A Macroecological Approach to Understanding Drivers

of Riverine Fish Community Composition

By

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Abstract

Macroecology is an evolving ecological discipline that analyzes regional through global processes whose temporal interactions are especially significant over decades to millennia. Understanding if and how variables acting on rivers at large spatiotemporal scales affect fish communities is key to better river management and ecological theory. Using the American Fisheries Society's standard sampling protocol, we sampled fish communities in contrasting (constricted and wide valley) hydrogeomorphic patches in both upland and lowland areas within terminal basin rivers in the Great Basin USA. We used species and trait-based community composition data, reach scale habitat data, and valley scale hydrogeomorphic data to analyze relationships between community composition and environmental variables. These relationships were evaluated using Mantel and partial Mantel tests to elucidate a causal network between the previously listed elements. Canonical correspondence analysis (CCA) was then used to illuminate specific variables within each environmental scale that may shape the composition of fish communities. Results indicated that valley scale hydrogeomorphic variables had a significant direct effect on fish community composition and explained more variation within the CCA than reach scale habitat variables. Correlations were stronger when based on a trait description of fish community composition with valley scale variables and more variance was explained in CCAs by environmental variables when a trait-based description was used.

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Background

Macroecology is an evolving ecological discipline that analyzes regional through global processes whose temporal interactions are especially significant over decades to millennia (Thorp, 2014). Riverine macrosystems in particular have been described as "…watershed-scale networks of connected and interacting riverine and upland habitat patches" (McCluney *et al.*, 2014). This thesis is part of a larger riverine macrosystem study focusing on roles of hierarchical scale, system drivers, and climate change in controlling hydrology, system metabolism, invertebrate trait composition, fish trait composition, and food webs. This larger project (Macroecological Riverine Synthesis – MACRO) compares rivers within three temperate steppe biomes on two continents (North America Great Plains in the USA and Euro-Asian Steppes of Mongolia). The present study analyzed two rivers within the Great Basin located in the western USA and evaluated the influences of environmental variables at differing spatial scales on fish community composition.

The primary goals of this thesis were to illustrate the importance of a multiscale environmental approach and a trait-based community description approach in analyzing fish community structure within riverine networks and to elucidate the influence of valley scale hydrogeomorphology on the structure of fish communities. The intrinsic hierarchical nature of riverine networks creates unique challenges to the study and management of rivers. Understanding if and how variables acting on rivers at large spatiotemporal scales affect fish communities is key to better river management and ecological theory. Asking questions which begin to unravel the immense complexity of these hierarchical systems requires a different practical and theoretical approach. In our study, we purposefully chose sites of contrasting hydrogeomorphic nature to maximize time and resources and increase our chances of illuminating patterns present within the complex spatiotemporal nature of riverine macrosystems.

The number of replicates per sample area in this project was necessarily smaller because of the immense geographical area covered, and the breadth of the questions asked. To counter restrictions to sample size, we analyzed our data using d-separation tests of path models (Shipley, 2000) which permits the testing of models with small data sets. Frenette-Dussault, Shipley, and Hingrat (2013) illustrated how Mantel and partial Mantel tests can be used in accordance with the theory of d-separation to test for plausible causal pathways between matrices.

Other challenges to this study were the lack of fish diversity present within the terminal basin rivers of the Great Basin and that many of the species were introduced. We focused on a trait-based approach to community analysis for the study. In this approach, biological traits of individual species are used as markers of diversity rather than the species themselves. An advantage of this approach is that it allows for more generality and predictability, creating a better framework to test ecological theories and examine patterns at large scales (McGill *et al.*, 2006).

These problems of low sample size and diversity made it difficult to expose ecological patterns using conventional community analytics. This reflects the observation that, macroecology requires thinking outside of conventional research methodology and becoming creative with how you frame your questions and interpret analyses. With this in mind, this thesis focuses on greater trends in riverine macroecology in relation to fish community composition rather than centering on detailed patterns related to fish communities and environmental factors. We hope that this body of work creates a foundation for future research in the MACRO project as well as the greater field of riverine macroecology by exposing the connection between valley scale hydrogeomorphic variables and fish community composition.

Chapter 1.

A Macroecological Approach to Understanding Drivers

of Riverine Fish Community Composition

Introduction

Rivers as one of the most heavily human influenced ecosystems on earth (Dudgeon et al., 2006) present unique challenges for research and management. A more comprehensive understanding of the functioning of riverine macrosystesms can be gained from a nontraditional approach incorporating a larger spatiotemporal view of riverine communities and processes (Thorp, 2014). This is especially true if we are to effectively assess and predict effects on riverine networks from climate change, invasive species, and alterations of river hydrology and geomorphology.

Macrosystems have been defined as: "... hierarchical dynamic networks, influenced by strong directional connectivity that integrates processes across multiple scales and broad distances through time" (McCluney et al., 2014). Macroecological studies can encompass a wide range of structural and functional attributes of the system, including nutrient cycling and system metabolism, food webs and food chain length, and traits of invertebrates and fish. Previous research has focused on the roles of large scale anthropogenic stressors in shaping community assemblage but has largely overlooked effects of valley scale hydrogeomorphic metrics on community structure (Hoeinghaus, Winemiller, & Birnbaum, 2007; Pease, Taylor, Winemiller, & King, 2015; Pool, Olden, Whittier, & Paukert, 2010). To better understand biotic community structure in riverine ecosystems, valley scale variables that shape long-term stream behavior and physical habitat structure need to be incorporated (Davies, Norris, & Thoms, 2000; Frissell, Liss, Warren, & Hurley, 1986).

Determining the mechanisms behind assembly and response rules at various scales to better predict community assemblages has a long history in ecological research (Keddy, 1992). Specific combinations of environmental variables function as "environmental filters" that influence stream

fish assemblages at both the reach/local and valley/regional scales (Angermeier & Winston, 1999; Hoeinghaus et al., 2007; Pease et al., 2015; Poff, 1997). For example, changes in local and regional hydrological regimes, particularly due to impoundments, are significantly associated with changes in fish assemblages (McManamay & Frimpong, 2014; Mims & Olden, 2013; Perkin et al., 2016).

Past studies exploring relationships between community assemblage and environmental variables using taxonomic approaches have been successful at multiple scales (Angermeier & Winston, 1999; Taylor, Winston, & Matthews, 1993), but taxonomic diversity metrics alone are insufficient to comprehend community functional structure (Villéger, Ramos Miranda, Flores Hernández, & Mouillot, 2010). Community ecologists are increasingly incorporating trait-based community analysis as an essential tool for assessing community composition (McGill, Enquist, Weiher, & Westoby, 2006). Traits have the unique ability to incorporate links among community structure, environmental variables, and ecosystem function (Cadotte, Carscadden, & Mirotchnick, 2011; Frimpong & Angermeier, 2010; C. T. Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010). The unique spatiotemporal scale at which riverine macrosystems function make trait-based approaches promising when assessing large-scale environmental filters on fish community assemblages.

The current study evaluates the plausible causal pathways between valley scale variables, reach scale variables, and community composition using the theory of d-separation (Frenette-Dussault, Shipley, & Hingrat, 2013; Shipley, 2000) within terminal-basin rivers located in the western USA. We hypothesized that valley scale environmental variables would have a direct effect on reach scale variables and fish community composition. We also expected a direct effect of reach scale variables on fish community composition. Within this analysis we anticipated that

the trait-based description of fish community composition would be more highly correlated with both environmental variables than would the taxonomic description.

Methods

Study Area

The large spatial extent of the study area and the ecological goals of our macrosystem project to sample a wide range of ecological properties (e.g. hydrology, system metabolism, invertebrate traits, fish traits, and food webs) in a short time span constrained the intensity and extent of research analyses at each sample site. The present project focused on the Carson and Bear Rivers, two terminal basin rivers in the Great Basin, a forested and semi-desert dominated region of the western United States (Fig. 1). The Carson River has a watershed of ~10,100 km^2 (Douglas K. Maurer, Angela P. Paul, David L. Berger, 2009). It originates high in the Sierra Nevada Mountains and flows down through the semiarid desert of western Nevada before evaporating in the Carson Sink. The Bear River flows from the Uinta Mountains of Utah north through southwestern Wyoming and southeastern Idaho before turning back south and flowing into Utah's Great Salt Lake, creating a drainage basin of 19,631 km^2. These basins were selected for analysis based on their diverse and unique geomorphologies and their reliable presence of water during our sampling period.

Sampling Design

The initial analysis of the two basins employed a set of GIS tools (RESonate; Williams et al., 2013). RESonate characterizes unique functional process zones (FPZs; Thorp, Thoms, & Delong, 2006), or river valley scale hydrogeomorphic patches, using a combination of catchment,

river valley, and river channel characteristics (10 parameters in our case). We characterized stream segments at 10-km lengths, and then selected sampling sites. Selection of stream segments was based both on their hydrogeomorphic classification created by the RESonate model and on their accessibility for sampling. Contrasting FPZ classifications were selected (e.g. wide vs. constricted valleys) to elucidate differences in community structure that traditional sampling methodologies may not have identified.

Sample sites in the Carson River were split into upland and lowland categories. Upland sites were located in two of the western most tributaries of the Carson River (West Fork Carson River and Wolf Creek) within the Sierra Nevada Mountains (Fig. 1). The lowland sites were located on the main channel of the Carson River just south of Carson City, NV and extended eastward (Fig. 1). The upland and lowland groups were further divided into two subcategories: wide valley sites and constricted valley sites. It is important to note that upland constricted and wide valley FPZs were not equivalent in physical characteristics to lowland constricted and wide valley sites. Three sites in each of the four contrasting FPZs were sampled, producing 12 sites in total.

Only upland sites were sampled on the Bear River due to challenges with accessibility and significant anthropogenic modifications in lowland areas. The upland sites were categorized into constricted valley and wide valley. Half of the sites were in the Wasatch National Forest at the headwaters of the Bear River. Two of the upland constricted valley sites (Bear River and the East Fork Bear River) and one of the upland wide valley sites (Mill Creek) were located in the headwater region (Fig. 1). The other three sites were distributed throughout the Bear River Mountain Range within the Cache National Forest and included two wide valley sites (Blacksmith Fork River and Eightmile Creek) and one constricted valley site (Cub River). These six sites

allowed for comparison to the upland data collected in the Carson basin and provided a more holistic analysis of upland sites within the Great Basin.

Data Collection

We sampled streams in July-August 2016 when stream flow was adequate at all sites to sustain fish populations. Two reaches were sampled per site, each approximately 10 times the wetted width of the stream, giving a sufficient measure of fish diversity and abundance within streams of this size (Patton, Hubert, Rahel, & Gerow, 2000). Our goal was to acquire adequate fish taxonomic and abundance data to characterize each sample site (FPZ segment) individually rather than to characterize the entire stream community. Stream size, depth, and low fish diversity helped us maximize data collection in a short sampling window. To gain an adequate measure of each site's fish community, we employed backpack electrofishing (with a Smith-Root LR24 and an ETS AB-3), seining, and gillnetting techniques, following guidelines of the American Fisheries Society's Standard Methods (Bonar, Hubert, & Willis, 2009). Collected fish were identified to species, weighed, and measured (standard length).

Environmental variables (valley and reach level)

Valley scale environmental variables relate to large scale ecosystem processes (9 of 10 variables extracted by RESonate) were used in this study due to their continuous nature (mean annual precipitation, elevation, valley width, valley floor width, ratio of valley width to valley floor width, left valley slope, right valley slope, down valley slope, and river channel sinuosity). Reach scale environmental variables relate to in-stream processes and habitat and were measured at each site following a standardized methodology (EPA, 2004). The reach variables used in the

analyses were averages of multiple measurements taken within the sample reaches of each site: depth (m), velocity (m/s), wetted width (m), bank full width (m), flow composition (percent riffle, run, pool), and substrate composition (percent boulder 250-4000 mm, cobble 64-250 mm, course gravel 16-64 mm, fine sand or other sediment <16 mm). A summary of valley and reach scale variables used in this study are presented in Table 1.

Taxonomic and trait-based approaches

Both taxonomic and trait-based approaches were used to describe fish community composition. Taxonomic community composition was described using the species abundance data from each site. To translate species abundance into functional trait abundance, species were assigned to 6 trait groups (Table 2). The reproductive group (1) was categorized following Balon (1975). The trophic trait group (2) was based on adult feeding habits following Olden, Poff, & Bestgen (2006). Life-history classifications (3) were obtained from the database described in Mims et al. (2010) following the opportunistic-periodic-equilibrium trichotomy (Winemiller & Rose, 1992). Habitat traits consisted of two groups: substrate preference (4) and current velocity preference (5) (Frimpong & Angermeier, 2013; Poff & Allan, 1995). Morphology was described as shape factor (6), the ratio of total body length to maximum body depth (or fineness ratio) (P. W. Webb & Weihs, 1986).

Statistical Analysis

All statistical analyses were run in the statistical environment R version 3.3.2 (R Development Core Team, 2016). To analyze community composition among sites, we created dissimilarity matrices from both species and trait-based community abundance matrices and both

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sets of environmental variables. The Euclidean distance among sites was used to create dissimilarity matrices for our valley and reach scale environmental variables (matrices: Valley and Reach). The Bray-Curtis index (Legendre & Legendre, 1998) was used to create dissimilarity matrices for both community composition approaches (matrices: Traits and Species). These dissimilarity matrices were then used to compute Mantel and partial Mantel correlations.

We tested for causal relationships between valley scale environmental variables, reach scale environmental variables, and fish species and trait composition using simple and partial Mantel correlations. The partial Mantel test extends the Mantel analysis to linear models with one dependent distance matrix and two or more independent matrices (Castellano & Balletto, 2002). This allowed us to quantify the degree of correlation between two distance matrices conditional on the third in the same respect as the partial Pearson correlation coefficient (Frenette-Dussault et al., 2013). We tested the plausibility of our hypothesized model using d-separation tests of path models (Shipley, 2000) based on the framework laid out by Frenette-Dussault, Shipley, and Hingrat (2013).

Lastly, canonical correspondence analysis (CCA) was used with both sets of environmental variables, separately and together, on both taxonomic and trait-based community structure matrices. This analyses was completed based on its ability to detect non-linear patterns between environmental variables and community abundance data (Ter Braak & Verdonschot, 1995). Significant variables were identified in CCA using forward selection with 5000 Monte Carlo permutations and alpha of 0.05. Only significant variables were included in the ordinations, and variables with variance inflation factors greater than 20 were excluded from ordinations (Hoeinghaus et al., 2007). All analyses were run in the statistical package 'vegan' using mantel, mantel.partial, and cca functions (Oksanen et al., 2016). This analysis was completed on the full

data set (including all sites - 18), and specifically on upland sites (12 – excluding lowland sites on Carson River) to study valley scale effects on communities in similar environmental settings.

Results

All Sites

Simple and partial Mantel tests indicated direct effects of both valley and reach scale environmental variables on both species and trait-based community approaches. Valley scale variables were more highly correlated with both community approaches than reach scale variables, and the trait based community approach was a better community descriptor across both environmental scales than the taxonomic approach due to higher correlations in simple and partial Mantel tests. The hypothesized models for both taxonomic and trait-based approaches were rejected based on the lack of direct effect between valley and reach scale variables. We created the most plausible model (Fig. 2) with separate direct effects from both valley and reach scale environmental variables on both descriptions of fish community composition based on the results presented in Table 3.

The CCA analyses comparing taxonomic and trait-based approaches resulted in similar patterns to the previous analysis. Valley scale variables accounted for more variation within the species and trait-based community ordinations than that of the reach scale variables. Elevation and down valley slope are significant valley scale variables in both fish community ordinations. Within the reach scale ordinations, more variation was explained in the species community composition approach than that of the trait-based approach. Significant reach scale variables within each ordination were more inconsistent with velocity, % fine sediment, and average depth being significant for the species ordination and only % riffle being significant within the traits ordination.

Combining valley and reach scale variables to look at overall environmental patterns within community structure explained the most variation within both the species and trait-based community ordinations. All variables significant in the trait ordination, including all environmental variables, were also significant in the species ordination (down valley slope, elevation, % fine sediment, and mean annual precipitation). For both community description approaches all valley scale variables that were significant in the separate ordinations were also significant when all environmental variables were included. Results from all ordinations are presented in Table 4.

Upland Sites

The results from the upland only analysis tell a slightly different story. Our series of Mantel and partial Mantel tests show a direct effect of valley scale variables on both community approaches, while a direct reach scale effect is absent. The trait-based approach continues to be more highly correlated with valley scale variables than that of the species approach, and the absence of correlation between the two scales of environmental data is still evident. The most plausible model based on the results presented in Table 2 is shown in Fig. 2.

CCA analysis for the upland sites showed the same trends as the analysis above. When analyzing the environmental scales separately, we observed no significant reach scale variables in either community ordination approach. Valley scale variables did significantly better in accounting for variation within species and trait-based community ordinations (Table 2). Valley width and left valley slope were both significant within all four ordinations completed that included valley scale variables on the upland sites.

CCA ordinations that combined both spatial scales explained more variation within both community composition approaches with < 2% increase in variance explained in the species

approach and slightly < 10% increase in variance explained in the trait-based approach (Table 2 or 3). Only one reach scale variable was deemed significant when both spatial scales were incorporated in the ordinations for both species and trait approaches, velocity and % pool respectively. Only ordinations involving both environmental scales are presented in Fig. 3 because they accounted for the most variation in all cases.

Discussion

Fundamental research in 'stream ecology' has previously focused on fine grain, main channel studies that evaluate local responses to habitat conditions and community interactions (Thorp, 2014). While this is important at the species and population levels, incorporating a macroecological approach allows for a connection between basic and applied research areas that can elucidate ecosystem service responses in the face of large-scale environmental changes such as climate change, large impoundments, and river channel mitigations of whole river segments (McCluney et al., 2014; Thorp, Flotemersch, Williams, & Gabanski, 2013). Our results illustrate the importance of a multiscale macroecological approach to riverine research by demonstrating the significant correlation between valley-scale hydrogeomorphic variables and fish community composition.

A goal of our study was to elucidate potential causal pathways between valley scale environmental variables and fish communities to better understand macroscale ecological processes. We initially hypothesized a direct effect of valley scale variables on reach scale variables. We also expected that valley and reach scale variables would have direct effects on fish community composition. However, we found no detectable effect of valley scale variables on reach scale variables. While this result initially seemed surprising, it could reflect the cumulative effects

of the many anthropogenic changes to these river channels which have occurred over the last 150 years, including impoundments and water diversions. Such changes could significantly alter the flow and substrate of the river channel (Brandt, 2000) while valley characteristics remain relatively stable. Although this physical link between valley and reach scales was not apparent, significant evidence from an analysis of all sites suggests that valley and reach scale environmental variables separately influence fish community composition with valley scale variables being more highly correlated with both community description approaches than reach scale variables.

Data from upland sites reveal a more unique pattern. When our analysis was limited to upland sites, however, the reach scale effect on fish community composition disappeared. It is important to consider that our intentional macroscale sampling design, as required for such large scale studies (Thorp et al., 2013), may have obscured finer scale patterns at the reach level. Remote pre-analysis of the area using the RESonate tool allowed us to choose sites with contrasting valley scale features to efficiently analyze differences in community composition at this scale.

Although our study was optimized for larger, valley scale analysis, it was important to incorporate local/reach scale variables in our analysis because of their known significance in structuring fish communities and populations (Gorman & Karr, 1978; Rahel & Hubert, 1991; Terra, Hughes, & Araùjo, 2016). Incorporating both reach and valley scale variables explained the greatest percentage of variation within our ordinations in both taxonomic and trait-based data sets than either scale separately. This is best illustrated within the species-based ordinations containing all sites where both sets of environmental variables explained ~20% more variation than valley scale variables alone, further illustrating the importance of multiscale approaches to understanding community composition (Poff, Pyne, Bledsoe, Cuhaciyan, & Carlisle, 2010; Ricklefs, 2004).

Analyzing associations between taxonomic and trait-based descriptions of fish community composition was an important aspect of our analysis. It is still somewhat unclear which approach best summarizes variation across scales because both taxonomic and trait-based community composition approaches have been successfully employed in accordance with regional/large scale variables (Hoeinghaus et al., 2007; Olden & Kennard, 2010) and local/reach scale variables (Lamouroux, Poff, & Angermeier, 2002; Pont, Hugueny, & Oberdorff, 2005). In the Great Basin, fish diversity is relatively low, only 18 species were collected in our study, over half of which were introduced species. This creates many holes in species abundance data between sites, especially when some sites had 3 or fewer species. This increases variation in the dataset and makes it harder to establish correlations between environmental factors and fish species composition. This scenario was better suited, however, for a trait-based approach as it can be applied across broad spatial scales and transcends taxonomy (Lima, Wrona, & Soares, 2016). We optimized our trait analysis by combining proven approaches to trait-based community description (Pyron, Williams, Beugly, & Jacquemin, 2011), as described in our methods.

Our study demonstrates the ability of trait-based community descriptions to reveal community-environment connections across large spatial scales, especially when diversity is low. Because species composition within habitats may change over large spatial scales simply due to geographical restrictions, a greater reliance on trait-based community approaches is justified when comparing communities at the basin, ecoregion, or continental scales (Heino, Schmera, & Erős, 2013; Lamouroux et al., 2002; Winemiller, 1991). A trait-based approach to community composition allows us to test general riverine ecological theory of community organization across river networks and ecoregional boundaries.

Within this system we have established plausible connections between valley scale environmental variables and fish community composition. This has potentially important implications for riverine ecosystem research because it demonstrates that valley scale variables that do not change predictably along the stream gradient (e.g., valley width and down valley slope characteristics of hydrogeomorphic patches) can create a patch-like pattern throughout a river network (Thorp, Thoms, & Delong, 2008). Nonetheless, multiscale approaches are still vital for understanding the hierarchical nature of riverine macrosystems. A multiscale approach is especially important when evaluating changes in community composition in relation to changes in valley and reach scale variables because these variables change at different temporal scales and respond differently to anthropogenic stressors (Thorp, 2014), thereby affecting riverine communities in different ways.

From a management perspective, these results demonstrate that valley scale variables can be important when considering where and how much restoration and mitigation should take place within riverine networks. Ecosystem services differ due to alternative configurations of valley scale variables or different hydrogeomorphic patches (Thorp et al., 2010) and rehabilitating river sections in relation to their hydrogeomorphology is important when attempting to restore ecosystem service to their original state. Thus, understanding the relationships that variables at the valley scale have on those at the reach scale and on biological communities is vital when predicting changes due to anthropogenic stressors or rehabilitation efforts.

Within the Great Basin we have demonstrated that both valley and reach scale environmental variables are significantly correlated with fish community structure. This study has shown that it is possible to elucidate patterns in fish community composition based on sampling contrasting hydrogeomorphic patches in a limited number of sites. We believe that this multiscale

framework coupled with a trait-based community approach can be used within and across ecoregions to study the structure of riverine biological communities and lead to a better understanding of the hierarchal nature of riverine macrosystems.

References

Angermeier, P. L., & Winston, M. R. (1999). Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. *Ecological Applications*, *9*(1), 335–349.

Balon, E. K. (1975). Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Board of Canada*, *32*(6), 821–864.

Bonar, S. A., Hubert, W. A., & Willis, D. W. (2009). Standard methods for sampling North American freshwater fishes.

Brandt, S. A. (2000). Classification of geomorphological effects downstream of dams. *Catena*, *40*(4), 375–401. https://doi.org/10.1016/S0341-8162(00)00093-X

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087.

Castellano, S., & Balletto, E. (2002). Is the Partial Mantel Test Inadequate? *Evolution*, *56*(9), 1871–1873. https://doi.org/10.1111/j.0014-3820.2002.tb00203.x

Davies, N. M., Norris, R. H., & Thoms, M. C. (2000). Prediction and assessment of local stream habitat features using large-scale catchment characteristics. *Freshwater Biology*, *45*(3), 343–369.

Douglas K. Maurer, Angela P. Paul, David L. Berger, and C. J. M. (2009). Analysis of Streamflow Trends , Ground-Water and Surface-Water Interactions , and Water Quality in the Upper Carson River Basin , Nevada and California, (March).

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, *81*(2), 163–82. https://doi.org/10.1017/S1464793105006950

EPA, U. S. (2004). Wadeable Streams Assessment: Field Operations Manual. Washington, DC: United States Environmental Protection Agency.

Frenette-Dussault, C., Shipley, B., & Hingrat, Y. (2013). Linking plant and insect traits to understand multitrophic community structure in arid steppes. *Functional Ecology*, *27*(3), 786–792. https://doi.org/10.1111/1365-2435.12075

Frimpong, E. A., & Angermeier, P. L. (2010). Traitbased approaches in the analysis of stream fish communities. In *Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society, Symposium* (Vol. 73, pp. 109–136).

Frimpong, E. A., & Angermeier, P. L. (2013). Fishtraits database. Retrieved from http://www.fishtraits.info

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, *10*(2), 199–214.

Gorman, O. T., & Karr, J. R. (1978). Habitat Structure and Stream Fish Communities. *Ecology*, *59*(3), 507–515.

Heino, J., Schmera, D., & Erős, T. (2013). A macroecological perspective of trait patterns in stream communities. *Freshwater Biology*, *58*(8), 1539–1555. https://doi.org/10.1111/fwb.12164

Hoeinghaus, D. J., Winemiller, K. O., & Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, *34*(2), 324–338. https://doi.org/10.1111/j.1365-

2699.2006.01587.x

Keddy, P. A. (1992). Assembly and Response Rules: Two Goals for Predictive Community Ecology. *Journal of Vegetation Science*, *3*(2), 157–164. https://doi.org/10.2307/3235676

Lamouroux, N., Poff, N. L., & Angermeier, P. L. (2002). Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, *83*(7), 1792–1807.

Legendre, P., & Legendre, L. F. J. (1998). *Numerical ecology* (Vol. 2nd Englis). Elsevier.

Lima, A. C., Wrona, F. J., & Soares, A. M. V. M. (2016). Fish traits as an alternative tool for the assessment of impacted rivers. *Reviews in Fish Biology and Fisheries*, 1–12. https://doi.org/10.1007/s11160-016-9446-x

McCluney, K. E., Poff, N. L., Palmer, M. A., Thorp, J. H., Poole, G. C., Williams, B. S., … Baron, J. S. (2014). Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Frontiers in Ecology and the Environment*, *12*(1), 48–58.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185.

McManamay, R. A., & Frimpong, E. A. (2014). Hydrologic filtering of fish life history strategies across the United States: implications for stream flow alteration. *Ecological Applications*, *25*(1), 243–263. https://doi.org/10.1890/14-0247.1

Mims, M. C., & Olden, J. D. (2013). Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology*, *58*(1), 50–62. https://doi.org/10.1111/fwb.12037

Mims, M. C., Olden, J. D., Shattuck, Z. R., & Poff, N. L. (2010). Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish*, *19*(3), 390–400.

Oksanen, A. J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., … Wagner, H. (2016). Vegan: Community Ecology Package. Retrieved from https://cran.r-project.org/package=vegan

Olden, J. D., & Kennard, M. J. (2010). Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. *American Fisheries Society Symposium*, *73*, 83–107. Retrieved from http://depts.washington.edu/oldenlab/wordpress/wp-content/uploads/2013/03/AFS_Chapter_2010.pdf

Olden, J. D., Poff, N. L., & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs*, *76*(1), 25–40.

Patton, T. M., Hubert, W. A., Rahel, F. J., & Gerow, K. G. (2000). Effort Needed to Estimate Species Richness in Small Streams on the Great Plains in Wyoming. *North American Journal of Fisheries Management*, *20*(2), 394–398. https://doi.org/10.1577/1548-8675(2000)020<0394:ENTESR>2.3.CO;2

Pease, A. A., Taylor, J. M., Winemiller, K. O., & King, R. S. (2015). Ecoregional, catchment, and reach-scale environmental factors shape functional-trait structure of stream fish assemblages. *Hydrobiologia*, *753*(1), 265–283. https://doi.org/10.1007/s10750-015-2235-z

Perkin, J. S., Knorp, N. E., Boersig, T. C., Gebhard, A. E., Hix, L. A., & Johnson, T. C. (2016). Life history theory predicts long-term fish assemblage response to stream impoundment. *Canadian Journal of Fisheries and Aquatic Sciences*, *239*(July 2016), 1–12. https://doi.org/10.1139/cjfas-2015-0593

Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, *16*(2),

391–409. https://doi.org/10.2307/1468026

Poff, N. L., & Allan, J. D. (1995). Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, *76*(2), 606–627.

Poff, N. L., Pyne, M. I., Bledsoe, B. P., Cuhaciyan, C. C., & Carlisle, D. M. (2010). Developing linkages between species traits and multiscaled environmental variation to explore vulnerability of stream benthic communities to climate change. *Journal of the North American Benthological Society*, *29*(4), 1441–1458.

Pont, D., Hugueny, B., & Oberdorff, T. (2005). Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints? *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(1), 163–173.

Pool, T. K., Olden, J. D., Whittier, J. B., & Paukert, C. P. (2010). Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(11), 1791–1807. https://doi.org/10.1139/F10-095

Pyron, M., Williams, L., Beugly, J., & Jacquemin, S. J. (2011). The role of trait-based approaches in understanding stream fish assemblages. *Freshwater Biology*, *56*(8), 1579–1592.

R Development Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Rahel, F. J., & Hubert, W. A. (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*(3), 319–332. https://doi.org/10.1577/1548-8659(1991)120<0319:faahgi>2.3.co;2

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, *7*(1), 1–15. https://doi.org/10.1046/j.1461-0248.2003.00554.x

Shipley, B. (2000). A New Inferential Test for Path Models Based on Directed Acyclic Graphs. *Structural Equation Modeling*, *7*(2), 206–218. https://doi.org/10.1207/S15328007SEM0702

Taylor, C. M., Winston, M. R., & Matthews, W. J. (1993). Fish Species-Environment and Abundance Relationships in a Great-Plains River System. *Ecography*, *16*(1), 16–23. https://doi.org/10.1111/j.1600-0587.1993.tb00054.x

Ter Braak, C. J. F., & Verdonschot, P. F. M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, *57*(3), 255–289.

Terra, B. de F., Hughes, R. M., & Araùjo, F. G. (2016). Fish assemblages in Atlantic Forest streams: the relative influence of local and catchment environments on taxonomic and functional species. *Ecology of Freshwater Fish*, *25*(4), 527–544. https://doi.org/10.1111/eff.12231

Thorp, J. H. (2014). Metamorphosis in river ecology: from reaches to macrosystems. *Freshwater Biology*, *59*(1), 200–210.

Thorp, J. H., Flotemersch, J. E., Delong, M. D., Casper, A. F., Thoms, M. C., Ballantyne, F., … Haase, C. S. (2010). Linking Ecosystem Services, Rehabilitation, and River Hydrogeomorphology. *BioScience*, *60*(1), 67–74. https://doi.org/10.1525/bio.2010.60.1.11

Thorp, J. H., Flotemersch, J. E., Williams, B. S., & Gabanski, L. A. (2013). Critical Role for hierarchical geospatial analyses in the design of fluvial research, assessment, and management. *Environmental Monitoring and Assessment*, *185*(9), 7165–7180. https://doi.org/10.1007/s10661-013-3091-9

Thorp, J. H., Thoms, M. C., & Delong, M. D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications*,

22(2), 123–147.

Thorp, J. H., Thoms, M. C., & Delong, M. D. (2008). *The Riverine Ecosystem Synthesis: Toward Conceptual Cohesiveness in River Science*. (J. H. Thorp, Ed.) (First). Elsevier.

Villéger, S., Ramos Miranda, J., Flores Hernández, D., & Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, *20*(6), 1512–1522. https://doi.org/10.1890/09-1310.1

Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, *13*(3), 267–283.

Webb, P. W., & Weihs, D. (1986). Functional locomotor morphology of early life history stages of fishes. *Transactions of the American Fisheries Society*, *115*(1), 115–127.

Williams, B. S., D'Amico, E., Kastens, J. H., Thorp, J. H., Flotemersch, J. E., & Thoms, M. C. (2013). Automated riverine landscape characterization: GIS-based tools for watershed-scale research, assessment, and management. *Environmental Monitoring and Assessment*, *185*(9), 7485–7499.

Winemiller, K. O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 343–365.

Winemiller, K. O., & Rose, K. A. (1992). Patterns of Life-History Diversification in North American Fishes: implications for Population Regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(10), 2196–2218. https://doi.org/10.1139/f92-242

Figures and Tables
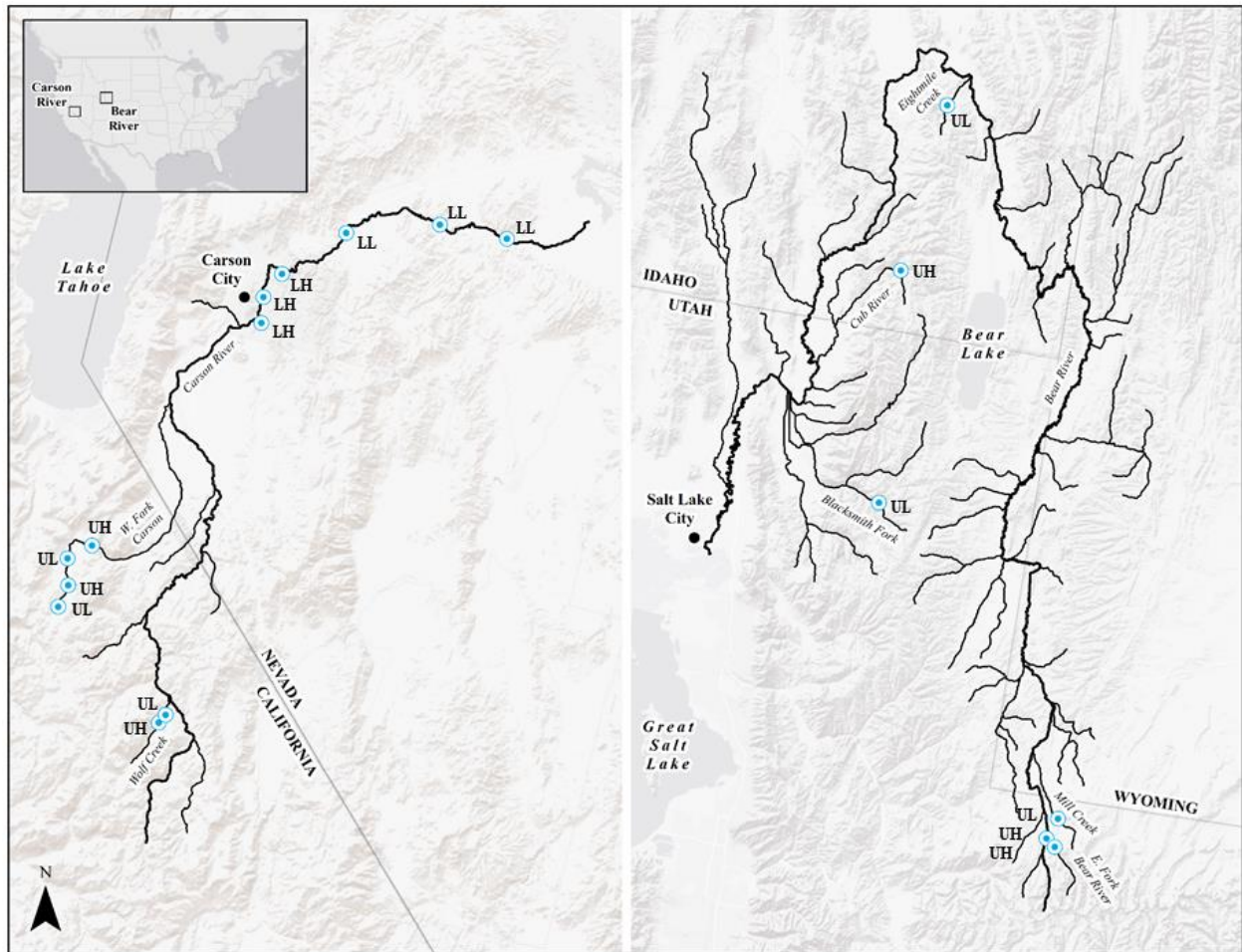
Fig. 1. Map of the Carson and Bear Rivers with dots representing sample sites (UL = upland low energy; UH = upland high energy; LL = lowland low energy; LH = lowland high energy).
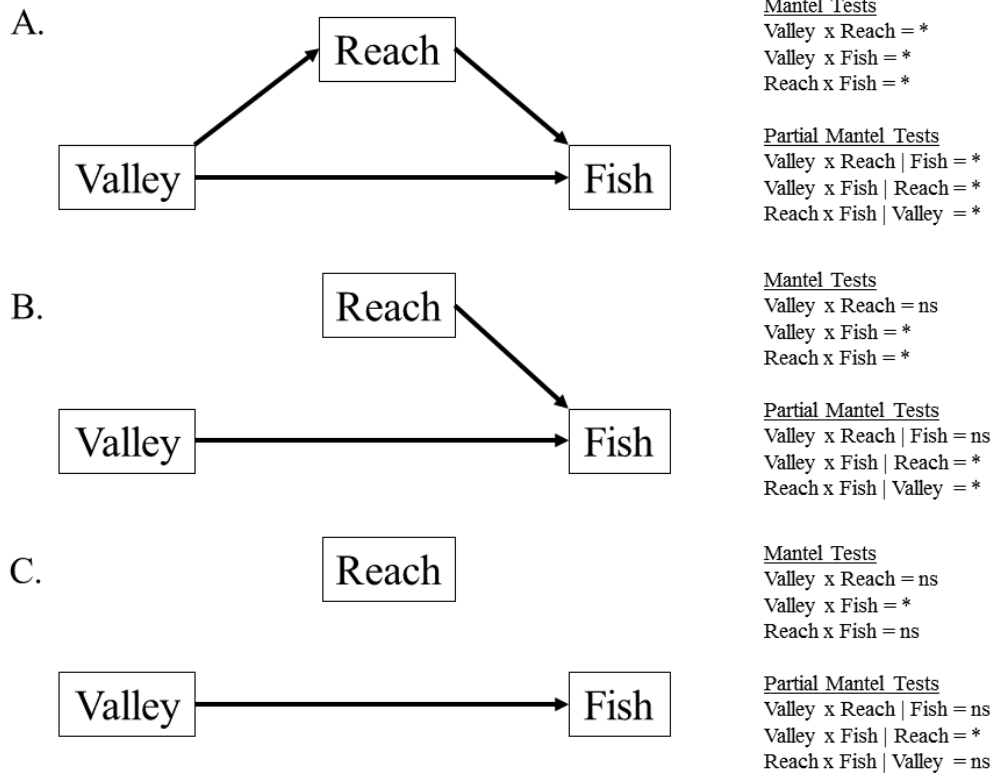
Fig. 2. The hypothesized model (A) and most plausible models for all sites (B) and upland sites (C) based on our analyses are shown here. Plausible causal relationships are illustrated by arrows. Valley scale environmental variables (Valley), reach scale environmental variables (Reach), fish community composition (Fish). Significant test results needed to assume plausibility of these models are shown (* = significant test). Note: same test results for Traits and Species.

Fig. 3. Canonical correspondence analysis ordinations of all sites for species (A) and traits (B) and upland sites for species (C) and traits (D).

Table 1. All environmental variables and abbreviations used in ordinations.

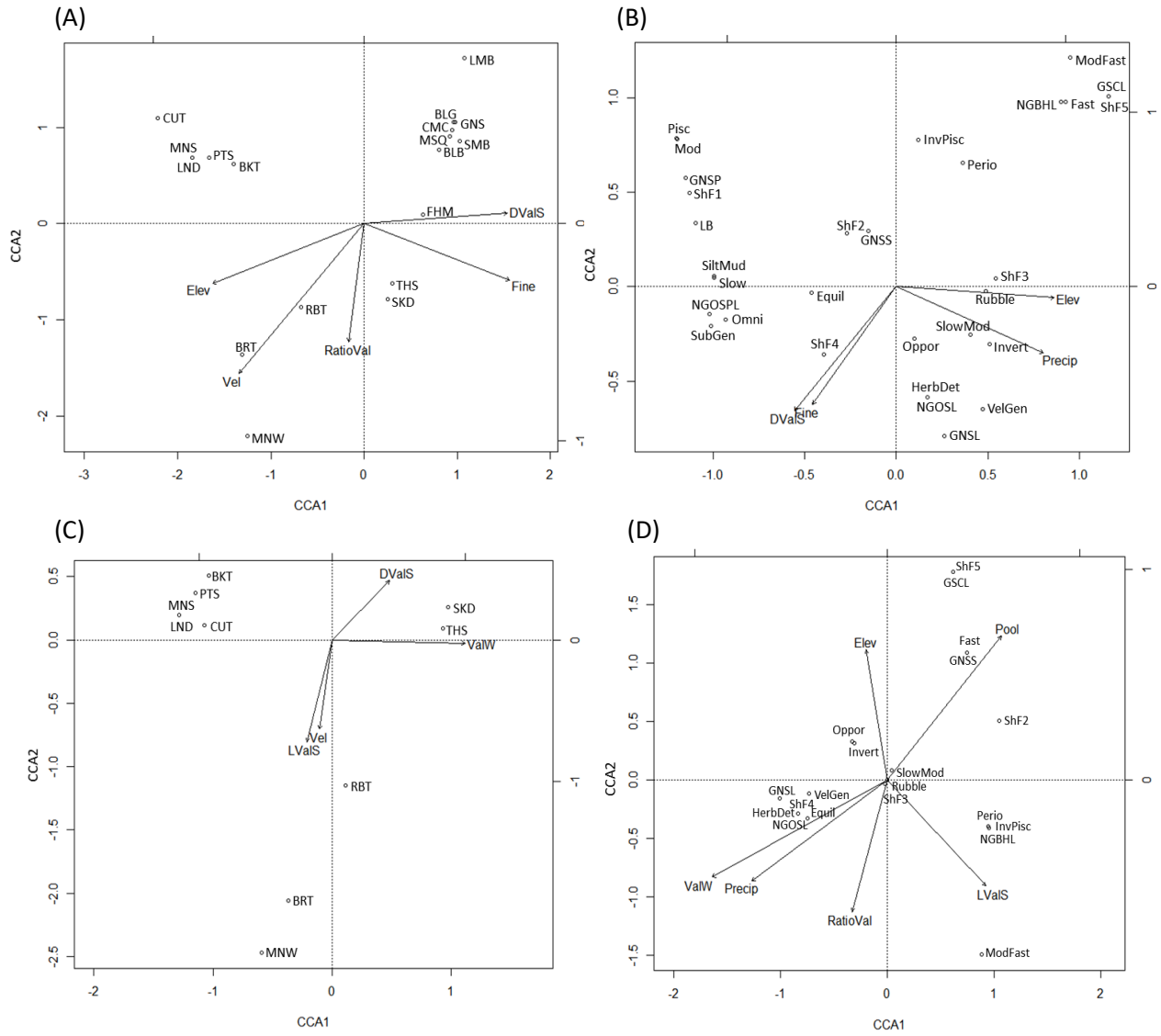| Valley Scale Variables (n = 9)		Reach Scale Variables (n = 11)	
Mean Annual Precipitation (mm)	Precip	Wetted Width (m)	WetW
Elevation (m)	Elev	Bank Full Width (m)	BFW
Valley Width (m)	ValW	Depth (m)	Depth
Valley Floor Width (m)	ValFW	Velocity (m s^-1)	Vel
Left Valley Slope	LValS	Pool (%)	Pool
Right Valley Slope	RValS	Run (%)	Run
Down Valley Slope	DValS	Riffle (%)	Riff
Sinuosity of the River Channel	Sinu	Boulder (%)	Bould
Ratio Valley Width to Valley Floor Width	RatioVal	Cobble (%)	Cobb
		Coarse Substrate (%)	Coar
		Fine Substrate (%)	Fine

Table 2. Trait groups and categories used in the analysis. See supplementary materials for in-depth explanations.

Trait Group	Trait Category	
Reproductive	Guarder - Nest Spawners - Lithophils	GNSL
	Guarder - Nest Spawners - Polyphils	GNSP
	Guarder - Nest Spawners - Speleophils	GNSS
	Guarder - Substratum Choosers - Lithophils	GSCL
	Live Bearer	LB
	Nonguarder - Brood Hiders - Lithophils	NGBHL
	Nonguarder - Open Substratum - Lithophils	NGOSL
	NonGuarder - Open Substratum - Phyto-Lithophils	NGOSPL
Trophic	Herbivore - Detritivore	HerbDet
	Omnivore	Omni
	Invertivore	Invert
	Invertivore - Piscivore	InvPisc
	Piscivore	Pisc
Life-history	Equilibrium	Equil
	Periodic	Perio
	Opportunistic	Oppor
Substrate Preference	Rubble	Rubble
	Silt - Mud	SiltMud
	Generalist	SubGen
Current Velocity Preference	Slow	Slow
	Slow - Moderate	SlowMod
	Moderate	Mod
	Moderate - Fast	ModFast
	Fast	Fast
	Generalist	VelGen
Shape Factor	2.0 - 3.0	ShF1
	3.0 - 4.0	ShF2
	4.0 - 5.0	ShF3
	5.0 - 6.0	ShF4
	6.0 - 7.0	ShF5

Table 3. Pearson correlation coefficients shown for each test performed. Format A x B indicates a Mantel test, A x B | C indicates a partial Mantel test (*ns*: nonsignificant; **P < 0.05; **P < 0.01, ***P < 0.001*).

Sites	Matrices	Correlation Coefficient	Significance
All	Valley x Reach	-0.021	*ns*
	Species x Valley	0.192	*
	Species x Reach	0.159	*
	Species x Valley | Reach	0.198	**
	Species x Reach | Valley	0.166	*
	Valley x Reach | Species	-0.053	*ns*
	Trait x Valley	0.270	*
	Trait x Reach	0.247	**
	Trait x Valley | Reach	0.284	*
	Trait x Reach | Valley	0.262	*
	Valley x Reach | Trait	-0.094	*ns*
Upland	Valley x Reach	-0.084	*ns*
	Species x Valley	0.405	***
	Species x Reach	-0.248	*ns*
	Species x Valley | Reach	0.398	**
	Species x Reach | Valley	-0.235	*ns*
	Valley x Reach | Species	0.019	*ns*
	Trait x Valley	0.553	*
	Trait x Reach	-0.157	*ns*
	Trait x Valley | Reach	0.549	*
	Trait x Reach | Valley	-0.133	*ns*
	Valley x Reach | Trait	0.004	*ns*

Table 4. Identifies the matrices involved in the CCA ordination. The variables listed are the environmental variables that were significant within each ordination (listed in order based on the forward selection method). The percent variance explained by each CCA model is also given.

Sites	Community Matrix	Environmental Matrix	Significant Variables	% Variance Explained
All	Species	Valley & Reach	Vel, DValS, RatioVal, Elev, Fine	0.5721
	Species	Valley	DValS, RatioVal, Elev	0.3748
	Species	Reach	Vel, Fine, Depth	0.2749
	Traits	Valley & Reach	Elev, DValS, Precip, Fine	0.587
	Traits	Valley	Elev, DValS, Precip	0.4885
	Traits	Reach	Riffle	0.2331
Upland	Species	Valley & Reach	ValW, LValS, Vel, DValS	0.763
	Species	Valley	ValW, LValS, RaioVal, DValS	0.7471
	Species	Reach	None	n/a
	Traits	Valley & Reach	ValW, LValS, Precip, Elev, Pool, RatioVal	0.96872
	Traits	Valley	ValW, LValS, Precip, Elev	0.87012
	Traits	Reach	None	n/a

Appendix 1.

Explanations of trait groups and categories. Codes used in ordinations and species assignment table below are also provided.

Reproductive Guilds	Codes	Explanations
Guarder - Nest Spawners - Lithophils	GNSL	Eggs are deposited on cleaned areas of rocks or in pits dug in gravel. Nest is guarded.
Guarder - Nest Spawners - Polyphils	GNSP	Not particular in the selection of nest material and substrate. Some attach eggs to any cleaned surface and guard clutchl; others build nests of seaweeds or stones.
Guarder - Nest Spawners - Speleophils	GNSS	Guard and spawn in natural holes and cavitites or in specially constructed burrows. Others deposit eggs on cleaded area of the undersurface of flat stones - male guards eggs.
Guarder - Substratum Choosers - Lithophils	GSCL	Choose rocks for attachment of their eggs. Eggs are guarded, and possibly cleaned and ventilated.
Live Bearer	LB	Gives live birth to young.
Nonguarder - Brood Hiders - Lithophils	NGBHL	Eggs are hidden in specially constructed places. In most cases the hiding places (called redds in salmonids) are excavated in gravel by the female. No parental care of eggs
Nonguarder - Open Substratum - Lithophils	NGOSL	Deposit eggs on rocks, rubble, or gravel. No parental care of eggs.
NonGuarder - Open Substratum - Phyto-Lithophils	NGOSPL	Deposit eggs in relatively clearwater habitats on submerged plants if available or on other submerged items.
Trophic Guild		
Herbivore - Detritivore	HerbDet	Approximately > 25% plant matter
Omnivore	Omni	Approximately < 5% plant matter
Invertivore	Invert	Diet consisting largely of invertebrates
Invertivore - Piscivore	InvPisc	Diet consisting of both invertebrates and fish
Piscivore	Pisc	Diet consisting largely of fish
Substrate Preference		
Rubble	Rubble	Including cobble and gravel
Silt - mud	SiltMud	Silt or muddy substrate
Generalist	SubGen	Does not have a preference
Current Velocity Preference		
Slow	Slow	Slow current
Slow - Moderate	SlowMod	Slow to moderate current
Moderate	Mod	Moderate current
Moderate - Fast	ModFast	Moderate to fast current
Fast	Fast	Fast current
Generalist	VelGen	Does not have a preference
Life-history Classification		
Equilibrium	Equil	Large eggs and parental care - produce relatively small clutches of larger or more advanced juveniles at the onset of independent life.
Periodic	Perio	Fishes that delay maturation in order to attain a size sufficient for production of a large clutch

			and adult survival during periods of suboptimal environemtna conditions.	
Opportunistic		Oppor	Early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover rates.	

Shape Factor				
2.0 - 3.0		ShF1	ratio of total body length to maximum body depth (fineness ratio)	
3.0 - 4.0		ShF2		
4.0 - 5.0		ShF3		
5.0 - 6.0		ShF4		
6.0 - 7.0		ShF5		

Trait category assignments for each species.

Scientific Name	Common Name	Code	Reproductive Guild	Trophic Guild	Substrate Pref.	Current Pref.	Life-history Class.	Shape Factor
Ameiurus melas	black bullhead	BLB	GNSL	InvPisc	SiltMud	Slow	Equil	ShF3
Catostomus platyrhynchus	mountain sucker	MNS	NGOSL	HerbDet	Rubble	SlowMod	Equil	ShF4
Catostomus tahoensis	Tahoe sucker	THS	NGOSL	HerbDet	Rubble	SlowMod	Equil	ShF4
Cottus beldingii	paiute Sculpin	PTS	GNSS	Invert	Rubble	Fast	Oppor	ShF3
Cyprinus carpio	common carp	CMC	NGOSPL	Omni	SiltMud	Slow	Perio	ShF2
Gambusia affinis	western mosquitofish	MSQ	LB	Invert	SiltMud	Slow	Oppor	ShF4
Lepomis cyanellus	green sunfish	GNS	GNSP	InvPisc	SiltMud	Slow	Equil	ShF1
Lepomis macrochirus	bluegill	BLG	GNSP	InvPisc	SubGen	Slow	Equil	ShF1
Micropterus dolomieu	smallmouth bass	SMB	GNSP	Pisc	Rubble	Mod	Equil	ShF2
Micropterus salmoides	largemouth bass	LMB	NGSP	Pisc	SiltMud	Slow	Equil	ShF2
Oncorhynchus clarkii	cutthroat trout	CUT	NGBHL	InvPisc	Rubble	VelGen	Perio	ShF3
Oncorhynchus mykiss	rainbow trout	RBT	NGBHL	InvPisc	Rubble	ModFast	Perio	ShF3
Pimephales promelas	fathead minnow	FHM	GNSS	Omni	SiltMud	Slow	Oppor	ShF4

Prosopium williamsoni	mountain whitefish	MNW	NGBHL	Invert	Rubble	VelGen	Equil	ShF3
Rhinichthys cataractae	longnose Dace	LND	GSCL	Invert	Rubble	VelGen	Oppor	ShF5
Rhinichthys osculus	speckled dace	SKD	GNSL	Invert	Rubble	VelGen	Oppor	ShF3
Salmo trutta	brown trout	BRT	NGBHL	InvPisc	Rubble	ModFast	Perio	ShF3
Salvelinus fontinalis	brook trout	BKT	NGBHL	InvPisc	Rubble	SlowMod	Perio	ShF2