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ARTICLE

# Influence of Stream Condition on Habitat Diversity and Fish Assemblages in an Impaired Upper Snake River Basin Watershed

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## Abstract

Habitat diversity reflects the range of available habitats used by species with different niche requirements and, therefore, influences species diversity. Land use influences stream condition, and streams in poor condition are often wide, shallow, sediment-laden channels with low instream habitat diversity. Our goal was to evaluate the effect of instream habitat diversity on fish species diversity, the effect of stream habitat condition on habitat diversity, and the effect of habitat diversity, stream condition, and other natural stream features on fish assemblage structure (proportional abundance) in an impaired upper Snake River basin watershed containing a locally diverse but regionally depauperate species pool. We sampled fishes and instream and riparian habitat at 41 sites, focusing on measures of instream habitat diversity and the following stream condition indicators: livestock trails on streambanks, streambank stability, channel width-to-depth ratio, percent fine substrates, and woody riparian vegetation. Multiple regression revealed that fish species diversity was positively associated with all four components of habitat diversity, that is, diversity in substrate, cover, water depth, and water velocity ( $P < 0.09$ , adjusted  $R^2 = 0.642$ ). All four components of habitat diversity increased with stream size, and each component was negatively but weakly associated with at least one stream condition indicator ( $P < 0.10$ , adjusted  $R^2 = 0.23$  to  $0.61$ ). Fish assemblage structure was influenced primarily by natural stream features (gradient, temperature) and secondarily by stream condition indicators and streamflow diversity. Our results connect fish species diversity increases in larger streams with concomitant increases in four dimensions of instream habitat diversity. The findings show how stream condition reflecting land uses, such as riparian over-grazing, can negatively impact habitat diversity within that stream-size continuum, thus emphasizing the role land management plays in maintaining fish species diversity.

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Structural diversity of habitat, often called habitat heterogeneity or complexity, has been associated with the diversity of many taxonomic groups. This habitat diversity–species diversity relationship is due to increased physical space, refuge, resource availability, and, consequently, niche availability to organisms with varying niche requirements (MacArthur and MacArthur 1961; Tews et al. 2004; St. Pierre and Kovalenko 2014). In streams, fish species diversity increases with habitat volume (Schlosser 1982; Angermeier and Schlosser 1989). Sheldon (1968) hypothesized the

positive association between fish diversity and water depth in a New York stream was due to increased habitat volume, which facilitated vertical niche partitioning by different species. Gorman and Karr (1978) found that the diversity in stream habitat positively influenced fish species diversity across both temperate and tropical streams. Their data showed that the relative contribution of diversity in stream substrates, water velocities, and depths to fish species diversity varied between their two study streams, and they argued that each component of habitat diversity varied in importance to

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different fish guilds. Subsequent studies have continued to document fish diversity associations with habitat diversity in streams (Schlosser 1982; Smith and Mather 2013).

Streams degraded from anthropogenic activities can often have low instream habitat diversity in addition to other symptoms (Gorman and Karr 1978; Lepori et al. 2005; Laub et al. 2012). Watershed land use influences instream habitat through connections within the aquatic system at multiple spatial scales (Frissell et al. 1986), and many studies have linked watershed and riparian land use to changes in stream habitat (Roth et al. 1996; Nerbonne and Vondracek 2001). Urban watersheds have impervious surfaces and development that encroaches into stream corridors that result in altered flow regimes and riparian vegetation. Urban watersheds, therefore, often have streams with incised channels, eroding stream banks, uniform bed morphologies, and small but sparse wood (Booth et al. 2016). Likewise, agricultural streams often have less riparian vegetation, more streambank erosion, higher levels of fines sediments, and increased nutrients (Vondracek et al. 2005). In the western United States, watersheds with higher levels of use (grazing, logging, mining, and roads) can have more unstable stream banks with fewer undercuts and shallower pools with more fine sediments embedded in pool tails (Kershner et al. 2004).

Domestic livestock grazing, primarily from cattle, is pervasive in the western United States and has had a large impact on native ecosystem health, including stream health (Fleischner 1994; Poff et al. 2011). Grazing impacts to streams result when cattle congregate in riparian areas for easy access to water, lush vegetation, and flatter terrain (Kauffman and Krueger 1984). Intense riparian grazing often alters the community composition of riparian vegetation with a reduction in grasses, forbs, sedges, and woody vegetation (Fleischner 1994; Beschta et al. 2013; Batchelor et al. 2015). Changes in riparian vegetation are negatively correlated with terrestrial invertebrate inputs that are an important prey source for fish (Saunders and Fausch 2009). Loss of riparian vegetation and stream shading leads to higher stream temperatures that can exceed fish thermal tolerances (Li et al. 1994). Reduction in woody vegetation (e.g., willows, alder, aspen) and streambank trampling cause streambank instability and erosion that, in turn, lead to wider, shallower, and warmer streams with higher concentrations of fine sediments, nutrients, and bacteria (Kauffman and Krueger 1984; Stuber 1985; Armour et al. 1991; Agouridis et al. 2005).

Many studies have shown negative associations between anthropogenic land use and fish occurrence and abundance (Wenger et al. 2008; Dauwalter et al. 2011) and fish assemblage richness, diversity, and integrity (Wang et al. 1997; Dauwalter and Jackson 2004; Perkin et al. 2016). The loss of biological diversity due to stream alteration and degradation from land uses is often attributed to the concomitant reduction in habitat diversity (Stuber 1985; Armour et al.

1991). Despite this common attribution, the link between indicators of stream condition and habitat diversity is rarely quantified (but see Gorman and Karr 1978; Schlosser 1982; Laub et al. 2012) despite habitat diversity (or complexity) often being the goal of stream restoration (Palmer et al. 2010; Laub et al. 2012).

We evaluated how different elements of instream habitat diversity influenced fish diversity and how stream habitat condition was related to different elements of habitat diversity in the Goose Creek watershed. Goose Creek is a tributary to the Snake River near the Idaho–Nevada–Utah border that has been affected by multiple land uses, but livestock grazing is the predominant use. Specifically, our objectives were to (1) determine how four dimensions of habitat diversity (cover, substrate, velocity, and depth) influence fish species diversity, (2) determine how woody riparian vegetation, stream channel dimensions, streambank conditions, and fine sediments—all indicators of stream condition reflecting land use and used to monitor grazing impacts—are associated with the four dimensions of habitat diversity, and (3) determine how instream habitat diversity and other instream and riparian habitat features, including stream condition indicators, influence fish assemblage structure (proportional abundance of species).

Our study provides insight into how stream condition influences instream habitat diversity and shows how all four elements of instream habitat diversity are associated with fish species diversity in small streams in the Columbia River drainage that are characterized by low fish species richness compared with other regions of the United States (e.g., southeastern USA: Abell et al. 2008).

## METHODS

*Study area.*—Goose Creek originates in southern Idaho on the Sawtooth National Forest at around 2,200-m elevation, and then flows into Nevada, Utah, and then back into Idaho and into Lower Goose Creek (Oakley) Reservoir (1,450-m elevation). Goose Creek below the reservoir is diverted entirely for irrigation purposes and never reaches the Snake River. The Goose Creek basin is a matrix of sage *Artemisia tridentata* steppe and pine–aspen–juniper forest; higher elevations contain forests of pine *Pinus* spp., Douglas-fir *Pseudotsuga* spp., and aspen *Populus tremuloides*, whereas lower elevations contain pinyon pine *Pinus monophylla*, juniper *Juniperus* spp., and mountain mahogany *Cercocarpus ledifolius*. Riparian areas are comprised of willows *Salix* spp., alders *Alnus* spp., cottonwoods *Populus* spp., and sedges *Cyperaceae*. Average annual precipitation is 18 cm, and streamflow patterns are dominated by snowmelt runoff. Goose Creek is one of the most fish-species-rich subbasins in the Snake River basin above Hells Canyon, in which 14 fish species have been documented (Table 1; Meyer et al. 2013).

TABLE 1. Fishes documented in the Goose Creek watershed (Meyer et al. 2006, 2013; Blakney 2012; Wallace and Zaroban 2013) and their prevalence (percent occurrence) and relative abundance from all 34 (of 41) sites with fish present (3,948 individuals in total) sampled from 2013 to 2015. Species codes are in parentheses. An asterisk indicates nonnative species.

Fish species	Prevalence (%)	Relative abundance (%)
Speckled Dace <i>Rhinichthys osculus</i> (SPD)	53.7	35.7
Paiute Sculpin <i>Cottus beldingii</i> (PSC)	46.3	14.9
Brook Trout <i>Salvelinus fontinalis</i> (BKT)*	36.6	9.2
Rainbow Trout <i>Oncorhynchus mykiss</i> (RBT)*	34.1	3.7
Longnose Dace <i>Rhinichthys cataractae</i> (LND)	31.7	8.4
Bluehead Sucker <i>Catostomus discobolus</i> (BHS) <sup>a</sup>	31.7	6.6
Redside Shiner <i>Richardsonius balteatus</i> (RSS)	24.4	17.4
Northern Leatherside Chub <i>Lepidomeda copei</i> (NLC)	22.0	1.7
Yellowstone Cutthroat Trout <i>Oncorhynchus clarkii bouvieri</i> (CUT)	17.1	2.1
Utah Sucker <i>Catostomus ardens</i> (UTS)	7.3	0.18
Yellow Perch <i>Perca flavescens</i> (YPC)*	2.4	0.05
Mottled Sculpin <i>Cottus bairdii</i> (MSC)	2.4	0.03
Mountain Sucker <i>Catostomus platyrhynchus</i> (MTS)	Not collected	
Utah Chub <i>Gila atraria</i> (UTC)	Not collected	

<sup>a</sup> Proposed reclassification as *Pantosteus virescens* (Unmack et al. 2014).

The Goose Creek subbasin was included on the Idaho priority list of impaired water (303(d)), and in 2004 a total maximum daily load (TMDL) for pollutants was developed and approved for listed impairments (IDEQ 2010); portions of the subbasin in Nevada have been or are currently on that state's list of impaired waters (NDEP 2014). Most major tributaries to Goose Creek are impaired; the major impairments are bacteria (fecal coliform and *Escherichia coli*), dissolved oxygen, total phosphorous, sediment and suspended solids, and temperature. Two tributaries and a portion of the main stem do not meet beneficial-use designations, and road and trail decommissioning, road management, livestock exclusion, fence repair, riparian management, and streambank protections are listed as TMDL implementation actions (IDEQ 2010). Cattle production is the predominant land use in the region (IDFG 2005), and long-term grazing is cited as having impacted Yellowstone Cutthroat Trout populations in the drainage (IDFG 2007). Lands adjacent to the Goose Creek main stem are used for surface-irrigated hay pasture and winter grazing.

**Fish sampling.**—We conducted fish and habitat surveys at 41 sites in the Goose Creek watershed (Figure 1). Our sites were selected based on the stratified-random design used by Meyer et al. (2006) for Goose Creek, while adding additional sites selected to increase spatial coverage to represent the range of stream conditions (including grazing impacts) in the watershed and increase sample size given access constraints to private land. Each site was sampled one time from July 15 to October 6 during low-flow periods from 2013 to 2015 (number of samples in July = 10, August = 19, September = 7, October = 5). Sites ranged in wetted width from 0.4 to 6.2 m, and contributing watersheds ranged in size from 1.7 to

1,480 km<sup>2</sup>. At each site, a stream reach was typically 100 m thalweg length (range, 47–165 m), similar to Meyer et al. (2006), and was isolated using block nets with 6.35 mm bar mesh; nets were not used where impassable beaver *Castor canadensis* dams coincided with upstream reach boundaries. Fish were sampled by means of single-pass electrofishing using a Smith-Root LR-24 backpack electrofisher with one or two netters at 37 sites. Main-stem Goose Creek sites wider than 5.4 m wetted width ( $n = 4$ ) were sampled with two LR-24 backpack electrofishers and four netters. Electrofishing was done using pulsed DC (40 Hz) and 200–450 V. All fish were identified to species and counted.

**Instream and riparian habitat associations.**—After completing electrofishing surveys, we assessed instream habitat, streambank condition, and riparian vegetation using transect-based sampling. At each site, one transect was established every 10 m along the reach beginning at the downstream reach boundary. Transects were placed across the stream channel at bankfull height, which was identified using the following indicators: height of depositional surfaces, perennial vegetation, topographic breaks, bank substrates, undercut banks, and water stain lines (Harrelson et al. 1994; Burton et al. 2011). Channel depth, water depth, water velocity, stream substrate, and cover were measured at 10 equidistant points along each transect (Platts et al. 1983). We measured velocities at 0.6× water depth using a Hach FH950 velocity meter (Hach Company, Loveland, Colorado). Stream substratum at each point was classified according to the modified Wentworth scale, whereby particles are classified as bedrock, silt–clay (<0.064 mm diameter on  $b$ -axis), sand (0.064–2 mm), gravel (2–15 mm), pebble (15–64 mm), cobble (64–256 mm), or

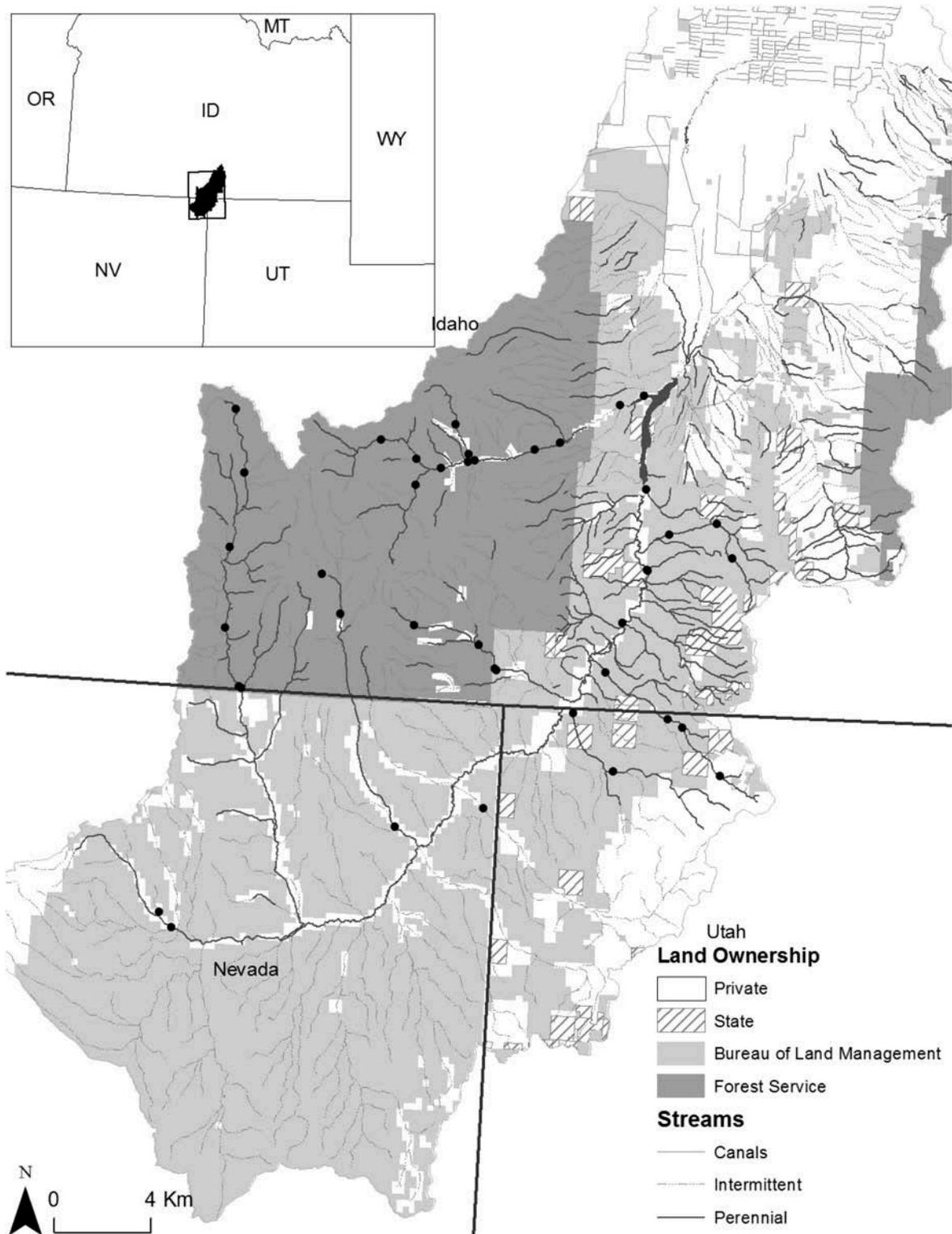


FIGURE 1. Locations of fish and habitat sample sites ( $n = 41$ ) in the Goose Creek watershed, Idaho–Utah–Nevada, 2013 to 2015.

boulder (>256 mm) (Cummins 1962). Cover was classified as boulder, large wood (>10 cm diameter, >4 m in length), small wood, aquatic vegetation (macrophytes), overhanging

bank vegetation, undercut bank (>10 cm depth), or absent. The surface water elevation difference between upstream and downstream reach boundaries was measured using a

survey level and stadia rod, and stream slope was computed as the elevation difference divided by the thalweg length (expressed as a percentage). Residual pool depth was calculated as maximum pool depth minus water depth at the downstream riffle crest for all pools identified using the classification of Hawkins et al. (1993). Woody vegetation height was classified above each transect endpoint at bankfull as 0.0–0.5 m, 0.5–1.0 m, 1.0–2.0 m, 2.0–4.0 m, 4.0–8.0 m, and >8.0 m (Burton et al. 2011), and we computed percent woody vegetation as the percentage of transect endpoints with woody vegetation greater than 1 m in height. Streambank stability was classified at each transect endpoint between the water's edge and bankfull height as fracture, slump, slough, eroding, or absent (Burton et al. 2011). Streambank alteration was defined as the presence of cattle trails within 5 m of transect endpoints and expressed as the percentage of transect endpoints with cattle trails present. Mean August stream temperature was measured using thermographs (TidbiT version2, Onset Computer Corporation, Bourne, Massachusetts) that recorded temperatures once each hour ( $n = 34$  in the Goose Creek watershed). Temperatures at sites without a thermograph were determined using data from the nearest one or two thermographs and distance interpolation or an elevation correction.

We evaluated associations among instream and riparian habitat variables using a principal components analysis (PCA). The PCA was fitted using the correlation matrix. A scree plot (PCA axis versus percent variance explained) was used to determine the number of interpretable PCA axes.

*Fish species diversity and habitat diversity.*—We evaluated how fish species diversity was associated with four dimensions of instream habitat diversity using multiple linear regression and data from sites where at least one fish species was present ( $n = 34$ ). Fish species diversity ( $H'_{spp}$ ) was computed using the Shannon–Wiener index:

$$H'_{spp} = - \sum_{i=1}^S p_i \cdot \log_e p_i \quad (1)$$

where  $p_i$  is the proportion of the total catch at a site comprised of species  $i$ , and  $S$  is species richness (i.e., total number of species) at a site (Legendre and Legendre 2012). Likewise, we computed four dimensions of habitat diversity. Cover diversity and substrate diversity were also computed using the Shannon–Wiener index ( $H'$ ), except that  $p_i$  represented the proportion of all cover (excluding the “absent” category) or substrates as type  $i$ . Diversity of water velocity and water depth was computed as the SD of water velocity (m/s) and SD of water depth (m), respectively.

Multiple linear regression was used to evaluate the effect of cover diversity ( $H'_c$ ), substrate diversity ( $H'_s$ ), SD of

velocity (m/s), and SD of depth (m) on fish species diversity. Each habitat diversity element was a separate variable in the model, and we evaluated significance of each variable at  $\alpha = 0.10$  (instead of the more traditional  $\alpha = 0.05$ ) because we were more interested in detection of associations that were real (statistical power: power =  $1 - \beta$ , where  $\beta$  is the type II error rate) along with their strength (i.e., effect size) versus safeguarding against interpreting an association as real when in fact it was not (i.e., type I error rate,  $\alpha$ , false positive) (Yoccoz 1991). We also used a commonality analysis (a.k.a., element analysis) to partition the variance in species diversity explained by the four dimensions of habitat diversity. Commonality analysis partitions variance in the response variable (species diversity) that is both unique to each explanatory variable as well as common to (or shared with) other explanatory variables, the latter of which cannot be discerned from standardized parameter estimates from multiple linear regression (Nimon et al. 2008). The analysis was done using the yhat package (Nimon et al. 2013) in Program R (R Core Team 2015).

*Habitat diversity and stream condition indicators.*—We evaluated the effect of riparian and instream habitat condition on habitat diversity by using multiple linear regression. Five measures of stream condition indicators that reflect impacts to streamside vegetation and streambanks were evaluated: streambank condition (percent bank sloughing and/or slumping), streambank alteration (percent cattle trails), percent woody riparian vegetation (woody vegetation > 1 m in height), percent fine substrates (sand, silt, and/or clay), and channel width-to-depth ratio (channel width divided by mean channel depth) (Eaglin and Hubert 1993; Kershner et al. 2004; Burton et al. 2011; Swanson et al. 2015). These five stream condition indicators were used as covariates in multiple linear regressions with each of the four dimensions of habitat diversity as response variables: cover diversity ( $H'_c$ ), substrate diversity ( $H'_s$ ), SD of water velocity (m/s), and SD of water depth (m). We included residual pool depth (m) as a covariate for stream size in each of the multiple regressions, as we expected the SDs in water velocity and depth to increase in larger streams and wanted to account for this expected variation. Significance of each habitat diversity dimension was evaluated at  $\alpha = 0.10$ . Models were refit with only significant terms to estimate parameters and variance explained (adjusted  $R^2$ ).

*Fish assemblage structure.*—We evaluated the effect of riparian and instream habitat, including the four dimensions of habitat diversity, on fish assemblage structure (i.e., relative [proportional] abundance of species) using a constrained correspondence analysis (CCA). The CCA is a direct gradient (constrained) ordination technique that uses a unimodal model to relate environmental variables to assemblage structure (ter Braak and Verdonschot 1995; Legendre and Legendre 2012). The species matrix used in

the CCA was comprised only of sites where fish were present ( $n = 34$ ) and species abundances were untransformed. The instream and riparian habitat variables evaluated for their influence on fish assemblage structure were placed into three categories: natural stream features, habitat diversity, and stream condition indicators. The suite of variables describing natural stream features were mean August stream temperature ( $^{\circ}\text{C}$ ), stream slope (%), percent aquatic vegetation (percentage of transect points), percent overhanging vegetation, and percent small wood. Habitat diversity variables were SD of depth, SD of velocity, substrate diversity ( $H'_s$ ), and cover diversity ( $H'_c$ ); percent cobble–boulder substrate was omitted from analysis because of its high correlation with substrate diversity ( $r = 0.85$ ). The stream condition variables were percent streambank sloughing–slumping, percent streambank alteration (cattle trails), percent woody vegetation, percent fine substrate (sand–silt–clay), and channel width-to-depth ratio. Each variable was evaluated for significance ( $\alpha = 0.10$ ) using a permutation test with 9,999 permutations. A final CCA was refit using only significant variables, and partial CCAs were then used to determine the amount of variation in fish assemblage structure explained by the three variable sets: natural features, habitat diversity, and stream condition indicators (Økland 1999).

## RESULTS

### Fish Sampling

At least one fish species was collected at 34 of the 41 sites sampled. Among all 12 species collected, Speckled Dace were collected at the highest percentage of sites and were the most abundant across all sites (Table 1). Brook Trout, Rainbow Trout, and Yellow Perch (collected at one site near Lower Goose Creek Reservoir) were the only nonnative fish species collected. Mottled Sculpin and Yellow Perch were only collected at one site each (2.4%) and were the least abundant. Species richness ranged from zero to eight fish species (mean = 3.1, SD = 2.5).

### Instream and Riparian Habitat Associations

The PCA suggested that variation in habitat among sites was attributable to two main habitat gradients—a longitudinal stream size gradient and an instream cover gradient. Axis 1 of the PCA explained 25.3% of the variance and axis 2 explained 21.5%. The scree plot suggested axes 3 (10.7% of variance) and higher did not explain substantially more variation than axes 1 and 2 and, therefore, they were not interpreted. A plot of axis 1 versus axis 2 showed a stream-size gradient where sites ranged from high gradient and cold temperature with more bank sloughing and slumping, more woody riparian vegetation, and more small wood (low axis 1 scores in Figure 2) to lower gradient sites with deeper residual pools, warmer temperatures, and more variation in water depths and

velocities (high axis 1 scores but low axis 2 scores in Figure 2). A second gradient represented sites dominated by high percentages of fine substrates, aquatic vegetation, and overhanging vegetation (high axes 1 and 2 scores in Figure 2) versus sites with more cobble and boulder substrates, and substrate and cover diversity (low axes 1 and 2 scores in Figure 2).

### Fish Species Diversity and Habitat Diversity

Fish species diversity ( $H'_{spp}$ ) averaged 0.61 (range, 0–1.65) and was positively associated with all four dimensions of habitat diversity (cover, substrate, water velocity, and water depth) in the Goose Creek watershed (Table 2). The overall multiple regression model fit the data well ( $F_{4,29} = 15.8$ ,  $P < 0.001$ ), and explained 64% of the variance in fish species diversity (adjusted  $R^2 = 0.642$ ). All variables were significantly different from zero, and only SD of water velocity would have been unsupported using a more restrictive type I error rate ( $P = 0.09$ ). Standardized parameter estimates showed SD of depth to have the strongest positive influence on fish species diversity in the watershed, followed by substrate diversity having the second strongest influence; SD of velocity was estimated to have the smallest effect (Table 2; Figure 3). The commonality analysis suggested that SD of depth explained most of the variation in species diversity independent of the other habitat diversity dimensions, confirming what was reflected by the standardized parameter estimates from the multiple regression. However, the commonality analysis also showed that, although cover diversity and SD of velocity explained little variation in species diversity individually, they both shared a substantial amount of variation with the other dimensions of habitat diversity and, in total, explained almost as much total variance in species diversity as did SD of depth (Table 2). This suggests that these different elements of habitat diversity covary with one another and have a shared influence on species diversity.

### Habitat Diversity and Stream Condition Indicators

Variation in each of the four dimensions of habitat diversity was explained, to varying degrees and in different ways, by stream condition indicators after a strong and persistent stream-size effect (by including the residual pool depth covariate) was accounted for. Residual pool depth had a significant, positive association with each of the four dimensions of habitat diversity, suggesting a stream habitat diversity gradient that increased downstream as streams became larger (Table 3). Cover diversity decreased as streams became wider and shallower with a higher prevalence of fine substrates. Substrate diversity also decreased when fine substrates were more prevalent, but unexpectedly increased as the number of livestock trails increased along the streambank. The SD of water velocity was lower with more streambank sloughing and

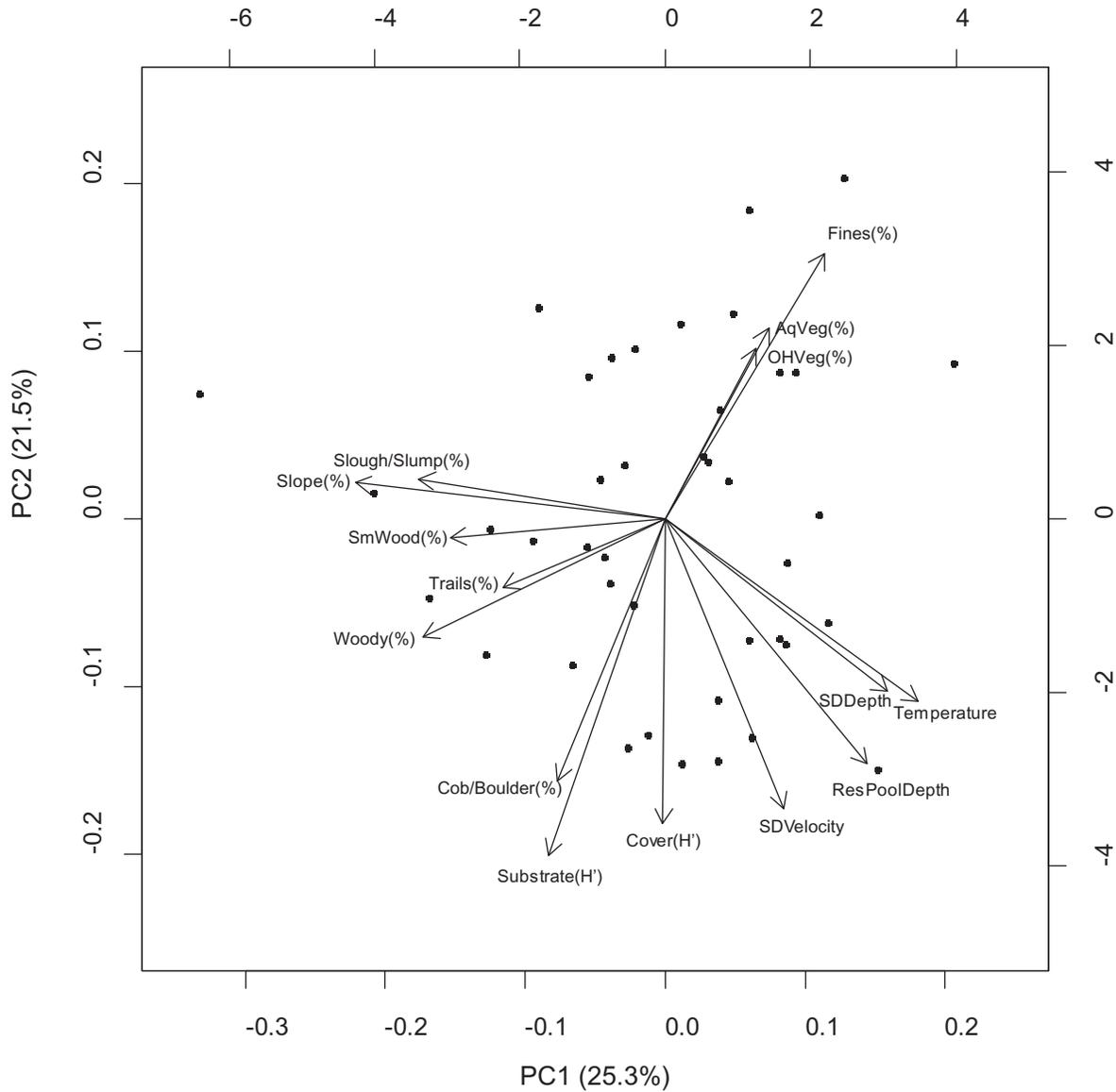


FIGURE 2. Plot of axis 1 versus axis 2 from a principal component analysis showing interrelationships among instream and riparian habitat variables in Goose Creek, 2013 to 2015.

TABLE 2. Parameter estimates, standard errors (including standardized estimates), *P*-values, and proportion of unique, common, and total variance from a multiple linear regression of four habitat diversity variables evaluated for their effect on fish species diversity in Goose Creek.

Variable	Unstandardized $\beta_i$ ( $\pm 1$ SE)	Standardized $\beta_i$ ( $\pm 1$ SE)	<i>P</i> -value	Variance contribution ( <i>p</i> )		
				Unique	Common	Total
Intercept	-0.993 (0.269)	<0.001 (0.103)	0.001 <sup>a</sup>			
Cover diversity ( $H'_c$ )	0.461 (0.185)	0.294 (0.118)	0.019	0.07	0.22	0.29
Substrate diversity ( $H'_s$ )	0.543 (0.183)	0.334 (0.112)	0.006	0.10	0.09	0.19
SD of velocity (m/s)	1.789 (1.020)	0.200 (0.114)	0.090	0.03	0.18	0.22
SD of water depth (m)	6.786 (1.493)	0.500 (0.110)	<0.001	0.22	0.12	0.34

<sup>a</sup> *P*-value for intercept is for standardized parameter estimate only.

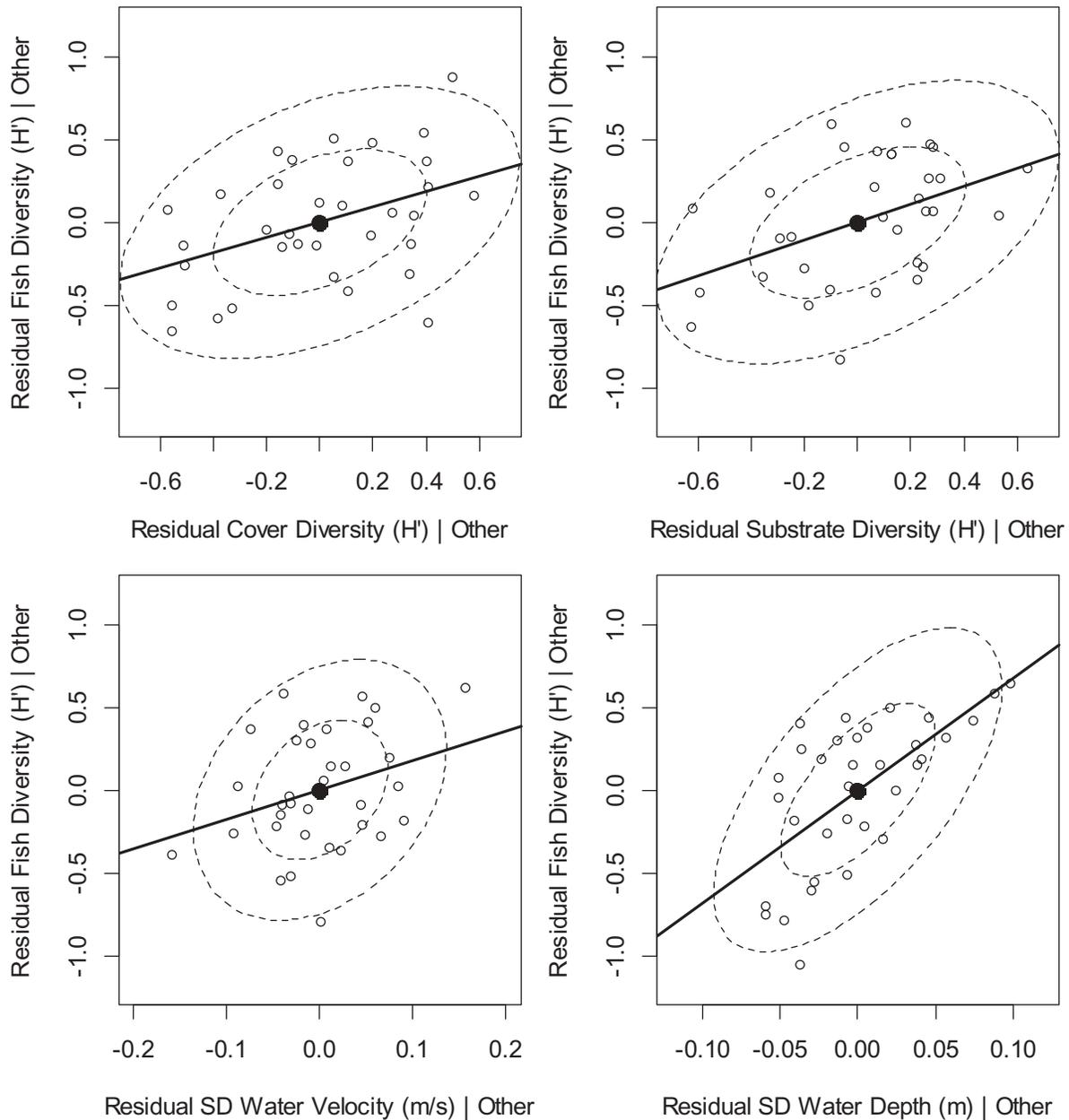


FIGURE 3. Partial regression plots showing the effect of four dimensions of stream habitat diversity on fish species diversity in Goose Creek, 2013 to 2015. Confidence ellipses represent the 50th and 90th percentiles of residual points.

slumping and more fine substrates, and SD of water depth decreased with more stream bank sloughing and slumping independent of stream size (Table 3). Only SD of water depth could be predicted with reasonable precision (adjusted  $R^2 = 0.61$ ; Table 3).

### Fish Assemblage Structure

Since Mottled Sculpin and Yellow Perch were collected at fewer than two sites they were omitted from the CCA. The CCA showed only a few instream and riparian habitat variables to be significantly associated with fish assemblage

structure: mean August stream temperature ( $P < 0.001$ ), slope ( $P = 0.012$ ), SD of velocity ( $P = 0.011$ ), and percent woody vegetation ( $P = 0.009$ ) (Table 4). Although percent fine substrates (clay-silt-sand) ( $P = 0.160$ ) did not meet our alpha criterion, we retained it in subsequent analyses to explore its association with fish assemblage structure as this has been shown in other studies (Waters 1995; Henley et al. 2000); it was the only variable close to our significance threshold. Refitting the CCA with only these variables showed a stream-size gradient where Brook Trout, Paiute Sculpin, Rainbow Trout, and Cutthroat Trout were most

TABLE 3. Parameter estimates ( $\pm 1$  SE),  $P$ -values, and adjusted  $R^2$  for models predicting four dimensions of stream habitat diversity as a function of indicators of stream condition. Parameter estimates and adjusted  $R^2$  are for models refit with only significant predictor variables ( $P < 0.10$ ).

Predictors	$\beta_i$ ( $\pm 1$ SE)	$P$ -value	Adjusted $R^2$
<b>Cover diversity (<math>H'_c</math>)</b>			
Woody vegetation (%)		0.602	0.23
Streambank slough–slump (%)		0.608	
Streambank trails (%)		0.171	
Channel width-to-depth ratio	−0.015 (0.008)	0.079	
Fine substrates (%)	−0.005 (0.002)	0.015	
Residual pool depth (m)	0.706 (0.288)	0.021	
<b>Substrate diversity (<math>H'_s</math>)</b>			
Woody vegetation (%)		0.739	0.45
Streambank slough–slump (%)		0.610	
Streambank trails (%)	0.007 (0.003)	0.095	
Channel width-to-depth ratio		0.715	
Fine substrates (%)	−0.011 (0.002)	<0.001	
Residual pool depth (m)	0.593 (0.286)	0.060	
<b>SD of velocity (m/s)</b>			
Woody vegetation (%)		0.210	0.28
Streambank slough–slump (%)	−0.002 (0.001)	0.012	
Streambank trails (%)		0.102	
Channel width-to-depth ratio		0.237	
Fine substrates (%)	−0.001 (0.0003)	0.015	
Residual pool depth (m)	0.116 (0.055)	0.042	
<b>SD of depth (m)</b>			
Woody vegetation (%)		0.580	0.61
Streambank slough–slump (%)	−0.001 (0.0003)	0.039	
Streambank trails (%)		0.856	
Channel width-to-depth ratio		0.216	
Fine substrates (%)		0.135	
Residual pool depth (m)	0.177 (0.026)	<0.001	

abundant in cold, high-gradient sites (CCA axis 1; top left panel of Figure 4). A secondary gradient showed Rainbow Trout and Paiute Sculpin to be more abundant at sites with more woody riparian vegetation and greater variation in water velocity (CCA axis 2; top left panel of Figure 4).

Variance partitioning using partial CCAs showed that the natural stream features—stream temperature and stream slope—explained more variation (51%) in assemblage structure than did the variable sets representing stream condition indicators (24%) and habitat complexity (22%). There was little explained variation in fish assemblage structure shared among the three variable sets (Table 5). Partial ordinations showed partitioning among the three trout species across cold streams, where Brook Trout were more abundant in high-gradient cold sites, and Rainbow Trout and Cutthroat Trout were more abundant at cold sites with intermediate gradients (bottom left panel of Figure 4). The partial ordination emphasizing stream condition indicators showed Cutthroat Trout to be more abundant at sites with less fine substrates and Paiute Sculpin to be more abundant at sites with more woody riparian

vegetation (top right panel of Figure 4). The partial ordination of habitat complexity showed Brook Trout to be more abundant at sites with less flow complexity (SD of velocity) and Rainbow Trout to be more abundant at sites with high flow complexity (lower right panel of Figure 4).

**DISCUSSION**

We found fish species diversity to be positively associated with all four dimensions of instream habitat diversity that we studied (cover, substrate, water velocity, and water depth), confirming that more diverse habitat is likely to have more of the unique niches available to potential species comprising fish assemblages in our disturbed study watershed. While we expected at least some dimensions of habitat diversity to influence fish species diversity, we were surprised that all four contributed to fish diversity in some way given the low number of species in our watershed compared with other regions. Numerous studies have associated habitat diversity with species diversity across taxa

TABLE 4. Significance (*P*-value) and variance inflation factor (VIF) of instream and riparian habitat variables (permutation test with 9,999 permutations) evaluated in a CCA for their influence on fish assemblage structure. The variable, percent cobble–boulder, was omitted due to high correlation with the variable, substrate diversity ( $r = 0.85$ ).

Variable	<i>P</i> -value	VIF
Temperature (°C)	<0.001	3.58
Slope (%)	0.012	2.07
Residual pool depth (m)	0.983	3.15
SD velocity (m/s)	0.011	1.99
SD water depth (m)	0.436	4.44
Woody vegetation (%)	0.009	3.36
Aquatic vegetation (%)	0.433	6.62
Small wood (%)	0.734	2.04
Overhanging vegetation (%)	0.625	2.41
Bank Trails (%)	0.745	3.02
Bank slough–slump (%)	0.603	2.39
Fine substrate (%)	0.160	6.02
Cover diversity ( $H'_c$ )	0.900	5.18
Substrate diversity ( $H'_s$ )	0.892	2.95

(MacArthur 1964; Rosenzweig and Winakur 1969; Allan 1975), but rarely has every element of habitat diversity under study contributed to fish species diversity (Gorman and Karr 1978; Jackson et al. 2001). For example, Gorman and Karr (1978) found that diversity in water velocity and depth influenced fish species diversity in both northern temperate and tropical streams, but found no influence of substrate diversity, and they did not evaluate cover diversity. Gorman and Karr (1978) suggested that the importance of habitat diversity dimensions to species diversity varies stream by stream and with the guilds represented in the species pool, such as the presence of riffle-dwelling species. Previous studies have mostly been conducted in species-rich streams, but we found that all four dimensions of habitat diversity were important to fish diversity despite our observed species pool comprising only 12 species, three of which are nonnative and two that were only collected at one site each. While Goose Creek represents a depauperate species pool compared with those elsewhere in the United States (Abell et al. 2000, 2008), it is one of the more speciose tributaries in the Snake River basin due to the

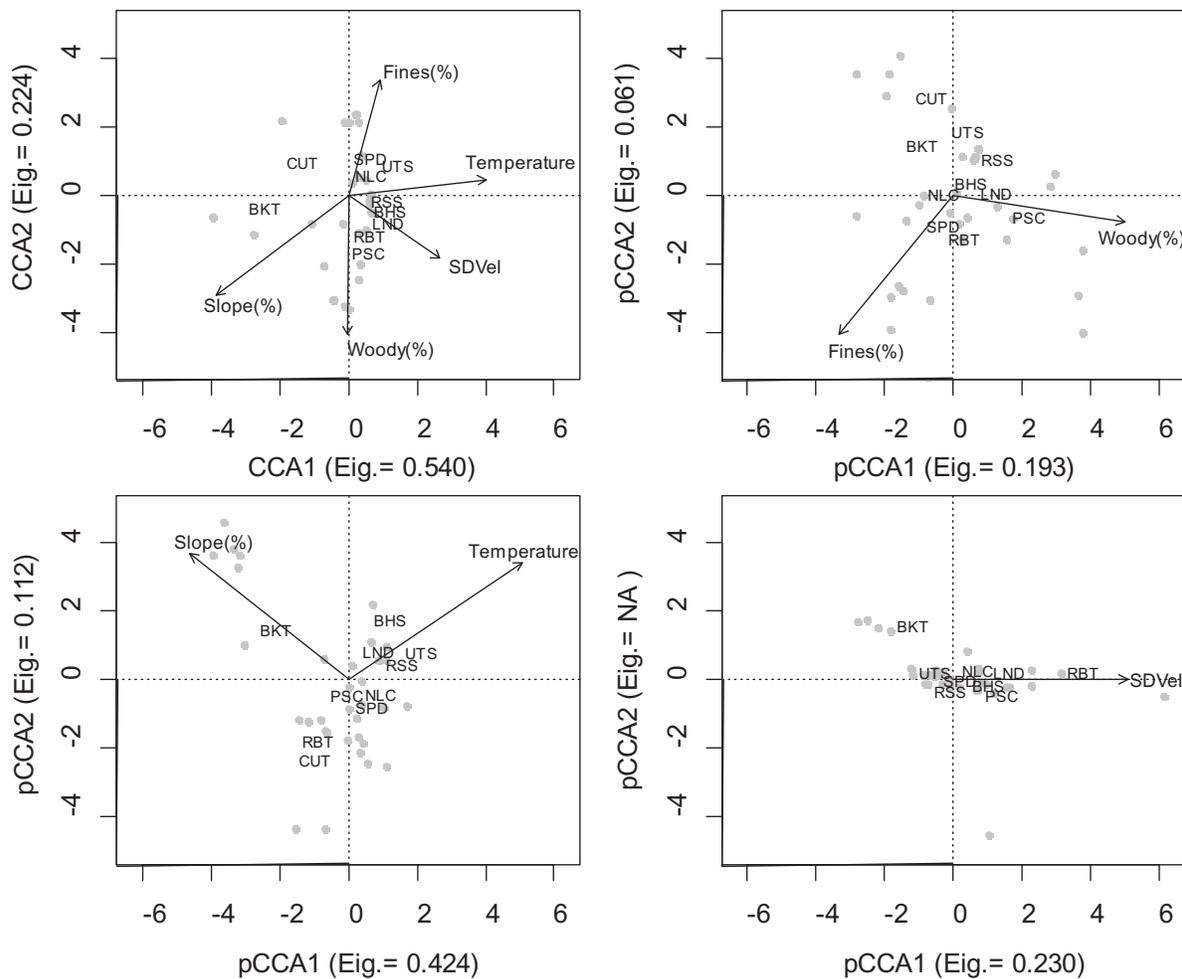


FIGURE 4. Constrained correspondence analysis (CCA) biplots showing associations of fish species to instream and riparian habitat in Goose Creek, 2013 to 2015. Top left panel shows biplot including all variables, bottom left panel shows partial CCA biplot with natural stream feature variables, top right panel shows partial CCA with stream condition variables, and bottom right panel shows partial CCA biplot with a habitat complexity variable. See Table 1 for fish species codes.

TABLE 5. Variance in fish assemblage structure attributable to natural stream features (Natural), indicators of stream condition (Condition), and habitat complexity (Complexity) and shared variances ( $\cap$ ) in the Goose Creek watershed.

Factor	Number of variables	$\Sigma$ of canonical eigenvalues	% variance	Mean % per variable
Natural features (% slope, temperature [ $^{\circ}$ C])	2	0.536	50.9	25.5
Condition (% woody vegetation, % fines)	2	0.255	24.2	12.1
Habitat complexity (SD velocity [m/s])	1	0.230	21.8	21.8
Natural $\cap$ Condition	4	0.010	1.0	0.25
Natural $\cap$ Complexity	3	0.050	4.8	1.60
Condition $\cap$ Complexity	3	-0.031	-3.0	-1.00
Natural $\cap$ Condition $\cap$ Complexity	5	0.005	0.4	0.08

occurrence of rare species such as Northern Leatherside Chub and Bluehead Sucker (Meyer et al. 2013).

Our analyses also suggested that habitat diversity persistently increased with stream size. Stream size is often positively associated with fish species diversity due to increased habitat volume and, presumably, a higher diversity of available resources (Vannote et al. 1980; Angermeier and Schlosser 1989), and our study shows this linkage directly with physical habitat availability. Sheldon (1968) found that fish assemblages in a New York watershed changed mainly through species additions (species replacement was minor) that occurred due to increases in water depth and habitat diversity, both of which generally, but not systematically, increased downstream. Rahel and Hubert (1991) found that coldwater species in the headwaters of a Rocky Mountain stream were replaced by warmwater species downstream whereby additional warmwater species were continually being added to the assemblage; that is, they found a strong longitudinal gradient in fish assemblages related to stream size (and the other habitat features associated with stream size). However, when using a coefficient of variation as a measure of habitat diversity they found habitat diversity to be uncorrelated with stream size. The strength of species diversity–habitat diversity associations, if present, likely depends on the range of stream sizes studied and how diversity and thus resource availability is quantified (Tews et al. 2004). We suspect that resource availability is best represented as an unstandardized measure of variability, such as with a standard deviation or diversity index (categorizing continuous data when needed), instead of a standardized measure such as a coefficient of variation. Habitat diversity, heterogeneity, and complexity have been defined and quantified in a myriad of ways (Schlosser 1982; Rahel and Hubert 1991; Tews et al. 2004; Taylor et al. 2006; Smith et al. 2016).

Although habitat diversity primarily increased along a stream-size gradient, we determined that stream condition influenced habitat diversity independent of this stream-size continuum, a novel aspect of our study. Degraded streams have wide, shallow channels dominated by fine sediments, a

lack of riffles and pools, and a lack of instream cover (Kauffman and Krueger 1984; Armour et al. 1991). In almost every case in our study, stream condition indicators had a negative association with the different dimensions of habitat diversity, with a presumably adverse effect on fish diversity as well. What requires further study, however, is whether streams with low habitat diversity also have habitat conditions that vary more over time. For example, grazing can compact soils and increase overland flow and storm runoff, thus increasing streamflow variability and habitat variability over time (Marston 1994; Trimble and Mendel 1995). Temporal variability in habitat, in turn, can negatively affect fish assemblage stability (Taylor et al. 2006) and decrease the strength of habitat diversity–fish diversity associations (Schlosser 1982). This phenomenon requires further study in species-poor systems such as stream fish communities in the northwestern United States.

While habitat diversity influenced fish species diversity, the constrained ordination showed that habitat diversity explained only a small fraction of fish assemblage structure. Fish assemblages were structured primarily along a longitudinal stream-size gradient in Goose Creek; streamflow diversity (SD of velocity) was the only dimension of habitat diversity to significantly influence assemblage structure directly (and was the weakest dimension associated with fish diversity). Therefore, while habitat diversity and species diversity increased in larger streams in our study area, the relative abundances of individual species in the assemblage were largely not influenced, *per se*, by habitat diversity. The one exception was that Brook Trout and Rainbow Trout were partitioned along a gradient of streamflow diversity in which Brook Trout were more abundant at cold stream sites with simple streamflows and Rainbow Trout were more abundant at cold sites with complex flows (lower right panel of Figure 4). Other studies have determined the structure of the fish assemblages to be primarily a function of stream size and longitudinal gradient (Schlosser 1982; Schultz et al. 2012). For example, Rahel and Hubert (1991) concluded that fish assemblages in a Wyoming stream were structured primarily along a longitudinal thermal gradient,

with a trout-dominated assemblage in the headwaters that transitioned to a warmwater assemblage that became more species rich downstream, a pattern also reflected in fish assemblages of Goose Creek.

Although salmonids dominated fish assemblages in small, cold streams, we also observed apparent partitioning by salmonids among the coldest headwater streams. Brook Trout were abundant in the high-gradient, cold streams, whereas Cutthroat Trout and Rainbow Trout were abundant only in the moderate-gradient, cold sites that we sampled, a pattern also observed by Maret et al. (1997) for least-disturbed streams in the upper Snake River basin. The mechanisms driving patterns of salmonid relative abundances requires further study, as those patterns could reflect negative competitive interactions (Peterson et al. 2004; Benjamin et al. 2011), hybridization (Meyer et al. 2006), and stocking and invasion history (Benjamin et al. 2007; Neville and Bernatchez 2013). Inconsistent capture of Rainbow Trout suggests this species has invaded only the lower portion of the watershed in streams nearest Lower Goose Creek Reservoir. The diverse fish community in the Goose Creek main stem may provide some resistance to invasion by Rainbow Trout into tributaries farther from the reservoir, as diverse communities have been suggested to resist invasion by nonnative species (Moyle and Light 1996). Continued monitoring of the fish community would help detect further invasions, species interactions and replacements, and any homogenization of the fish community in the watershed over time (Rahel 2002; Meyer et al. 2014).

In addition to fish assemblages being structured along a natural longitudinal gradient, variance partitioning suggested that the two indicators of stream condition included in the ordination explained 24% of the fish assemblage structure independent of the observed longitudinal gradient. This suggests that while land management can have some influence on habitat diversity (and thus species diversity), it can have a stronger influence on the specific habitat components structuring fish assemblages. It is well documented that logging, road building, grazing, and other land uses lead to sedimentation in streams (Eaglin and Hubert 1993; Waters 1995). Regardless of the source, fine sediments smother and embed larger substrates and adversely affect lithophilic spawning and insectivorous fishes (Berkman and Rabeni 1987; Dauwalter et al. 2003). These land uses can also result in reductions in woody riparian vegetation, streambank stability, and terrestrial invertebrate prey inputs and, in turn, negatively impact stream fishes (Bayley and Li 2008; Saunders and Fausch 2012). Mature riparian vegetation results in more overhanging vegetation in other habitats used by fishes in the upper Snake River basin (Meyer et al. 2013; Dauwalter et al. 2014, 2015). Thus, strategic management of timber harvest, roads, grazing, and other land uses can aid the protection and enhancement of stream habitats and fishes; for example, implementation of best management

practices for timber harvest and road construction (e.g., stream buffers) can minimize impacts to stream ecosystems (Angermeier et al. 2004). Likewise, grazing management, such as riparian exclosures, off-stream watering facilities, rotational grazing, and reduced cattle stocking densities, can reduce the negative effects of grazing on stream ecosystems (DelCurto et al. 2005; Saunders and Fausch 2009; Tufekcioglu et al. 2013; Swanson et al. 2015). Active restoration in heavily affected stream reaches can also improve riparian vegetation, instream habitat, and overall habitat diversity (Laub et al. 2012). Thus, both land management and active restoration will likely play roles in the conservation of fish assemblages, such as those in Goose Creek, that represent a diversity “hotspot” within a larger river basin impacted by land and water uses and show a close linkage to instream habitat diversity (Hauer and Lorang 2004; Meyer et al. 2013).

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## REFERENCES

- Abell, R. A., D. M. Olson, E. Dinerstein, P. T. Hurley, J. T. Diggs, W. Eichbaum, S. Walters, W. Wettengel, T. Allnutt, C. J. Loucks, P. Hedao, R. A. Abell, D. M. Olson, E. Dinerstein, P. T. Hurley, J. T. Diggs, W. Eichbaum, S. Walters, W. Wettengel, T. Allnutt, C. J. Loucks, and P. Hedao. 2000. Freshwater ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.
- Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. C. Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E. Wikramanayake, D. Olson, H. L. Lopez, R. E. Reis, J. G. Lundberg, M. H. S. Perez, and P. Petry. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58:403–414.
- Agouridis, C. T., S. R. Workman, R. C. Warner, and G. D. Jennings. 2005. Livestock grazing management impacts on stream water quality: a review. *Journal of the American Water Resources Association* 41:591–606.
- Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56:1040–1053.
- Angermeier, P. L., and I. J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70:1450–1462.
- Angermeier, P. L., A. P. Wheeler, and A. E. Rosenberger. 2004. A conceptual framework for assessing impacts of roads on aquatic biota. *Fisheries* 23 (12):19–29.
- Armour, C. L., D. A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. *Fisheries* 16(1):7–11.
- Batchelor, J. L., W. J. Ripple, T. M. Wilson, and L. E. Painter. 2015. Restoration of riparian areas following removal of cattle in the northwestern Great Basin. *Environmental Management* 55:930–942.

- Bayley, P. B., and H. W. Li. 2008. Stream fish responses to grazing exclosures. *North American Journal of Fisheries Management* 28:135–147.
- Benjamin, J. R., J. B. Dunham, and M. R. Dare. 2007. Invasion by nonnative Brook Trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. *Transactions of the American Fisheries Society* 136:875–888.
- Benjamin, J. R., K. D. Fausch, and C. V. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. *Oecologia* 167:503–512.
- Berkman, H. E., and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285–294.
- Beschta, R. L., D. L. Donahue, D. A. DellaSala, J. J. Rhodes, J. R. Karr, M. H. O'Brian, T. L. Fleischner, and C. Deacon Williams. 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management* 51:474–491.
- Blakney, J. R. 2012. Historical connectivity and contemporary isolation: population genetic structure of a rare high-desert minnow, the Northern Leatherside Chub (*Lepidomeda copei*). Master's thesis. Idaho State University, Pocatello.
- Booth, D. B., A. H. Roy, B. Smith, and K. A. Capps. 2016. Global perspectives on the urban stream syndrome. *Freshwater Science* 35:412–420.
- Burton, T. A., S. J. Smith, and E. R. Cowley. 2011. Riparian area management: multiple indicator monitoring (MIM) of stream channels and streamside vegetation. U.S. Bureau of Land Management, BLM/OC/ST-10/003+1737, Technical Reference 1737-23, Denver.
- Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist* 67:477–504.
- Dauwalter, D. C., K. A. Fesenmyer, and R. Bjork. 2015. Using aerial imagery to characterize Redband Trout habitat in a remote desert landscape. *Transactions of the American Fisheries Society* 144:1322–1339.
- Dauwalter, D. C., and J. R. Jackson. 2004. A provisional fish index of biotic integrity for assessing Ouachita Mountains streams in Arkansas, U.S.A. *Environmental Monitoring and Assessment* 91:27–57.
- Dauwalter, D. C., E. J. Pert, and W. E. Keith. 2003. An index of biotic integrity for fish assemblages in Ozark Highland streams of Arkansas. *Southeastern Naturalist* 2:447–468.
- Dauwalter, D. C., S. J. Wenger, and P. Gardner. 2014. The role of habitat complexity in habitat use and selection by stream fishes in a Snake River basin tributary. *Transactions of the American Fisheries Society* 143:1177–1187.
- Dauwalter, D. C., S. J. Wenger, K. R. Gelwicks, and K. A. Fesenmyer. 2011. Land use associations with declining native fishes in the upper Colorado River basin. *Transactions of the American Fisheries Society* 140:646–658.
- DelCurto, T., M. Porath, C. T. Parsons, and J. A. Morrison. 2005. Management strategies for sustainable beef cattle grazing on forested rangelands in the Pacific Northwest. *Rangeland Ecology and Management* 58:119–127.
- Eaglin, G. S., and W. A. Hubert. 1993. Effects of logging and roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. *North American Journal of Fisheries Management* 13:844–846.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629–644.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–214.
- Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59:507–515.
- Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. U.S. Forest Service General Technical Report RM-245.
- Hauer, F. R., and M. S. Lorang. 2004. River regulation, decline of ecological resources, and potential for restoration in a semi-arid lands river in the western USA. *Aquatic Sciences* 66:388–401.
- Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6):3–12.
- Henley, W. F., M. A. Patterson, R. J. Neves, and A. D. Lemly. 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science* 8:125–139.
- IDEQ (Idaho Department of Environmental Quality). 2010. Goose Creek subbasin: TMDL five year review. IDEQ, Twin Fall Regional Office, Twin Falls.
- IDFG (Idaho Department of Fish and Game). 2005. Idaho comprehensive wildlife conservation strategy. IDFG, Idaho Conservation Data Center, Boise.
- IDFG (Idaho Department of Fish and Game). 2007. Management plan for conservation of Yellowstone Cutthroat Trout in Idaho. IDFG, Boise.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* 37:430–438.
- Kershner, J. L., B. B. Roper, N. Bouwes, R. Henderson, and E. Archer. 2004. An analysis of stream habitat conditions in reference and managed watersheds on some federal lands within the Columbia River basin. *North American Journal of Fisheries Management* 24:1363–1375.
- Laub, B. G., D. W. Baker, B. P. Bledsoe, and M. A. Palmer. 2012. Range of variability of channel complexity in urban, restored, and forested reference streams. *Freshwater Biology* 57:1076–1095.
- Legendre, P., and L. Legendre. 2012. *Numerical ecology*. Elsevier, Oxford, UK.
- Lepori, F., D. Palm, E. Brannas, and B. Malmqvist. 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15:2060–2071.
- Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day basin, Oregon. *Transactions of the American Fisheries Society* 123:627–640.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. *American Naturalist* 98:387–397.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Maret, T. R., C. T. Robinson, and G. W. Minshall. 1997. Fish assemblages and environmental correlates in least-disturbed streams of the upper Snake River basin. *Transactions of the American Fisheries Society* 126:200–216.
- Marston, R. A. 1994. River entrenchment in small mountain valleys of the western USA: influence of beaver, grazing, and clearcut logging. *Revue de Geographic de Lyon* 69:11–15.
- Meyer, K. A., J. A. J. Lamansky, D. J. Schill, and D. W. Zaroban. 2013. Nongame fish species distribution and habitat associations in the Snake River basin of southern Idaho. *Western North American Naturalist* 73:20–34.
- Meyer, K. A., E. I. Larson, C. L. Sullivan, and B. High. 2014. Trends in the distribution and abundance of Yellowstone Cutthroat Trout and nonnative trout in Idaho. *Journal of Fish and Wildlife Management* 5:227–242.
- Meyer, K. A., D. J. Schill, J. A. Lamansky Jr., M. R. Campbell, and C. C. Kozfay. 2006. Status of Yellowstone Cutthroat Trout in Idaho. *Transactions of the American Fisheries Society* 135:1329–1347.

- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78:149–161.
- NDEP (Nevada Department of Environmental Protection). 2014. Nevada 2012 water quality integrated report with EPA overlisting. NDEP, Carson City.
- Nerbonne, B. A., and B. Vondracek. 2001. Effects of local land use on physical habitat, benthic macroinvertebrates, and fish in the Whitewater River, Minnesota, USA. *Environmental Management* 28:87–99.
- Neville, H. M., and L. Bernatchez. 2013. Coding gene single nucleotide polymorphism population genetics of nonnative Brook Trout: the ghost of introductions past. *Transactions of the American Fisheries Society* 142:1215–1231.
- Nimon, K., M. Lewis, R. Kane, and R. M. Haynes. 2008. An R package to compute commonality coefficients in the multiple regression case: an introduction to the package and a practical example. *Behavior Research Methods* 40:457–466.
- Nimon, K., D. Oswald, and J. K. Roberts. 2013. yhat: interpreting regression coefficients. Available: <http://CRAN.R-project.org/package=yhat>. (May 2016).
- Økland, R. H. 1999. On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science* 10:131–136.
- Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology* 55:205–222.
- Perkin, J. S., M. J. Troia, D. C. R. Shaw, J. E. Gerken, and K. B. Gido. 2016. Multiple watershed alterations influence fish community structure in Great Plains prairie streams. *Ecology of Freshwater Fish* 25:141–155.
- Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of brook trout on native Cutthroat Trout. *Ecological Applications* 14:754–772.
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Poff, B., K. A. Koestner, D. G. Neary, and V. Henderson. 2011. Threats to riparian ecosystems in western North America. *Journal of the American Water Resources Association* 47:1241–1254.
- R Core Team. 2015. R: a language and environment for statistical computing, version 3.0.2. R Foundation for Statistical Computing, Vienna.
- Rahel, F. J. 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33:291–315.
- Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society* 120:319–332.
- Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitat and environmental complexity. *Ecology* 50:558–572.
- Roth, N. E., J. D. Allan, and D. E. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11:141–156.
- Saunders, W. C., and K. D. Fausch. 2009. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. *Transactions of the American Fisheries Society* 136:1216–1230.
- Saunders, W. C., and K. D. Fausch. 2012. Grazing management influences the subsidy of terrestrial prey to trout in central Rocky Mountain streams (USA). *Freshwater Biology* 57:1512–1529.
- Schlösser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52:395–414.
- Schultz, L. D., S. J. Lewis, and K. N. Bertrand. 2012. Fish assemblage structure in Black Hills, South Dakota streams. *Prairie Naturalist* 44:98–104.
- Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193–198.
- Smith, C. D., M. C. Quist, and R. S. Hardy. 2016. Fish assemblage structure and habitat associations in a large western river. *River Research and Applications* 32:622–638.
- Smith, J. M., and M. E. Mather. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology* 58:1523–1538.
- St. Pierre, J. L., and K. E. Kovalenko. 2014. Effect of habitat complexity attributes on species richness. *Ecosphere* 5:1–10.
- Stuber, R. J. 1985. Trout habitat, abundance, and fishing opportunities in fenced vs unfenced riparian habitat along Sheep Creek, Colorado. U.S. Forest Service General Technical Report RM-GTR-120:310–314.
- Swanson, S., S. Wyman, and C. Evans. 2015. Practical grazing management to maintain or restore riparian functions and values on rangelands. *Journal of Rangeland Application* 2:1–28.
- Taylor, C. M., T. L. Holder, R. A. Fiorillo, L. R. Williams, R. B. Thomas, and M. L. Warren Jr. 2006. Distribution, abundance, and diversity of stream fishes under variable environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 63:43–54.
- ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57:255–289.
- Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31:79–92.
- Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent: a critical review. *Geomorphology* 13:233.
- Tufekcioglu, M., R. C. Schultz, G. N. Zaines, T. M. Isenhardt, and A. Tufekcioglu. 2013. Riparian grazing impacts on streambank erosion and phosphorus loss via surface runoff. *Journal of the American Water Resources Association* 49:103–113.
- Unmack, P. J., T. E. Dowling, N. J. Laitinen, C. L. Secor, R. L. Mayden, D. K. Shiozawa, and G. R. Smith. 2014. Influence of introgression and geological processes on phylogenetic relationships of western North American mountain suckers (*Pantosteus*, Catostomidae). *PLoS (Public Library of Science) ONE* [online serial] 9:e90061.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.
- Vondracek, B., K. Blann, C. B. Cox, J. F. Nerbonne, K. G. Mumford, and B. A. Nerbonne. 2005. Land use, spatial scale, and stream systems: lessons from an agricultural region. *Environmental Management* 36:775–791.
- Wallace, R. L., and D. W. Zaroban. 2013. Native fishes of Idaho. American Fisheries Society, Bethesda, Maryland.
- Wang, L., J. Lyons, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22(6):6–12.
- Waters, T. F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society, Monograph 7, Bethesda, Maryland.
- Wenger, S. J., J. T. Peterson, M. C. Freeman, B. J. Freeman, and D. D. Homans. 2008. Stream fish occurrence in response to impervious cover, historic land use, and hydrogeomorphic factors. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1250–1264.
- Yoccoz, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bulletin of the Ecological Society of America* 72:106–111.