayflies (76 sites), coenagrionid damselflies (75 sites), and caenid mayflies (74 sites). The taxa that were numerically dominant in my collections were again chironomid (21,195 individuals) and ceratopogonid Diptera (10,432 individuals), followed by amphipods (8,765 individuals), caenid mayflies (6,207 individuals), coenagrionid damselflies (2,720 individuals), oligochaetes (2,596 individuals), and baetid mayflies (2,229 individuals). For other groups, well under 600 individuals were collected in most cases. The spring 2004 benthic macroinvertebrate fauna was similarly diverse, although the total number of individuals collected, and the average, minimum, and maximum taxonomic groups collected at each site were somewhat lower than those in the summer collection. In spring 2004, 51,500 benthic macroinvertebrates were collected at the 96 sites sampled (three samples per site). This included 52 taxonomic groups that were collected over the course of the spring (several of these were different than groups collected in the summer). The average taxa richness was 13.32 taxonomic groups per site, the maximum taxa richness was 23, and the minimum was four. The most frequently collected groups were chironomid (95 sites) and ceratopogonid Diptera (90 sites), followed by oligochaetes (89 sites), gastropods (75 sites), and baetid mayflies (70 sites). The taxa that were numerically dominant in spring 2004 collections were chironomid Diptera (14,978 individuals), caenid mayflies (7,801 individuals), and ceratopogonid Diptera (7,706 individuals), followed by amphipods (6,095 individuals), oligochaetes (4,802 individuals), gastropods (1,860 individuals), pelecypods (1,761 individuals), and baetid mayflies (1,284 individuals). For other groups, well under 800 individuals were collected in most cases.

The benthic macroinvertebrate collections were typical for the area. Although few studies of entire invertebrate assemblages exist for Texas streams, two studies that were conducted nearby can be cited. Davis (1980) investigated benthic macroinvertebrates at multiple stations in the Pecos River. At the station closest to the Pedernales, which was the most downstream (upstream of Amistad Reservoir) that he sampled, 50 taxa were collected. Fries and Bowles (2002) conducted a study in the San Marcos River. Although they do not report overall taxa richness, taxa richness at their stations ranged from 22 to 33 during three sampling periods in summer and spring months. Because both of these rivers are permanent and much larger than the streams I sampled, they would be expected to have much higher species richness than my study sites. Additionally, Davis (1980) identified insects to genus level, whereas I only identified insects to family. This discrepancy in level of identification would naturally lead to higher taxa richness in the other studies. Thus, taxa richness in my collections seems to be typical for the area.

Relative to the fish fauna, the benthic macroinvertebrate fauna was more similar between the two seasons. Many invertebrate groups have shorter life spans than fish, reproduce in less time, and may have multiple life cycles per year (Merritt and Cummins 1996). Therefore, their populations should recover from dry conditions more quickly, and immigration/emigration should occur earlier after dry periods due to their smaller body sizes and ability of many of the adults to disperse terrestrially.

Species-environment relationships

A major goal of this study was to identify species (or taxa) relationships with environmental factors. First, species matrices were ordinated using CA, an indirect gradient technique. From CA, we observed species patterns and inferred environmental gradients. Next, CCA was used to determine the linear relationship of species assemblages with suites of environmental variables in multidimensional space. Three sets of CCA's were run, two involving only local-scale environmental factors (water depth, canopy cover) or landscape scale factors (basin area, vegetation coverage), and a third in which local and landscape factors were considered simultaneously. Of course, from the perspective of an organism, this last scenario is the most realistic because it illustrates the relative influences of various environmental factors acting simultaneously from different scales; however it is a useful exercise to consider the two scales separately. CA and CCA analyses were conducted for fish (and crayfish) and benthic macroinvertebrate assemblages collected during both sampling seasons. Since fish were collected at so few of the sites, approximately 43% in summer 2003 and 27% in spring 2004, I further investigated this phenomenon using binary logistic regression. There was one dependent variable representing fish presence/absence, and the independent variables were the non-redundant environmental variables used in the local-scale and landscape CCA's.

Fish (and crayfish) assemblages

CA and CCA ordinations

The principle gradient for spring 2004 fish (and crayfish) assemblages may contrast sites containing assemblages more highly influenced by abiotic extremes, whereas the principle gradient for summer 2003 fish may incorporate relatively more influence by biotic factors. As discussed earlier, the spring sampling occurred after a relatively dry period, whereas the summer sampling occurred after a relatively wet period. Additionally, Schlosser (1987) found that fish density is lowest in spring because age 0 to age 1 fish do not survive the winter in areas where there are no deep pool refugia. Accordingly, total fish abundance in spring 2004 was less than 15 % that of summer 2003 and overall species richness was much lower, as was the number of sites containing fish. Grossman et al. (1998) found that flow had a much stronger effect on fish assemblages than either interspecific competition or predation during a temporal period which included a drought. Peckarsky (1983) suggested that benthic invertebrate communities may be more influenced by biological interactions as physical conditions become more benign.

The primary gradient in spring contrasted sites containing crayfish and/or central stonerollers (these occurred most frequently and were therefore most likely to occur with no other fish species), and sites containing multiple fish species. In these ephemeral streams, some key factors that influence macrofauna assemblages are connectivity and frequency of connectivity, or time since the pool last dried. It is well-documented that assemblages in headwater streams are heavily influenced by high environmental variability at the local scale (ex. lack of connectivity or frequency of connectivity lapses) (Taylor 1997, Herbert and Gelwick 2003). Since connectivity or time since last connectivity lapse was not measured in this study, probably the closest surrogates are water velocity and discharge. Since velocity was highly associated with sites containing minnows and multiple species, these sites are probably better connected, and thus create less of a barrier to colonization dynamics. In contrast, sites containing crayfish and no fish or just central stonerollers, may have loaded on the end of the gradient associated with relatively poor habitat (i.e. low velocity and discharge) for several reasons. First, these sites did not contain fish, a major component of the aquatic macrofauna. Second, crayfish may be more tolerant of lower water quality than fishes (Seiler and Turner 2004) and seemed to occur at many sites containing lower dissolved oxygen concentrations. Third, crayfish are known to burrow in wet mud and survive periods of drought (Jordan et al. 2000), while the fish in this region have no way of surviving drying pools.

For summer 2003, biotic factors, such as predation, may have influenced assemblage structure. I observed a principle CCA gradient mainly contrasting sites containing mosquitofish versus everything else. Although mosquitofish frequently occurred with other fishes, they were usually the most abundant species at the site, and did not occur at sites with large numbers of green sunfish, which probably prey on them. Green sunfish have been used as predators in lab experiments on mosquitofish (Johansson and Leonardsson 1998, Smith and Belk 2001). Of the commonly captured small fishes, including central stoneroller, blacktail shiner, and roundnose minnow, mosquitofish are the smallest at maturity (Page and Burr 1991) and probably the slowest swimmers (J. Birnbaum, *personal observation*); therefore, they would be the most vulnerable to predation. Of these fishes, the only recent studies documenting swimming speeds were conducted on mosquitofish and blacktail shiner. Adams et al. (2003) documented mean critical swimming speeds for blacktail shiners that were approximately 25 times faster than the fastest documented by Johansson and Leonardsson (1998), although the experimental blacktail shiner were only about two times the size of the mosquitofish. Since the mosquitofish fits Winemiller and Rose's (1992) description of the colonizing, opportunistic life-history strategy, individuals of this species may colonize habitats that are unsuitable for green sunfish.

The secondary gradient for both summer 2003 and spring 2004 fish (and crayfish) assemblages may contrast mesohabitats- relatively favorable pool habitats (large area, deep, with flow, as opposed to isolated pools) versus flowing runs (relatively deep, high discharge, high average dissolved oxygen) with most of the sites remaining in the middle of the gradient. In summer 2003, this pattern is confounded with the addition of landscape variables to the analysis. In the combination CCA analysis, sites with crayfish and no fish loaded high on the axis, and since this score represents a range of sites, it is difficult to interpret a pattern. Of the sites containing fish, those with green sunfish (and crayfish) were associated with the pool habitats, and those containing the other species, which included the three minnow species, were associated with the flowing run habitats. Differences in mesohabitat communities are well-documented. Schlosser (1995) suggests that small fish and/or earlier life stages tend to be found in relatively shallow habitats, while large and/or later life stages occur more frequently in deeper pool habitats. Other studies have documented a similar pattern (Muhlfield et al. 2001, Erős et al. 2003).

The secondary CCA gradient for spring 2004 contrasted sites with relatively good habitat for more sensitive species. Most fish species were associated with aquatic vegetation, high average dissolved oxygen, and gravel substrate, whereas crayfish and mosquitofish were associated with more woody debris and greater canopy cover. However, this CCA axis was even more difficult to interpret than the one for summer 2003 and there was not a clear enough gradient to say that there was a contrast between large pools and large runs. One interesting thing to note is that percent cover of juniper in the watershed was the highest loading variable for the end of the gradient that was associated with most of the fish species and may be associated with flowing runs.

Logistic regression

The logistic regression for the summer 2003 analysis of environmental variables predicting fish presence indicated that the most important variables associated with fish presence were average velocity (positive relationship), average depth (positive relationship), and latitude (negative relationship). If velocity is a good surrogate for connectivity, this result supports the notion that connectivity is an important factor determining fish presence. Depth is obviously important as well, because more speciose fish communities are associated with habitats containing areas of greater depth (Schlosser 1995). Latitude may be strongly related to fish presence, because many of the streams we surveyed flow from South to North, and many of the streams also dry up at some point downstream of the spring source. Other landscape-scale factors had little effect on fish presence, although fish presence was weakly associated with decreases in juniper cover between 1999 and 2003.

The spring 2004 logistic regression indicated that fish presence was highly associated with maximum depth (positive relationship), average pH (positive relationship), and sites with mud as the dominant substrate (negative relationship). The relationship with depth is again logical. The strong relationship with pH could indicate that water quality changes when pools dry and fill repeatedly. The negative relationship with mud may be associated with requirements for dissolved oxygen (Schenková et al. 2001). Moreover, sites with mud as the dominant substrate occurred in areas where livestock had access to the stream. Livestock have multiple impacts on streams, from trampling the stream bed and causing erosion of the bank, to defecating in or near the stream, thereby enriching nutrient loads (Belsky et al. 1999). In this analysis, there was no significant relationship with juniper cover in the watershed and fish presence.

Benthic macroinvertebrate assemblages

CA and CCA ordinations

The primary gradient for summer 2003 CCA’s contrasted shaded, flowing run habitats with shallow pools and pool-like runs with low velocity and canopy cover. Landscape variables were relatively important, as they loaded highest on either end of the gradient. The runs were characterized by greater canopy cover, variation in water temperature at different points in the site, gravel substrates, a range of depths in the habitat, high average dissolved oxygen, and occurred in watersheds where juniper had increased between 1999 and 2003. The pools were characterized by fine silt/clay/detritus substrate, and were found in watersheds at higher latitudes with a large percentage of cropland in the watershed, and increasing oak cover. They may also be characterized by high average water temperature, and larger average widths. Similar to fish assemblages, as was discussed earlier, more sensitive taxa inhabit areas with coarse substrate, canopy cover, and flow. Coarse substrate provides habitat for invertebrates in the interstitial spaces between particles, and is more likely to protect organisms during high flow events (Kilbane and Holomuzki 2004). Obviously, shade and flow help regulate oxygen concentration and are therefore beneficial to sensitive taxa.

The primary gradient for spring 2004 CCA's again may contrast shaded, flowing runs, with shallow pools and pool-like runs characterized by low flow and canopy cover. However, for this collection the pattern was not quite as clear. Since the spring sampling was done during/after harsher conditions than the summer sampling, the pattern may be obscured by multiple environmental factors. Runs were characterized by cobble substrate, increased juniper in the watershed between 1999 and 2003, a high percentage of canopy cover over the stream, and possibly more woody debris in the stream. The pools and pool-like runs were characterized by high latitudes, and greater maximum depth, were found in larger watersheds, and had higher average water temperatures, and possibly higher average widths. Landscape factors again were fairly important predictors of invertebrate assemblages, but vegetation cover was not as important as in summer 2003, perhaps reflecting the role proximal environmental factors play during harsher conditions.

The secondary gradient for summer 2003 CCA's appeared to contrast sites containing lentic-littoral groups with those favoring lotic and open-water habitats. The gradient was very difficult to interpret, but seemed to contrast sites containing high average dissolved oxygen and sites with a range of dissolved oxygen concentrations at the site (i.e., there were some areas of low oxygen within a sampling locality). Sites with varying dissolved oxygen concentrations were also associated with high average pH values and fine substrates such as silt/clay/detritus, mud, and sand. Sites with high average dissolved oxygen concentrations were found in large watersheds, had high discharge, and were found at high latitudes in watersheds dominated by rangeland. To a lesser degree, these sites were also associated with cobble substrate. The importance of oxygen, discharge, and coarse substrates to benthic organisms has been discussed earlier.

The secondary gradient for spring 2004 CCA's also was difficult to interpret but may have emphasized velocity and substrate. This gradient seemed to contrast sites with an increase in juniper coverage between 1999 and 2003, woody debris in the stream, high maximum velocity, and cobble substrate with sites containing silt/clay/detritus as the dominant substrate, an increase in rangeland in the watershed, and a large amount of oak in the watershed. The notion of substrate and velocity being the important components of the gradient is supported by the fact that naucorid Hemiptera and tabanid Diptera were associated with the fine substrate end of the gradient; these groups are often found buried in sediments (Merritt and Cummins 1996). In contrast, organisms that are usually associated with lotic habitats (which have relatively higher velocity and therefore usually coarser substrate), such as dixid flies, Collembola, and polycentropodid Trichoptera, had high scores on the opposite end of the axis (Merritt and Cummins 1996).

Summary of species-environment relationships

In all CCA analyses, the cumulative amount of variation in species abundances explained by environmental variables (given by the score for the cumulative percentage variance of species-environment relation) was higher in landscape analyses than the local analyses. However, in the combination analyses containing variables from both sets, the cumulative amount of variation in species abundances explained by environmental variables was similar to or usually lower than the amount explained by the local variables. This indicates complex patterns of covariance between local and landscape variables. The analyses for fish (and crayfish) assemblages in summer 2003 and spring 2004 explained relatively large amounts of variation, 51.7% and 68.6%, respectively (Tables 4, 8). The CCA analyses for benthic macroinvertebrate assemblages explained less variation, 45.6% for summer 2003 and 38.7% for spring 2004 (Tables 12, 16). Insects were only identified to family, and invertebrates were identified to class or order. Since insect members of one family may occur in different functional feeding groups, different habitats, and have different tolerances to environmental stressors, classification to the family level may obscure patterns that would otherwise be evident with greater taxonomic resolution. Additionally, fish assemblage patterns might have been strengthened by including a greater number of survey sites. Although 91 sites in summer 2003 and 96 sites in spring 2004 were included in fish analyses, only 39 and 26 sites, respectively, actually contained fish.

Relative importance of juniper cover

Several analyses were conducted to examine the relative importance of juniper cover (or change in juniper cover between 1999 and 2003) in relation to other environmental variables. Linear regressions of CA axis 1 and 2 site scores versus percent juniper cover and the percent change in juniper cover were conducted for seine and macroinvertebrate samples from both seasons. A significant coefficient of variation ($R^2 > 0.10$) value was obtained for percent change in juniper cover versus axis 1 and 2 for the CA involving summer 2003 seine samples. Positive relationships indicate that increased juniper cover in the watershed is associated with sites containing crayfish, Mexican tetra, and green sunfish for the primary gradient, and crayfish and Mexican tetra for the secondary gradient. Those sites on the primary gradient that were positively associated with increasing juniper cover were generally longer sites with higher discharge and coarse substrate, while those on the secondary gradient were generally large, connected pools. A significant relationship ($R^2 > 0.10$) was obtained for the regression between percent change in juniper cover and axis 1 for the summer 2003 invertebrate CA. Since this relationship was positive, an increase in juniper tended to be associated with sites containing Elmidae (Coleoptera), Amphipoda, Simuliidae (Diptera), Heptageniidae (Ephemeroptera), Calamoceratidae (Trichoptera), and

Ephemeridae (Ephemeroptera). These sites were characterized by variable water temperature at the site, dense canopy cover, a range in depths, and high average dissolved oxygen. This end of the gradient appears to be associated with shaded, flowing run habitats. There were no significant relationships between juniper cover variables and CA axis scores for the spring seine and invertebrate samples. This indicates that juniper has a weak influence, at most, on macrofauna during harsh conditions (low water depth, loss of connectivity).

This analysis reveals that increasing juniper coverage in the watershed is associated with more sensitive organisms found in higher quality habitats (shaded, flowing runs with coarse substrate; deep, connected pools). However, associations were relatively weak ($R^2 < 0.20$) and were not detected at all in many analyses. Moreover, there were no significant relationships incorporating the actual amount of juniper cover near the time of sampling. There may be some optimum amount of juniper cover. Although others have assumed that a decrease in juniper cover on the landscape should result in a linear increase in discharge, and therefore a direct increase in species richness (Fig. 19), this may not be the case. Ward and Stanford (1983) proposed that the Intermediate Disturbance Hypothesis (IDH) (Connell 1978) could explain the high diversity in natural stream systems. In support of this, a study by Stewart and Samways (1998) found that dragonfly species richness among several rivers in South Africa was highest on the rivers with moderate disturbance. Assessing the effect of juniper coverage on instream macrofauna is complicated by the fact that we do not know how much of a disturbance to discharge regimes is constituted by current juniper densities

(Fig. 19). It is possible that a decrease in juniper could result in an increase in species richness, but it is also plausible that current juniper coverage could be at the optimum level and a reduction would lead to decreased species richness. Further supporting this idea of an optimum amount of juniper cover are preliminary results of a rainfall simulation study. They suggest that water from large rain events may quickly be routed off-site from juniper covered hillslopes via sub-surface interflow (B. Wilcox, *in review*). This means that juniper might actually facilitate recharge of groundwater, despite the fact that it obviously must use some water itself. This idea certainly warrants further research.

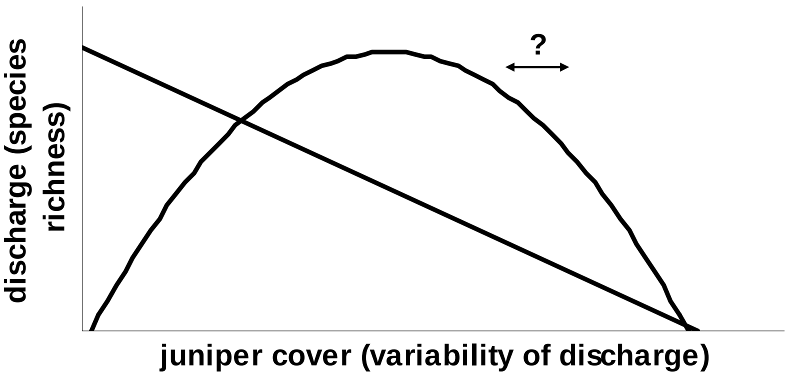

FIG. 19. Theoretical linear relationship between juniper cover and discharge (predicted by others), and quadratic relationship proposed here in support of the Intermediate Disturbance Hypothesis (Connell 1978).

I performed a suite of bivariate linear regressions to explore individual relationships between species (taxa) richness and several key environmental variables of interest (percent juniper cover, change in percent juniper cover, percent total woody cover, basin area, and discharge). I also performed a multiple regression to investigate the influence of these variables on species (taxa) richness simultaneously. These analyses were conducted for fish and invertebrate collections from summer 2003 and spring 2004. For fish collected in both seasons, basin area was the only significant key variable to explain a relatively large amount of variation in species richness ($0.30 < R^2 < 0.35$, Table 24). Basin area should be related to the amount of water available to stream habitats, and greater water availability should increase fish species richness (Gorman and Karr 1978, Schlosser 1987). However, discharge was not significantly related to fish species richness in this analysis. The significant model for the multiple regression ($R^2 = 0.412$) indicated a positive relationship of basin area and percent juniper coverage, and a negative relationship of change in juniper coverage (1999-2003) with fish species richness (Table 25). The model was contradictory, indicating that juniper coverage was positively correlated with species richness, but that a recent decrease in juniper coverage was also associated with higher species richness. The significant model for spring 2004 fish only included basin area ($R^2 = 0.181$, Table 25). As described earlier from CCA analyses, it is not surprising that the land cover variables drop out of the model in the spring. Since the spring sampling occurred during/after a relatively dry period of time, species richness should be more related to local environmental factors that influence colonization dynamics.

For invertebrate bivariate regressions, juniper cover and discharge were the only significant variables correlated with taxa richness in summer 2003. Lower amounts of juniper and higher discharge were associated with increased taxa richness. However, these relationships were extremely weak ($R^2 < 0.10$, Table 26). There were no significant relationships for spring 2004 analyses (Table 26). In the multiple regression analyses, juniper cover was again negatively related to taxa richness and discharge was again positively related. However, the relationship was very weak ($R^2 = 0.137$, Table 27). In the spring multiple regression, discharge was weakly and positively related to taxa richness ($R^2 = 0.045$, Table 27). Overall, these linear and multiple regression models gave conflicting results for the influence of juniper cover on fish and invertebrate species/taxa richness. In highly fluctuating or severe environments, organisms should respond strongly to local abiotic factors (Peckarsky 1983, Jackson et al. 2001).

It is instructive to examine juniper coverage in watersheds relative to other environmental variables derived from the CCA analyses involving combined local and landscape environmental factors. Juniper cover and change in juniper cover (1999-2003) were not the most influential variables for the summer fish/crayfish. However, for the spring analysis, percent juniper coverage was the most influential variable on axis 2, which probably corresponded with large, deep pools that were connected to the rest of the stream (as opposed to being isolated). In the combined CCA for summer invertebrates, increase in juniper cover was the most influential variable on axis 1. This contrasted with the negative end of the axis, which was strongly associated with greater cropland and oak coverage in the watershed. Increase in juniper was associated with shaded, flowing, run habitats containing gravel as the dominant substrate. In spring 2004, increasing juniper in the watershed was the most influential variable on positive axis 2, and had the second highest loading (negative) on axis 1. Negative scores on axis 1 seemed to correspond with shallow pools and pool-like runs characterized by low velocity, dense canopy cover, and higher average temperatures. However, there was not a very clear pattern in this analysis. Axis 2 corresponded with a gradient based on velocity and substrate, in which case the positive end was associated with higher maximum velocity and cobble substrate.

To summarize, juniper coverage and change in juniper coverage (1999-2003) were not always the most important variables in CCA's including combined local and environmental variables. However, in most instances when they were among the most influential variables for an axis, they were associated with sites containing relatively higher quality habitat (deep connected pools or flowing runs). Juniper cover in the riparian zone may provide canopy cover over the stream, thus regulating temperature and dissolved oxygen concentrations. Additionally, juniper may actually be very efficient at funneling precipitation below ground (C. Munster, *personal communication*), which might then provide baseflow to streams and thereby benefit aquatic macrofauna.

In addition to its influence on hydrology, removal of woody vegetation can have indirect effects. For example, coarse debris (e.g., leaf litter) from woody vegetation provides food for invertebrates, shelter for smaller macrofauna from predators, and alleviation of impacts from flood events (Wallace et al. 1997, Fairchild and Holomuzki 2002, Neumann and Wildman 2002). Removal of coarse debris impacts invertebrate density, richness, and assemblage composition (Wallace et al. 1997, Collier and Bowman 2003), as well as fish abundance, richness, and assemblage composition (Erskine and Webb 2003, Wright and Flecker 2004). Trimble et al. (1987) documented a decrease in water yield with reforestation of the southern Piedmont, mainly in Georgia.

However, they also point out that there was severe erosion in this area before reforestation (the land was forested before it was cleared for cropland). Siltation due to erosion can have negative impacts on aquatic macrofauna. Sutherland et al. (2002) documented decreased abundance of fishes requiring coarse substrate for spawning in streams with increased non-forested land cover. Likewise, Jones III et al. (1999) observed decreased fish abundance and suggested that there may be shifts in fish assemblage structure due to increases in fine sediments associated with longer patches where riparian zones had been deforested. Besides reducing sediment loads, the riparian zone also may act as a nutrient filter (Lowrance et al. 1984). These findings are not surprising, and are probably applicable to the study system, given that Wilcox's (*in review*) preliminary results indicate there is little overland runoff of heavy simulated rainfall on hillslopes covered with juniper. Although land managers may be most concerned with increasing water yields (however, that connection with juniper cover was not conclusively demonstrated in this study), they need to take into consideration the effects that removal of at least the riparian zone has on aquatic macrofauna, and strive for a balance between these two objectives.

One study with contrasting results was TAES (2002), which documented higher biotic integrity of fish where there was less juniper cover in sub-basins. However, this relationship was proposed for a higher spatial scale than the one presented in my study. Jackson et al. (2001) noted that small-scale studies are usually more limited in the range of environmental variation of abiotic variables, making it difficult to detect significant effects of these factors. Although an index of biotic integrity was not calculated in this study, this may explain the weak association of juniper cover with species/taxa richness and many of the environmental gradients proposed in this study. Further evidence that this study may have been limited in the range of juniper cover associated with different springs can be derived from Stednick (1996). Stednick reviewed studies documenting the effects of timber harvest on annual water yield and reported measurable water yield increases with a 78% harvest of pinyon juniper (similar species to ashe juniper) in an Arizona watershed. Since no studies were available in this area in which a lower percentage of a juniper species was harvested, I cannot say that increased water yield does not occur at lower rates of harvest. However, Stednick suggests that, in general, approximately 20% of the catchment vegetation cover must be harvested to achieve a measurable increase in water yield. Since most of the watersheds in this study contained less than 20% juniper coverage and the maximum percent coverage was less than 41% (Fig. 20), there may not have been a large enough range of variation in juniper coverage among watersheds to detect an effect on fish and benthic macroinvertebrate assemblages.

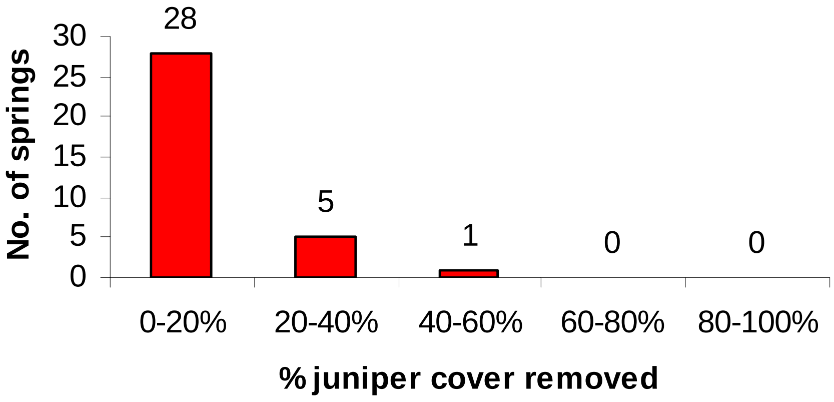

FIG. 20. Histogram depicting the number of study springs divided into different percent juniper cover removal categories. Total number of springs is 34 and maximum percent removal is 40.63%.

Another explanation for the weak link between juniper cover and aquatic macrofauna is that environmental variables not included in this study could play large roles. For example, detailed data on livestock density was not available. The impact of livestock on nutrient levels, bank stability, and faunal diversity, among others, is well established (Allan 2004). A post hoc logistic regression was conducted to determine whether there was a relationship between intensity of livestock signs (live animals, feces) and percent juniper cover in the watershed. It was possible that areas with low juniper cover might contain higher densities of livestock, which would then have a greater impact on streams. The dependent variable in the analysis was a binary categorical value where one equaled greater signs of livestock near the stream and zero equaled light to no signs of livestock. Three independent variables were percent juniper cover in the watershed, percent rangeland, and percent total woody cover. Only percent total woody cover was retained in the final significant model, and it was negatively correlated with the category for greater livestock signs ($p = 0.035$, $B = -0.081$, Cox & Snell $R^2 = 0.122$). Although this test was based on rudimentary livestock data, it suggests that future studies might benefit from including livestock data in analyses, along with other variables, such as nutrient load, bank quality, and percent woody vegetation.

CONCLUSION AND RECOMMENDATIONS

Several strong patterns emerged from this study. Fish diversity is extremely low in headwater tributaries of the Pedernales River, and in spring 2004, fish abundance was less than 15% of that in summer 2003. Fish presence at sites was positively correlated with average velocity and average depth in summer 2003, and in spring 2004 with maximum depth, average pH (both positive), and sites with mud as the dominant substrate (negative relationship). This seasonal pattern of reduced diversity and abundance in the spring should be examined over multiple years to see if it recurs over a longer temporal scale. Although benthic macroinvertebrate abundance was lower in spring 2004, it was less than 15% different from that in the previous summer. The invertebrate community was diverse and appeared characteristic for the region. One of the most interesting results from CCA's was that fishes in the streams sampled may respond more to abiotic factors during harsher periods, and biotic factors, such as predation, during relatively benign conditions. Additionally, relationships between fish and macroinvertebrate assemblages were fairly similar to those in many other studies. Different taxa were associated with deep as opposed to shallow water, and areas with differing amounts of velocity. More sensitive taxa, such as minnows seemed to be associated with flowing runs containing coarser substrates, often with higher canopy cover of riparian vegetation over the stream.

Juniper cover was sometimes a strong component of environmental gradients, often associated with higher quality habitat, such as large, deep pools (as opposed to unconnected, shallow pools) or flowing runs. Juniper cover was positively associated with fish species richness and negatively associated with invertebrate taxa richness, although for the invertebrates this variable was only significant in the multiple regression model for the summer 2003 collection. This relationship could be confounded by fish presence, however, because fish predation might also reduce invertebrate richness. In general, juniper cover appeared to have a very weak influence on fish and benthic macroinvertebrate assemblages in the streams I sampled. Stednick (1996) suggested that approximately 20% of catchment vegetation cover must be harvested to achieve a measurable increase in water yield and most of the watersheds in this study contained less than 20% juniper coverage. Therefore, there may not have been a large enough range of variation in juniper coverage among watersheds in this study to detect an influence on fish and benthic macroinvertebrate assemblages. Another possible reason for the weak relationship between juniper coverage and aquatic macrofauna was that the streams were harsh habitats for aquatic organisms, with water levels dropping to very low levels or drying completely at times during the year. Related to this, water temperature was sometimes extremely high and dissolved oxygen extremely low, which may also be due to the nature of the spring water source. In this system, local scale variables are most likely the dominant influence on fish and benthic macroinvertebrate assemblages. Expanding on this, it is possible that the relationship between juniper coverage and aquatic macrofauna was relatively weak because environmental variables not measured in this study are of primary importance. Such variables may include livestock density, total woody cover, nutrient levels, as well as many others. Future studies in this area should incorporate these variables.

Although many studies have investigated species-environment relationships for fish and invertebrate assemblages (Vannote et al. 1980, Schlosser and Ebel 1989, Wallace et al. 1997), few have investigated the role that juniper coverage in the watershed may play in structuring stream macrofauna communities. In fact, literature searches for “juniper and macroinvertebrate” or “juniper and fish” in four databases revealed no studies that actually dealt with the issue of juniper cover and its influence on stream organisms. Thus, this study incorporated a unique set of questions. Although a criteria of the study was to focus on lower order streams, because I believed these would more likely show an effect of juniper cover, this provided some complications.

The sample size of the study, on coarse observation, was fairly large; I sampled approximately 97 sites (not all sites were the same in both seasons) associated with 34 springs. However, due to the intermittent nature of many of the streams, many did not contain fish, and the sample size for fish ended up being relatively small. I sampled nearly every stream in the basin that was 1) associated with a spring and not overly human-modified, and 2) for which landowner access was granted. Future studies might be conducted in watersheds with even more tributaries.

Future studies should incorporate the temporal scale, even if this means focusing on fewer streams. It would be valuable to incorporate frequent observations over a long period of time regarding frequency of drying and duration of lapse of connectivity into the environmental variable pool. Since the amount of variation in assemblages explained by CCA’s was not large, I believe that these other types of variables that were not measured may be the overriding factor determining assemblage structure in these intermittent streams. If future researchers interested in the question of juniper influence on aquatic macrofauna are interested in fish, they may need to incorporate these types of variables and/or move to streams of a slightly higher order, in order to reduce the heavy influence of environmental harshness. However, if they are interested in benthic macroinvertebrates, greater taxonomic resolution is needed. Identification to the genus level could have added much to this study; however due to time constraints it was not undertaken. Studies of longer duration would be ideal in order to fully explore fish and invertebrates simultaneously. Additionally, collaboration among different stream ecologists to concurrently investigate these different groups would strengthen the body of knowledge in this area.

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VITA

Name:	Jenny S. Birnbaum
Permanent Address:	c/o Marcia Parks 20017 Wanegarden Ct. Germantown, MD 20874 jennybirnbaum@hotmail.com
Education:	B.S. Biology (Ecology, Evolution & Behavior option), The University of Texas at Austin, May 2002

Professional Experience:

Fall 2004	Graduate Teaching Assistant, Department of Wildlife and Fisheries Sciences, Texas A&M University
Summer 2001	National Science Foundation (NSF) Research Experience for Undergraduates (REU) Internship, Texas A&M University (Dr. Daniel Roelke)
Summer 2000	NSF REU Internship, University of Michigan Biological Station (Dr. Paul Webb)

Publications:

Fejes, E., J. Birnbaum, F. Gelwick, and D. Roelke. Vertical distribution of herbivorous zooplankton in a well-mixed lake system in which the main predator is a non-selective filter-feeding fish. *Journal of Freshwater Ecology (18):2, 2003.*

Honors/Awards:

2002-2004	Academic Scholarships (three), Department of Wildlife and Fisheries Sciences, Texas A&M University, Amount: $3,400.
2002-2003	Merit Fellowship, Texas A&M University, Amount: $25,846.