

ASSOCIATIONS OF WATERSHED VEGETATION AND ENVIRONMENTAL VARIABLES WITH FISH AND CRAYFISH ASSEMBLAGES IN HEADWATER STREAMS OF THE PEDERNALES RIVER, TEXAS

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ABSTRACT

Intermittent headwater streams serve important functions for humans and wildlife in semi-arid rangelands. Increases in ashe juniper coverage in central Texas over recent decades are believed to have negatively impacted stream flows. Few studies have examined relationships between aquatic species and environmental factors in these systems as well as the influence of juniper coverage on assemblage structure. During summer 2003 and spring 2004, we examined species–environment relationships to infer potential effects of juniper cover on aquatic ecology relative to local-scale and watershed-scale environmental variables. Fish and crayfish species assemblages and physicochemical variables were investigated in spring-fed headwater tributaries of the Pedernales River, Texas. Fish abundance was much higher in summer 2003, whereas crayfish abundance was higher in spring 2004. Fish species richness was lower during spring 2004, possibly due to below average precipitation during spring 2004 that reduced deep-water refugia. Higher abundance of crayfish in spring 2004 samples was probably due to their ability to survive low-flow conditions, and a release from fish predation pressure. Fish assemblage structure was more strongly associated with local abiotic factors during spring 2004 when flow was reduced, whereas structure during summer 2003 samples suggested a relatively greater influence of predation. In general, juniper cover was weakly associated with fish and crayfish assemblages, although it tended to be positively associated with relatively high-quality habitat for sensitive taxa (flowing runs with coarse substrate; deep, connected pools). We suggest that intermediate levels of juniper cover in the region provide indirect benefits to aquatic organisms. However, short-term, local environmental factors appear to have a much greater influence than watershed vegetation on fish and crayfish assemblages in these intermittent streams. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS: ashe juniper; brush management; hydrology; species assemblage; spring flow

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INTRODUCTION

Watershed vegetation and surface water in semi-arid landscapes

As human populations continue to develop and impact freshwater resources, improved methods of allocating and protecting the quality of water become critical. In semi-arid landscapes, those 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 agriculture and other human uses. In these regions, development of new water sources and strategies that increase efficiency of use are critical natural resource issues that limit economic activity. A strategy for increasing the water supply in semi-arid regions is management of brush encroachment. Removal of deep-rooted woody species, such as mesquite (*Prosopis glandulosa* Torrey) and ashe juniper (*Juniperus ashei* Buchholz), 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 from a

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wide range of study areas and vegetation types concluded that both the direction and magnitude of water yield changes could be predicted (Bosch and Hewlett, 1982).

The few studies that have focused on rangelands of the Edwards Plateau in central Texas have yielded conflicting interpretations. For example, a study 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 (Dugas *et al.*, 1998). In contrast, a study on mechanical removal of mixed woody vegetation in another Edwards Plateau watershed predicted an approximately 20% decrease in surface runoff (Richardson *et al.*, 1979). Given the shallow soils and fractured limestone substratum of that region, 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. First, average annual precipitation should be above 450 mm year⁻¹. In order to reduce the soil water deficit, the ratio of precipitation to potential ET must be high. Second, a greater effect on streamflow is expected when a high-density patch of woody vegetation is cleared compared to when a low-density patch is cleared. Third, in regions, 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, surface water yields from brush management are more likely. Fourth, trees with high leaf density that produce relatively high litter mass are better candidates for brush management than deciduous trees with low leaf density producing low litter mass, because the former intercept more precipitation. Although ashe juniper is largely restricted to central Texas, other juniper species are found throughout North America, making this study relevant for extensive regions with similar precipitation and geological characteristics.

Macrofauna as an ecological indicator

Because they are strongly influenced by anthropogenic disturbances as well as natural environmental factors, aquatic macrofaunal components, such as arthropods and fish, are useful ecological indicators for streams and rivers (Karr, 1991; Harding *et al.*, 1998). Relationships between species abundance, richness, and composition with water depth, dissolved oxygen (DO) concentration, substrate composition and other environmental factors have been described in many systems (Schlosser, 1987; Chipps *et al.*, 1994; Landman *et al.*, 2005). Furthermore, several recent studies have revealed the relative influence of local and regional environmental factors on community structure of aquatic macrofauna (Hugueny and Paugy, 1995; Marsh-Matthews and Matthews, 2000; Jackson *et al.*, 2001).

Vegetation cover on the landscape is a multi-scale environmental influence on fish and invertebrate communities. At the local scale, riparian vegetation provides shade, which in turn influences water temperature and therefore DO concentration. Woody debris from dead trees, or parts of trees (such as leaf litter) that fall in the water, provides important habitat for aquatic organisms and food for invertebrates (Wallace *et al.*, 1997; Fairchild and Holomuzki, 2002; Neumann and Wildman, 2002). At a larger scale, riparian and watershed vegetation influence surface hydrology, siltation rates in streams and rates of pesticide/fertilizer runoff, all of which impact aquatic macrofauna (Cooper, 1993; Stednick, 1996; Jones *et al.*, 1999; Whiles *et al.*, 2000).

Study objectives

This study examines relationships between macrofauna (fish and crayfish) and environmental factors at multiple spatial scales, to indicate the influence of riparian/watershed vegetation composition and density on headwater stream habitat in central Texas. The study formed a part of a larger multi-disciplinary project assessing the ecological effects of ashe juniper management within the Pedernales River basin. Based on common conceptions that juniper removal increases water yields, we hypothesized a trend of higher species richness of aquatic macrofauna in streams where juniper had been managed in the watershed, as opposed to streams where juniper encroachment was unabated (Schlosser, 1987; Schlosser and Ebel, 1989). The key assumption here is that increase in stream discharge (and species richness of aquatic macrofauna) is directly proportional to decrease in juniper coverage.

With this in mind, the objectives of this study were to (1) describe fish and crayfish assemblages in headwater streams of the Pedernales River basin; (2) identify species–environment relationships at multiple spatial scales and

(3) evaluate the influence of juniper coverage, at both local- and landscape-levels, on the structure of fish and crayfish assemblages. We expected that (1) species assemblage structure would be highly correlated with water depth and/or related variables and (2) species richness would be higher in watersheds with lower juniper coverage due to increased discharge.

METHODS

Study area

The Pedernales River basin, largely in Blanco and Gillespie Counties within the Edwards Plateau formation of central Texas, was chosen for this study, because the landscape satisfies Wilcox's (2002) criteria for successful brush management. Annual precipitation is over 450 mm year⁻¹. Ashe juniper is a dominant tree in the area and, though native to Texas, has increased in density over the last 50 years largely due to fire suppression (Fuhlendorf and Smeins, 1997). Since soils are shallow and underlain by fractured parent rock formations, water can quickly percolate beyond the root zone to groundwater sources, thus minimizing overland runoff (Wilcox, personal observation). The presence of springs further indicates good surface to sub-surface connectivity. Any influence of brush management on water yield and subsequently on aquatic macrofauna should be local in nature, because recharge to streams, reservoirs and aquifers in the area tends to occur quickly following large, infrequent rain events (Wilcox, unpublished work). All sampling sites were located on spring-fed, headwater tributaries of the Pedernales River.

Selection of sampling sites

To ensure consistency in geological features associated with spring outflow, streams were selected based on identification of spring sources located at or near the geologic interface between the Edwards and the Upper Glen Rose Formation, or between the Lower Glen Rose and the Hensell Formations. Sub-watersheds associated with these springs contained variable densities of juniper cover. Sampling sites for fish and crayfish (Decapoda, Cambaridae) 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 (e.g. runs, pools, riffles). The goal was to sample four stream sites below each spring. However, due to the intermittent 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 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*.

Physicochemical characterization of sites

At each stream site, the date, time of day, general weather conditions and general land-use categories were recorded, as well as Global Positioning System (GPS) coordinates and length of each survey reach. The qualitative parameters per cent canopy coverage, per cent coverage of woody debris and per cent coverage of aquatic vegetation were calculated by estimating the amount of sky or substrate area containing the parameter. Wetted channel width was measured at three transects per stream reach. Water depth and water velocity were measured at five points on each transect. DO, water temperature, conductivity and pH were measured at two to three points on the middle transect, depending on water depth. These variables and wetted channel width were entered into subsequent multivariate analyses as the average and coefficient of variation (CV). Water depth was entered as the maximum, average and CV, whereas water velocity was entered as the maximum and average (a CV often could not be calculated since the velocity was zero at many points). Presence/absence (dummy) variables included dominant substrate categories (excluding bedrock, which was the parent substrate of all streams). According to a modified Wentworth scale, the silt/clay/detritus category consisted of particles less than 0.062 millimeters (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. The velocity-area method was used to calculate discharge at the upstream or

downstream end of the site. For this calculation, velocity was measured in the centre of the channel cross-section at the surface, middle and near the bottom, while depth was measured at the centre of the stream and on either edge.

Derivation of watershed-scale variables

Basin area associated with each spring sampled was delineated using the Better Assessment Science Integrating Point and Nonpoint Sources (BASINS) Version 3.0 software from the U.S. Environmental Protection Agency (EPA). The geographic information system (GIS) data sets required by the BASIN software for the catchment area delineation included USGS digital elevation models (DEMs), stream location files and the coordinates of the sampling locations. The DEMs were in a grid format covering a full 7.5-min USGS quadrangle, the stream files were obtained from the National Hydrography Dataset (NHD) and the coordinates of the sampling locations were obtained in the field using GPS equipment.

Land cover in the surface catchment of each spring was classified into cropland, rangeland, juniper, and 'oak' (mainly *Quercus virginiana* Miller and other woody vegetation). Land classification was determined using Landsat imagery and an ISODATA classifier. The images used in the study were retrieved from Landsat 7 ETM+ (Enhanced Thematic Mapper) launched in 1999. Multi-spectral visible bands (bands 1,2,3,4,5 and 7) were used in the analysis. Images from both 1999 and 2003 were used to determine land cover changes. Two scenes covered the study area for the 1999 images, path 27 row 39 on 20 October 1999 and path 28 row 39 on 14 December 1999. The two scenes included in the 2003 images were path 27 row 39 on 21 March 2003 and path 28 row 39 on 31 May 2003. Forty-three reference areas located in the study area were used to 'train' the classifier of the Landsat remote sensing data. Each land cover reference area contained approximately 4.1 ha of uniform land cover. Three reference areas were included for each land cover class. Land cover maps generated from the 2003 Landsat data were verified with field observations. Randomly chosen map pixels were compared with field data for each land cover classification at each spring sampling site. Variables included in multivariate analyses were per cent cover of cropland, rangeland, juniper and oak, and change in per cent cover (1999–2003) for each of those land cover categories.

Biotic characterization of sites

Fish and crayfish were collected with a seine (3.66 m × 1.83 m with 4.76-mm mesh). A second seine was used to block the downstream portion of the stream segment being sampled. Seine hauls were repeated until a haul captured 10% 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, fish and crayfish 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 and counted. Fish were identified to species according to Hubbs *et al.* (1991) and Page and Burr (1991). Crayfish were identified to family and grouped with fish in most statistical analyses (except for analyses involving species richness).

Data analysis

Description of assemblages. Correspondence analysis (CA) was performed to investigate patterns of species assemblage structure without the influence of environmental variables. CA is a multivariate ordination technique that uses reciprocal averaging in an iterative process to reveal gradients of species abundances. Its main assumption is that species abundance distributions are unimodal and reflect an approximately normal distribution in response to an environmental gradient (Gotelli and Ellison, 2004). CA was performed separately for the summer 2003 and spring 2004 fish/crayfish datasets using the software CANOCO (ter Braak and Smilauer, 1998). In order to reduce bias from rare species, fish species that were not collected from at least two sites were excluded from analyses.

Species–environment relationships with an emphasis on ashe juniper. 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 variables with potentially strong influences on assemblage structure. CANOCO was used to perform CCA incorporating the combined local- and landscape-scale environmental variable datasets for each season separately. Additional analyses not presented here included separate CCAs for datasets with local versus watershed environmental variables. The CCAs 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 criterion for frequency of occurrence at sites used in CA was also used to exclude rare species from CCA.

Since fish were not collected at many sites (52 out of 91 sites in summer 2003 and 70 out of 96 sites in spring 2004 did not contain fish), fishless sites were, in effect, excluded by CANOCO (ter Braak and Smilauer, 1998) from the CA and CCA analyses. To determine those environmental variables that might predict the fishless condition, logistic regression was performed, whereby environmental variables were 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 CCAs. 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 per cent juniper coverage or change in per cent juniper coverage (1999–2003). Additionally, we determined the influence of certain key environmental variables (per cent juniper cover, change in per cent juniper cover, per cent total woody cover, basin area and discharge) on fish species richness. A multiple regression was performed to model the simultaneous influence of these environmental variables. Since a multiple regression assumes normality of variables and these variables did not have a normal distribution, they were log transformed as $\log(x + 20)$. These analyses were performed using SPSS (SPSS, Inc., 2002).

RESULTS

Description of assemblages

A total of 4181 individual fish was collected during summer 2003, and 551 fish were collected during spring 2004. In comparison, 636 crayfish were collected during summer 2003, while 2405 crayfish were collected during spring 2004. Thirty-nine of 91 sites contained fish and crayfish in summer 2003; an additional 20 sites contained crayfish but no fish. Twenty-six of 96 sites contained fish and crayfish in spring 2004; an additional 27 sites contained crayfish but no fish. Benthic macroinvertebrates were collected at all sites, including ones where fish and crayfish were not collected. These data appear in TAES (2004).

CA ordination of fish and crayfish abundance data from the summer 2003 survey revealed a dominant assemblage gradient (modelling 25% of variation) that contrasted assemblages containing crayfish (Cambaridae), Mexican tetras (*Astyanax mexicanus* de Filippi), green sunfish (*Lepomis cyanellus* Rafinesque), and central stoneroller (*Camptostoma anomalum* Rafinesque) with assemblages containing mosquitofish (*Gambusia affinis* Baird and Girard) and longear sunfish (*Lepomis megalotis* Rafinesque) (Table I, Figure 1). The second axis (modelling an additional 21.9% of variation) contrasted species assemblages with abundant crayfish and tetras with those having larger numbers of the four cyprinid species and plains killifish.

CA ordination of fish and crayfish from the spring 2004 survey revealed a principal gradient (modelling 40.6% of variation) that was dominated by crayfish (Cambaridae) and stonerollers at one end of the gradient (negative loadings), but the other end of the gradient described assemblages that included the two sunfish species (*Lepomis* spp.), mosquitofish, a minnow (roundnose minnow, *Dionda episcopa* Girard) and the greenthroat darter (*Etheostoma lepidum* Baird and Girard) (Table I, Figure 2). The plains killifish (*Fundulus zebrinus* Jordan and Gilbert) and both shiner species (blacktail shiner, *Cyprinella venusta* Girard, and red shiner, *Cyprinella lutrensis* Baird and Girard) were not captured or rarely captured at the same sites during spring 2004. The second axis (modelling 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 I. Species loadings from CA of summer 2003 and spring 2004 data

	Axis 1	Axis 2
Eigenvalue	0.883	0.776
Cumulative % variance of species data	25.0	46.9
Summer 2003		
<i>Astyanax mexicanus</i>	4.462	1.405
<i>Campostoma anomalum</i>	1.962	-2.750
<i>Cyprinella lutrensis</i>	2.252	-3.421
<i>Cyprinella venusta</i>	1.716	-3.047
<i>Dionda episcopa</i>	0.477	-3.048
<i>Fundulus zebrinus</i>	1.848	-3.481
<i>Gambusia affinis</i>	-2.744	0.878
<i>Lepomis cyanellus</i>	3.300	0.705
<i>Lepomis megalotis</i>	-1.493	-0.140
Cambaridae	5.045	3.241
Spring 2004		
Eigenvalue	0.818	0.480
Cumulative % variance: species data	40.6	64.4
Spring 2004		
<i>Campostoma anomalum</i>	-0.812	3.190
<i>Dionda episcopa</i>	6.901	2.544
<i>Etheostoma lepidum</i>	6.853	2.978
<i>Gambusia affinis</i>	6.890	-1.249
<i>Lepomis cyanellus</i>	3.134	6.617
<i>Lepomis megalotis</i>	7.426	0.825
Cambaridae	-0.847	-0.327

Species–environment relationships with an emphasis on ashe juniper

CCA for summer 2003 performed with species abundance and combined local and landscape environmental variables yielded a principal gradient (modelling 22.5% of species variation, 29.7% of environment variation) that associated high abundances of eight of the ten taxa (including crayfish, sensitive minnow species, and tolerant green sunfish) 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

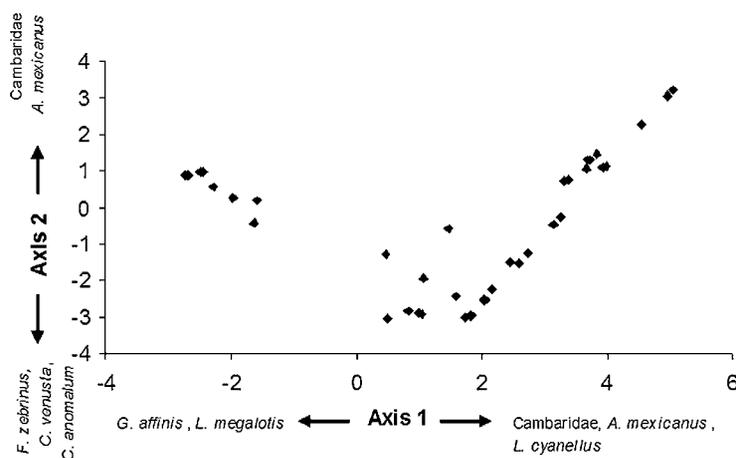


Figure 1. Plot of site scores from CA of summer 2003 seine data. Groups with high or low loadings on each axis are highlighted

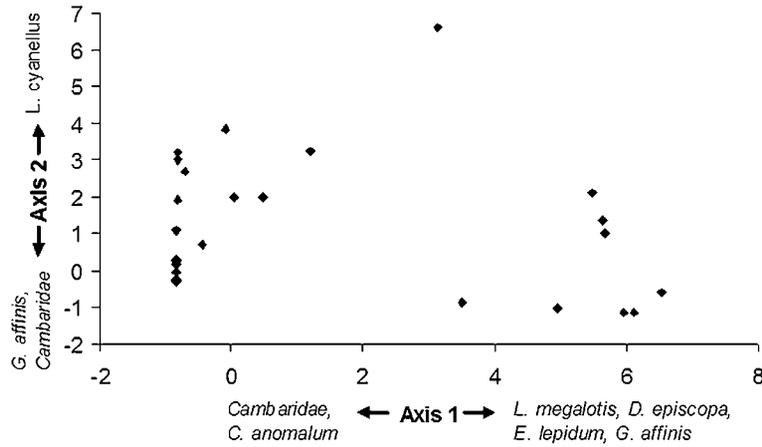


Figure 2. Plot of site scores from CA of spring 2004 seine data. Groups with high or low loadings on each axis are highlighted

stream (high positive axis 1 loadings) and low coverage of aquatic vegetation (negative loading) (Table II). The positive end of this axis was weakly associated with greater coverage of juniper. The opposite suite of landscape attributes was associated with higher abundances of mosquitofish and longear sunfish. The most influential environmental variables for the second CCA axis (modelling 16.7% of species variation, 22% of environment variation) were change in oak coverage (negative loading), average water temperature (negative loading) and CV of channel width (positive loading) (Table II, Figure 3).

CCA for spring 2004 performed with species abundance and combined local and landscape environmental variables yielded a principal gradient (modelling 37.2% of species variation, 45% of environment variation) that associated high abundance of five of seven 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, lower watershed basin area and decrease in the coverage of rangeland between 1999 and 2003 (negative loading) (Table III, Figure 4). The opposite suite of landscape attributes was associated with higher abundances of stonerollers and crayfish. Vegetation cover did not have a strong association with other environmental variables or fish and crayfish. The most influential environmental variables for CCA axis 2 (modelling 19.6% of species variation, 23.6% of environment variation) were per cent coverage of juniper in the

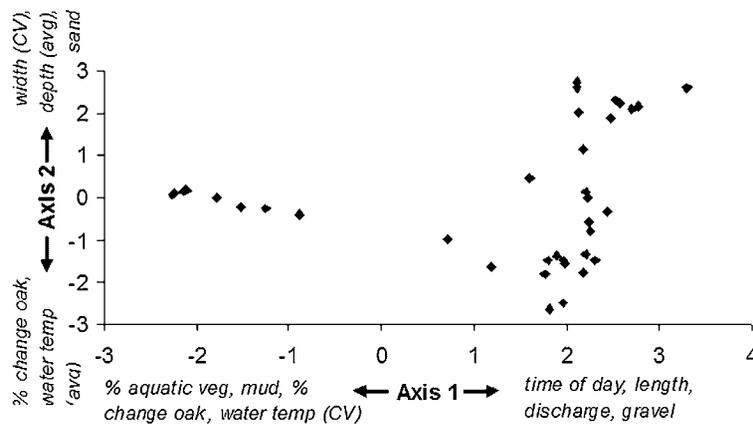


Figure 3. Plot of site scores from CCA of summer 2003 seine data and combined environmental variables. Variables with high or low loadings on each axis are highlighted

Table II. Species and environmental loadings (local- and landscape-scale variables) from CCA of summer 2003 data

	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
<i>Astyanax mexicanus</i>	3.725	2.958
<i>Campostoma anomalum</i>	2.286	–1.704
<i>Cyprinella lutrensis</i>	2.447	–2.980
<i>Cyprinella venusta</i>	1.757	–2.734
<i>Dionda episcopa</i>	1.788	–1.470
<i>Fundulus zebrinus</i>	1.738	–4.286
<i>Gambusia affinis</i>	–2.275	0.077
<i>Lepomis cyanellus</i>	2.698	2.106
<i>Lepomis megalotis</i>	–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
% 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

Redundant variables were removed.

watershed (high positive loading) and change in oak coverage between 1999 and 2003 (high negative loading) (Table III).

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 scales (Tables IV–VI). Separate analyses were performed for summer 2003 and spring 2004 data. Both analyses yielded highly significant models that successfully predicted over 85% of observations (Table VI).

Table III. Species and environmental loadings (local- and landscape-scale variables) from CCA of spring 2004 data

	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
<i>Campostoma anomalum</i>	−0.192	4.480
<i>Dionda episcopa</i>	6.811	0.933
<i>Etheostoma lepidum</i>	6.781	0.791
<i>Gambusia affinis</i>	5.718	−0.877
<i>Lepomis cyanellus</i>	2.813	3.329
<i>Lepomis megalotis</i>	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
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

Redundant variables were removed.

In the summer 2003 analysis, the largest positive coefficient was for average water velocity (Table V), meaning that velocity was a strong determinant of the presence of fish at survey sites (i.e. greater velocity resulting in a higher likelihood of fish being present). Average depth was also positively associated with the presence of fish. Latitude was strongly negatively associated with the presence of fish (Table V). The presence of fish was weakly and negatively associated with the per cent change in juniper (1999–2003) in watersheds, indicating a slight association of fish presence at sites where juniper cover was decreasing (Table V). Thus, findings from logistic regression are consistent with ordinations that show weak relationships between land cover variables and fish assemblages.

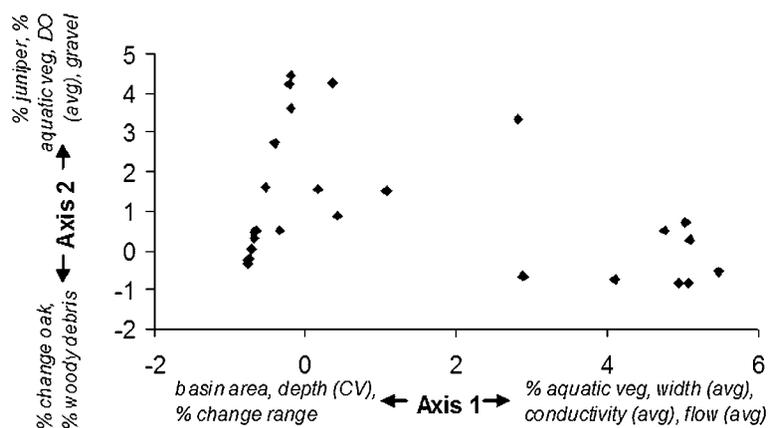


Figure 4. Plot of site scores from CCA of spring 2004 seine data and combined environmental variables. Variables with high or low loadings on each axis are highlighted

In the spring 2004 analysis, the largest positive coefficient was for maximum water depth (Table VI), meaning that the probability of fish presence was higher at a site with greater maximum depth. Average pH was also positively associated with the presence of fish. Mud was the strongest negative correlate (and the strongest overall correlate) with the presence of fish (Table VI), indicating that sites with mud as the dominant substrate were less likely to contain fish. In this analysis, there was no significant relationship between juniper coverage in the watershed and fish presence/absence.

Table IV. 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

Variables tested were non-redundant variables included in local- and landscape-scale CCAs.

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

Variable	<i>B</i>	SE	Wald	<i>p</i> -value
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

Bolded variables are those that are highly correlated with the presence of fish at a site (indicated by a high *B* value).

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

Variable	<i>B</i>	SE	Wald	<i>p</i> -value
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

Bolded variables are those that are highly correlated with the presence of fish at a site (indicated by a high *B* value).

Relationship between juniper cover and CA axis scores

To examine further the potential relationships between juniper cover and aquatic faunal composition, we performed linear regressions of CA axis 1 and 2 site scores versus per cent juniper cover and the per cent change in juniper cover (1999–2003) for summer 2003 and spring 2004 seine samples. For summer 2003 seine samples, the only statistically significant coefficients of variation ($R^2 > 0.10$) were obtained for per cent change in juniper cover (1999–2003) versus CA axis 1 and CA axis 2 (Table VII). Thus, changes in juniper cover seem to be weakly associated with the species gradients derived from summer surveys of fish and crayfish.

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

Relationship between key landscape variables and fish species richness

To test for significant associations between key landscape variables (per cent juniper cover, change in per cent juniper cover, per cent total woody cover, basin area and discharge) and fish species richness, multiple regression was performed for summer 2003 and spring 2004. Independent variables were selected for retention in the

Table VII. Linear regressions of per cent juniper cover or change in per cent juniper cover versus CA axis 1 and axis 2 scores for summer 2003 and spring 2004 data

Analysis: <i>X</i> , <i>Y</i>	Coefficient of <i>X</i>	R^2	<i>p</i> -value
Summer 2003			
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
Spring 2004			
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

Bolded variables are those significant ones with an R^2 value greater than 0.10.

Table VIII. Multiple regressions with fish species richness as the dependant variable

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	—	—	—	—
Spring 2004	% change juniper	-0.038	—	—	—	—
		—	0.181	1	20.749	<0.001
	basin area	0.022	—	—	—	—

Independent variables included were basin area, per cent juniper cover, change in per cent juniper cover, per cent total woody cover and discharge. Dependent and independent variables were log transformed as $\log(x+20)$.

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 modelled. Only those independent variables with significant coefficients are reported in Table VIII. For summer 2003, basin area, per cent juniper cover in watersheds and per cent 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 contain more fish species. The coefficient for per cent 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, with a positive relationship (Table VIII).

DISCUSSION

Although we expected to collect fewer fish during the summer when conditions tend to be drier, collections revealed the opposite trend. Summer collections were made during a relatively wet period. Average monthly precipitation for Blanco and Gillespie Counties was 28 mm in May 2003 (prior to summer collections), 118 mm in June, 109 mm in July and 60 mm in August (the last collection was made on 1 September) (NOAA, 2006). In contrast, the spring collections were made during a relatively dry period. Precipitation was 73 mm in February 2004 (prior to spring collections) and 54 mm in March 2004 (the last collection was made on 4 April) (NOAA, 2006). The relatively wet period prior to and during summer 2003 might have stabilized aquatic habitats of headwater streams, whereas lower flows during early spring 2004 probably restricted fish dispersal among isolated reaches.

Species–environment relationships

The principle CA gradient for spring 2004 species assemblages seemed to contrast species assemblages based on tolerance of extreme abiotic conditions. The principle CA gradient for species assemblages during summer 2003 seemed to contrast species vulnerability to piscivores. Again, spring sampling occurred after a relatively dry period, and summer sampling occurred after a relatively wet period. In these intermittent streams, this translates into differences in water depth, flow and connectivity between pools. Schlosser (1987) found that fish density was lowest in midwestern North American streams during spring, because many age-0 to age-1 fish do not survive the winter in areas lacking deep pool refugia. Fish abundance in Pedernales streams during spring 2004 was less than 15 % of the abundance during summer 2003, and overall species richness was much lower, as was the number of sites containing fish. Similarly, Grossman *et al.* (1998) found that flow had a stronger effect on fish assemblages than either interspecific competition or predation during a period that included a drought.

The primary CA gradient during spring contrasted sites containing crayfish and/or central stonerollers (the taxa with highest frequencies of occurrence at sites, and also the taxa most likely to occur at sites with no other fish species), and sites containing multiple fish species. In these ephemeral streams, major factors that influence macrofauna assemblages are the degree and frequency of connectivity, and the time elapsed since the most recent

drying of the stream reach. It is well documented that assemblages in headwater streams are strongly influenced by environmental variability at the local scale (e.g. frequency of connectivity) (Taylor, 1997; Herbert and Gelwick, 2003). Connectivity variables were not measured in this study, but related variables were water velocity and discharge. In the spring CCA, velocity was strongly associated with sites containing multiple species (discharge was also weakly positively associated with the first axis), sites with high positive scores (more species) probably were more connected and more frequently colonized. In contrast, sites containing only crayfish, or crayfish and central stonerollers, had axis 1 scores associated with the end of the gradient reflecting frequently disconnected habitats (i.e. low velocity and discharge). Crayfish tend to be more tolerant of low water quality than most North American stream fish (Seiler and Turner, 2004; Landman *et al.*, 2005), and in our study, crayfish occurred at several sites with relatively low DO. Moreover, some crayfish burrow into mud to survive periods of drought (Jordan *et al.*, 2000), whereas fish of this region cannot survive in dry streambeds. Lower discharge likely restricted the distribution of predatory green sunfish, so that populations of crayfish and stonerollers would have been able to increase following colonization of intermittently disconnected habitats (Lemly, 1985). Crayfish have been shown to select habitats lacking predatory fish (Magoulick, 2004).

Biotic factors, such as predation, could have influenced assemblage structure during summer 2003. The principle CCA gradient contrasted sites containing mosquitofish versus those with crayfish plus several other fish species (except longear sunfish, which tended to be uncommon in summer samples). Although mosquitofish frequently occurred with other fish, they usually were among the most abundant species at sites where they occurred, and did not occur at sites with large numbers of predatory green sunfish. Green sunfish frequently have been used as efficient predators in lab experiments with mosquitofish (Johansson and Leonardsson, 1998; Smith and Belk, 2001). Of the commonly captured small fish in our study, including central stoneroller, blacktail shiner and roundnose minnow, mosquitofish are the smallest at maturity (Page and Burr, 1991) and probably the slowest swimmers (Birnbaum, personal observation); therefore, they probably are the most vulnerable to predation by sunfish. Adams *et al.* (2003) documented mean critical swimming speeds for blacktail shiners which were approximately 25 times faster than the fastest documented by Johansson and Leonardsson (1998) for mosquitofish (the blacktail shiners were about twice the size of the mosquitofish used in experiments). The mosquitofish fits Winemiller and Rose's (1992) description of the colonizing, opportunistic life-history strategy, and we suspect this species colonizes frequently disturbed and marginal habitats that are unsuitable for larger green sunfish. The high loading for time of day on CCA axis 1 during summer could have been associated with microhabitat use, but more likely was a spurious association since it is difficult to imagine how this variable could have influenced our capture efficiency for crayfish and fish in these small aquatic habitats.

Logistic regression model predicting fish presence

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 species-rich fish assemblages are associated with deeper stream habitats (Schlosser, 1995). Latitude was a variable that significantly influenced fish presence/absence. Most of the streams we surveyed flow from south to north, and also tended to retain water near their spring sources during periods of drought. Other landscape-scale factors had little influence on models predicting fish presence/absence, 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 significantly associated with maximum depth (positive relationship), pH (positive relationship) and mud as the dominant substrate (negative relationship). The relationship with depth is logical and again supports the notion that connectivity-related variables are important in these intermittent streams (assuming areas with greater depth are more likely to be connected). When water erodes limestone (the overlying geology in the study area), there may be a slight increase in pH. The strong relationship of fish presence with pH may be another indicator that the probability of fish presence is greater at sites with a more constant supply of water (and where more water-related erosion can occur). The negative relationship with mud

may be associated with species intolerance of lower DO that tends to be associated with muddy habitats (Schenkova *et al.*, 2001). Moreover, sites with mud as the dominant substrate occurred in areas where livestock had access to the stream (Birnbaum, personal observation). Livestock have multiple impacts on streams, including physical disturbance of the streambed, bank erosion, and deposition of waste that increases nutrient loads (Belsky *et al.*, 1999). In this analysis, there was no significant relationship between juniper cover within watersheds and the presence of fish.

Associations with ashe juniper cover

Several analyses were conducted to examine the strength of associations between aquatic biota and juniper cover (or change in juniper cover between 1999 and 2003) relative to other environmental variables. For summer 2003, linear regression yielded positive trends between juniper coverage in the watershed and scores on CA axis 1 and 2, which implies that greater juniper coverage is associated with streams having more crayfish, Mexican tetras and green sunfish. Sites on the first gradient that were positively associated with an increase in juniper cover were generally longer reaches with higher discharge and coarser substrates, whereas those on the second gradient tended to be large, connected pools. Again, sub-basins where juniper coverage had increased tended to be associated with larger pools containing green sunfish. This contradicts the notion that removing juniper will increase surface water yields. There were no significant relationships between juniper cover variables and CA axis scores for the spring 2004 samples. This suggests that juniper cover has little influence on macrofauna during dry conditions (low water depth and longitudinal connectivity).

It has been proposed frequently that a decrease in juniper cover on the landscape should result in a linear increase in discharge, and therefore one would predict a direct increase in species richness. However, this would not be the case if there were an optimum amount of juniper cover (Figure 5). Ward and Stanford (1983) proposed that the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978) could explain the high diversity found in natural streams. The IDH 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 IDH was originally applied to sessile organisms, such as trees and corals, Ward and Stanford (1983) suggest that 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 head (relatively constant environment) or an intermittent stream (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). This view was supported by a study that found higher dragonfly species richness among several rivers in South Africa in the rivers with moderate disturbance (Stewart and Samways, 1998). Assessing effects of juniper coverage on instream macrofauna is complicated by the fact that we do not know the level of alteration to historic discharge regimes represented by current juniper densities (Figure 5). A decrease in juniper could result in an increase in species richness, but it is also plausible that current juniper coverage could be at an optimum level for stream habitat, and reductions would cause a decline in species richness. Wilcox *et al.* (2005) found that removal of 70 or 100% of ashe juniper from several of the nine small watersheds in the Edwards Plateau of central Texas had 'little influence on the amount, timing, or magnitude of

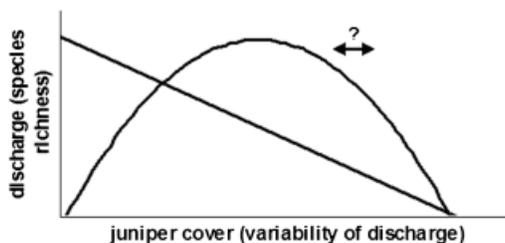


Figure 5. Traditionally assumed linear relationship predicting lower stream discharge and lower species richness with greater juniper cover in the watershed, and a hypothesized curvilinear relationship illustrating maximum stream discharge and species richness at intermediate levels of juniper cover. The optimum amount of juniper coverage for streams of the Pedernales Basin is undetermined at present

streamflow.' Coupled with the information derived in this study on the correlation between canopy cover over the stream and the relative abundances of many faunal groups (Table II), it seems likely that the relationship between juniper cover and aquatic organisms is complex.

We also performed a multiple regression to investigate the influence of several key environmental variables (per cent juniper cover, change in per cent juniper cover, per cent total woody cover, basin area and discharge) on species richness simultaneously. These analyses were conducted for fish collections from summer 2003 and spring 2004. The significant model ($R^2 = 0.41$) indicated a positive relationship between fish species richness and basin area and per cent juniper coverage, and a negative relationship between fish richness and changes in juniper coverage (1999–2003) (Table VIII). 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 model indicated that juniper coverage was positively correlated with species richness, but that a recent decrease in juniper coverage was also associated with higher species richness. This supports the idea that there is an optimal level of juniper coverage, or it may imply that our variables lacked appropriate precision or resolution. The regression model for spring 2004 identified basin area as the only significant landscape variable ($R^2 = 0.18$, Table VIII). Because spring sampling occurred during a relatively dry period, species richness was apparently more strongly influenced by local environmental factors, as inferred from our CCA results.

CONCLUSIONS

Juniper coverage and change in juniper coverage from 1999–2003 were not among the most influential variables in our analyses. When juniper coverage was statistically significant (e.g. juniper coverage in the spring CCA), it tended to be positively associated with deeper or more connected habitats. Juniper coverage in the riparian zone may provide canopy cover over the stream, thus regulating temperature and DO concentrations. Additionally, juniper roots can increase the movement of precipitation from surface to subsurface (Munster and Wilcox, unpublished work), which could increase stream base flow.

In addition to its influence on hydrology, removal of woody vegetation can have indirect effects on aquatic macrofauna. For example, coarse debris (e.g. leaf litter) from woody vegetation provides food for invertebrates, shelter for smaller macrofauna from predators and moderation of direct flood impacts (Wallace *et al.*, 1997; Fairchild and Holomuzki, 2002; Neumann and Wildman, 2002). Removal of coarse debris affects 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 Appalachian Piedmont in Georgia. However, they also pointed out that there was severe erosion in this area before reforestation. Siltation from erosion negatively impacts many stream organisms (Jones *et al.*, 1999; Sutherland *et al.*, 2002). In addition to reducing sediment loads, the riparian zone also functions as a nutrient filter (Anbumozhi *et al.*, 2005). These points, along with the results of this study, constitute an argument to maintain intermediate levels of juniper cover for management purposes. This could be accomplished by maintaining juniper in the riparian zone, which would provide coarse debris and canopy cover over streams, and reduce erosion. Removal of juniper in other parts of the watershed should help preserve stream flows.

Additionally, the influence of juniper on fish/crayfish assemblages in this study may have been masked by other environmental variables not included in our analysis. For example, livestock density was not estimated. Impacts of livestock on nutrients, bank stability and faunal diversity are well established (Allan, 2004). A *post hoc* logistic regression was conducted to determine whether there was a relationship between livestock (recorded as presence/absence of livestock or their feces) and per cent juniper cover in the watershed. It was possible that areas with low juniper cover might contain higher densities of livestock, which then might have a greater impact on streams. The dependent variable in the analysis was a binary categorical value where one indicated evidence of livestock near the stream and zero indicated absence of livestock. The three independent variables assessed were per cent juniper cover in the watershed, per cent rangeland and per cent total woody cover. Only per cent total woody cover was retained in the final model, and it was negatively correlated with the presence of livestock ($p = 0.035$, $B = -0.08$,

Cox & Snell $R^2 = 0.12$). Although this test was based on crude livestock data, it suggests that future studies might benefit from including quantitative livestock data in analyses, along with other variables, such as nutrient levels, bank condition and per cent woody vegetation.

Our study provides a first step toward understanding ecological effects of juniper removal on species assemblages in intermittent streams. We suggest that future studies should include long-term data on species assemblages both before and after juniper removal. Inclusion of additional variables, such as distance to upstream/downstream colonization sources, livestock density and width of the riparian zone, might provide greater insight into the mechanisms directly affecting community dynamics in these habitats.

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