

A MECHANISTIC FRAMEWORK FOR UNDERSTANDING PRAIRIE STREAM FISH
DISTRIBUTIONS

by

MATTHEW JOHN TROIA

B.S., University of Wisconsin – Eau Claire, 2008
M.S., University of Texas at Tyler, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2014

Abstract

A fundamental goal of ecology is to understand environmental associations of species. These associations can provide a basis for predicting spatial distributions in contemporary habitats as well as how those distributions might change in response to anthropogenic environmental change. Developing species distribution models is limited by an incomplete understanding of functional traits, spatial scaling, and the mechanisms and generalities of correlations among abundance and environmental gradients. I address these four issues using observational and experimental approaches. First, I tested opposing mechanisms of community assembly by measuring the dispersion (i.e., diversity) of three types of functional strategies at three spatial scales and along environmental gradients. I found that communities are assembled via abiotic environmental filtering, but the strength of this filtering depends on the spatial scale of investigation, longitudinal network position, and type of functional strategy. Second, I quantified community-environment relationships across thirteen sub-basins, nested within the three major basins within Kansas to evaluate the consistency (i.e., generality) in predictive capability of environmental variables among sub-basins and across spatial extents. I found that longitudinal network position is consistently the strongest predictor of community composition among sub-basins, but in-stream and catchment predictors become stronger correlates of community composition with increasing spatial extent. Third, I used environmental niche models to quantify distributions of four pairs of congeneric cyprinids and found that species within each pair exhibited contrasting stream-size preferences. I then used field experiments to test for differences in individual-level performance between one pair of species (*Pimephales notatus* and *P. vigilax*) along a gradient of stream size. I found that adult spawn success and juvenile growth and condition increased with stream size for both species, indicating that these congeners respond similarly to abiotic gradients associated with the river continuum. I concluded that complementary distributions are a consequence of biotic interactions, differential environmental filtering evident in an unmeasured performance metric, or differential environmental filtering by an environmental factor operating at longer timescales. These studies demonstrate the context dependencies of characterizing habitat associations of stream fishes, but also reveal the general

importance of stream size and associated environmental gradients in structuring stream fish communities.

MECHANISTIC UNDERPINNINGS OF PRAIRIE STREAM FISH DISTRIBUTIONS

by

MATTHEW JOHN TROIA

B.S., University of Wisconsin – Eau Claire, 2008

M.S., University of Texas at Tyler, 2010

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2014

Approved by:

Major Professor
Keith B. Gido

Copyright

MATTHEW J TROIA

2014

Abstract

A fundamental goal of ecology is to understand environmental associations of species. These associations can provide a basis for predicting spatial distributions in contemporary habitats as well as how those distributions might change in response to anthropogenic environmental change. Developing species distribution models is limited by an incomplete understanding of functional traits, spatial scaling, and the mechanisms and generalities of correlations among abundance and environmental gradients. I address these four issues using observational and experimental approaches. First, I tested opposing mechanisms of community assembly by measuring the dispersion (i.e., diversity) of three types of functional strategies at three spatial scales and along environmental gradients. I found that communities are assembled via abiotic environmental filtering, but the strength of this filtering depends on the spatial scale of investigation, longitudinal network position, and type of functional strategy. Second, I quantified community-environment relationships across thirteen sub-basins, nested within the three major basins within Kansas to evaluate the consistency (i.e., generality) in predictive capability of environmental variables among sub-basins and across spatial extents. I found that longitudinal network position is consistently the strongest predictor of community composition among sub-basins, but in-stream and catchment predictors become stronger correlates of community composition with increasing spatial extent. Third, I used environmental niche models to quantify distributions of four pairs of congeneric cyprinids and found that species within each pair exhibited contrasting stream-size preferences. I then used field experiments to test for differences in individual-level performance between one pair of species (*Pimephales notatus* and *P. vigilax*) along a gradient of stream size. I found that adult spawn success and juvenile growth and condition increased with stream size for both species, indicating that these congeners respond similarly to abiotic gradients associated with the river continuum. I concluded that complementary distributions are a consequence of biotic interactions, differential environmental filtering evident in an unmeasured performance metric, or differential environmental filtering by an environmental factor operating at longer timescales. These studies demonstrate the context dependencies of characterizing habitat associations of stream fishes, but also reveal the general

importance of stream size and associated environmental gradients in structuring stream fish communities.

Table of Contents

List of Figures	xi
List of Tables	xiv
Acknowledgements.....	xvi
Preface.....	xviii
Chapter 1 - Environmental associations of temperate stream fishes	1
Assembly of Freshwater Fish Communities.....	1
Spatial Scale and Fish-Environment Relationships	2
Mechanistic Underpinnings of Fish-Environment Relationships.....	3
References.....	4
Chapter 2 - Multi-trait functional strategies drive community assembly of stream fishes along environmental gradients and across spatial scales.....	7
Abstract.....	7
Introduction.....	7
Methods	12
Fish and Environmental Sampling.....	12
Functional Trait Data	12
Data Analysis	13
Results.....	15
Functional Strategies.....	15
Associations among Strategy Categories.....	17
Dispersion of Functional Strategies and Environmental Correlates	17
Discussion.....	18
Community Assembly in Stream Fishes.....	18
Individual Traits versus Multi-trait Strategies	19
Spatial Scale.....	20
Environmental Gradients	21
Conclusions.....	22
References.....	23

Chapter 3 - Predicting community-environment relationships of stream fishes across multiple drainage basins: Insights into model generality and the effect of spatial extent	40
Abstract	40
Introduction	41
Objectives and Hypotheses	43
Methods	44
Study Area and Datasets	44
Statistical Analysis	46
Environmental Variation among Sub-basins	46
Preparation of Environmental Predictor Variables for Community Models	46
Community Modeling	47
Results	48
Environmental Variation among Sub-basins	48
Derived Environmental Predictor Variables	48
Model Performance	49
Importance of Environmental Variables	49
Species-Environment Relationships	49
Discussion	50
Conclusions	52
References	53
Chapter 4 - Towards a mechanistic understanding of fish species niche divergence along a river continuum	72
Abstract	72
Introduction	73
Methods	76
Environmental Niche Models	76
Field Experiments	77
Experiment 1 – Spawning Success	78
Experiment 2 – Juvenile Survival, Growth, and Condition	79
Experimental Data Analysis	81
Results	82

Environmental Niche Models	82
Field Experiments	82
Experiment 1 –Spawning Success	82
Experiment 2 – Juvenile Survival, Growth, and Condition	83
Discussion.....	83
Complementary Distributions of Congeners	83
An Analytic Framework for Mechanistic Niche Modeling	86
References.....	87
Chapter 5 - Conclusions.....	107
References.....	108

List of Figures

- Figure 2.1 Conceptual diagram outlining three types of context dependency in community assembly. (A) Abiotic environmental filtering and competitive exclusion operate on different types of traits which may or may not be correlated among species. S1, S2, S3, etc. denote hypothetical species. (B) Increasing the spatial extent of the regional pool or local community can influence the amount environmental heterogeneity within and among local communities and shift the perceived mechanism of community assembly. Grey scaling represents a continuous environmental gradient. (C) Increasing severity and frequency of abiotic disturbance can maintain populations below carrying capacity, reduce resource limitation and decrease competitive..... 28
- Figure 2.2 Study area in the Big Blue River basin showing locations of 40 reaches (Upper Panel). The dashed lines represent EPA Level III ecoregion boundaries and circles represent five headwater reaches on the Flint Hills (black), nine headwater reaches off the Flint Hills (white), and twenty six mainstem sites (gray). Mesohabitats sampled from a reach on the Little Blue River (Lower Panel). Black lines represent stream margins, light gray areas are sandbars, dark gray areas are log complexes, and open rectangles represent sampled mesohabitats..... 30
- Figure 2.3 Multi-trait dendrograms for reproductive life history, feeding, and locomotion strategies. Shaded boxes indicate low (black) to high (white) values of individual traits representing each functional strategy type for each species. See Appendix A for trait abbreviations and numerical trait values area in the Big Blue River basin showing locations of 40 reaches (Upper Panel)..... 31
- Figure 2.4 Dispersion of reproductive life history (A–C), feeding (D–F), and locomotion (G–I) strategies at three spatial scales: mesohabitat within reach (A, D, G), mesohabitat within basin (B, E, H), reach within basin (C, F, I). Functional strategy dispersion was calculated as the standardized effect size (SES) of the mean nearest neighbor distance (MNND). Boxplots show the distribution of SES values and asterisks indicate statistically significant underdispersion (i.e., SES values significantly greater than zero) at $\alpha < 0.003$ based on Wilcoxon signed-rank tests. Squares show mean (\pm 95% confidence intervals) SES for

headwater reaches/mesohabitats on Flint Hills (black) and off Flint Hills (white) and different letters denote statistically significant differences based on Wilcoxon rank sum tests. Scatterplots show the relationship between stream network position (link magnitude) and SES values for headwater reaches/mesohabitats on Flint Hills (black) and off Flint Hills (white) and mainstem reaches/mesohabitats (gray). Best fit lines are shown for linear relationships with $R^2_{adj} > 0.10$. See Table 2.3 for summary of statistical tests.-trait dendrograms..... 33

Figure 2.5 As in Figure 2.4, except standardized effect size (SES) is calculated from mean pairwise distance (MPD)..... 35

Figure 3.1 Study area in Kansas located in the central United States showing the seventeen modeling units: State of Kansas, three basins, and thirteen sub-basins. See Table 3.1 for sub-basin codes. River mainstems are 4th order or larger streams. 58

Figure 3.2 Variation in (a) network position, (b) local characteristics, and (c) catchment characteristics among 13 sub-basins. Points represent mean link magnitude (a) or mean PC axis scores (b and c) for all sample sites within a sub-basin (± 1 standard error). Horizontal and vertical axes represent 1st and 2nd PC axes, respectively for b and c. See Table 3.1 for sub-basin codes and sub-basin sample sizes. 59

Figure 3.3 Model performance among thirteen sub-basins. Bars represent adjusted proportion of inertia constrained by all five environmental variables in a canonical correspondence analysis. All models were statistically significant based on randomization tests ($P < 0.01$).61

Figure 3.4 Predictive capability of five environmental predictor variables among thirteen sub-basins. Values indicate percent reduction in constrained inertia with that variable removed as an environmental constraint in a canonical correspondence analysis. 62

Figure 3.5 Predictive capability of environmental variables at three spatial extents: Entire state (white), three basins (light gray), and thirteen sub-basins (dark gray). Values represent percent reduction in constrained inertia with that variable removed as an environmental constraint in a canonical correspondence analysis. Error bars represent ± 1 standard error for basin ($n = 3$) and sub-basin ($n = 13$) extents. 63

Figure 4.1 (A) Study area in Kansas, USA, (B) locations of 221 KDWPT stream surveys sites in the Flint Hills EPA Level III ecoregion used for niche models, and (C) locations of small, medium, and large streams (Kings Creek, Wildcat Creek, and Kansas River, respectively) in

northern Flint Hills where field experiments were conducted. Dashed line indicates the drainage divide separating the Kansas River basin from the Arkansas River basin. 94

Figure 4.2 (A) Male *P. notatus* under a spawning tile. (B) *P. notatus* eggs on the underside of a spawning tile. (C) Experimental enclosures in the Kansas River, Riley County, Kansas. 96

Figure 4.3 Mean (\pm 95% confidence intervals) predictive capability of environmental variables included in niche models of eight species. Predictive capability was calculated as the reduction in deviance explained by a model without a predictor variable relative to a global model containing all predictor variables. 97

Figure 4.4 Smoothing functions (solid lines) and 95% confidence bands (dotted lines) generated from GAMs showing the relationship between stream size (link magnitude) and abundance of (A-D) tributary and (E-H) river mainstem species. Arrows in (D) and (H) indicate link magnitudes of Kings Creek, Wildcat Creek, and the Kansas River (from left to right) where field experiments were conducted for *P. notatus* and *P. vigilax*. Vertical gray dashes indicate the distribution of the 221 KDWPT sites along the stream-size gradient. 98

Figure 4.5 Individual performance for *P. notatus* (white bars) and *P. vigilax* (gray bars) from experimental enclosures in small, medium, and large streams. (A) Number of deposited ova per gram of wet somatic female mass per day for adults. (B) Probability of daily survival, (C) percent increase in total length per day, and (D) lipid content as percent of dry somatic mass for juveniles. Bars represent means for each treatment and circles represent values for each enclosure. Zero values are expressed as 0.1 in panel A to facilitate plotting on a \log_{10} scale. Overlapping circles are offset on the x-axis in panels A and B. 100

Figure 4.6 A three step analytic framework for the development of mechanistically-based environmental niche models using the congeners *P. notatus* and *P. vigilax* as a model study system. Red and blue lines represent *P. notatus* and *P. vigilax*, respectively. Solid lines represent known relationships from the current study and dashed lines represent additional relationships that should be quantified. 101

List of Tables

Table 2.1 Trait values for 38 fish species collected in the Big Blue River basin.	36
Table 2.2 Percent of local communities that were significantly underdispersed ($\alpha < 0.025$) or overdispersed ($\alpha > 0.975$) based on reproductive life history, feeding, and locomotion traits at three spatial scales: reach-mesohabitat (n = 440), basin-mesohabitat (n=440), and basin-reach (n = 40). Trait dispersion metrics were mean nearest neighbor distance (MNND) and mean pairwise distance (MPD).	38
Table 2.3 Summary of statistical tests presented in Figures 2.4 and 2.5. Statistically significant P-values at $\alpha < 0.003$ are bolded.	39
Table 3.1 Abiotic and biotic characteristics of 13 sub-basins, 3 basins, and the state of Kansas in which the fish community composition was modeled. Catchment area is only the area within the state of Kansas, does not include sub-basins removed from the analysis for the basin and state extents, and represents the spatial extent of each modeling unit.....	64
Table 3.2 Twenty nine environmental predictor variables representing three categories: local characteristics, network position, and catchment characteristics.....	65
Table 3.3 Summary of principal component analysis for the state of Kansas, three basins, and thirteen sub-basins. Variables with strongest loading are listed for PC axis 1 and PC axis 2 for local and catchment variable sets. Proportion of total variance explained by PC axis 1 and PC axis 2 are listed.	66
Table 3.4 Loadings of local variables on the first two principal component axes for 17 modeling units. See Tables 3.1 and 3.2 for modeling unit codes and local variable codes, respectively. Bolded values indicate highest positive and negative loadings.	67
Table 3.5 Loadings of catchment variables on the first two principal component axes for 17 modeling units. See Tables 3.1 and 3.2 for modeling unit codes and catchment variable codes, respectively. Bolded values indicate highest positive and negative loadings.....	68
Table 3.6 Number of sub-basins occupied and correlation of \log_{10} abundance with environmental predictor variables for all species. Values represent Pearson correlation coefficients averaged across occupied sub-basins. See Appendices A and B for environmental variable loadings on derived local and catchment variables.....	69

Table 4.1 Principal Components Analysis (correlation matrix) loadings of 23 environmental predictor variables on interpretable PC axes. Axis interpretability was determined from broken stick models. Percent of variance explained by each axis is shown in parentheses. Superscripts indicate variables loading most strongly (negatively or positively) on each PC axis, which were used as predictor variables in environmental niche models..... 102

Table 4.2 Environmental characteristics of the small, medium, and large streams (Kings Creek, Wildcat Creek, and the Kansas River, respectively) where field experiments were carried out. 103

Table 4.3 Experimental replication and body size of *P. notatus* and *P. vigilax* in enclosures from small, medium, and large streams (Kings Creek, Wildcat Creek, and the Kansas River, respectively) containing *P. notatus* or *P. vigilax*. 104

Table 4.4 Degrees of freedom for smoothing function and F- and P-values for six environmental variables used in niche models for eight study species. Bolded parameters indicate statistically significant ($\alpha < 0.05$) smoothing functions..... 105

Table 4.5 Two-way analysis of variance showing effect of stream size, species, and stream size * species interaction on four individual performance currencies measured during experiments. Bolded parameters are indicate statistically significant effects ($\alpha = 0.0125$ following Bonferroni adjustment). See Figure 4.5 for pair-wise comparisons between treatment levels. 106

Acknowledgements

I thank many funding sources for financial support of my dissertation research. The Kansas State University Division of Biology provided a teaching assistantship. Travel, equipment, supplies, and undergraduate technician salaries were provided by extramural research grants from the National Science Foundation, Southwestern Association of Naturalists, Kansas Academy of Science, and Prairie Biotic Research, Inc. I thank the Biology Graduate Student Association for providing a travel grant during my time at K-State. Eric Johnson and Mark Van Skoyok of the Kansas Department of Wildlife, Parks, and Tourism and Ram Raghaven provided extensive fish survey and environmental data that greatly enhanced my productivity.

I am indebted to my major advisor, Keith Gido, for his excellent guidance and constantly reminding me to salt the fish. I do, however, disapprove of his ability to hit a golf ball farther than I can. I thank those who served on my advisory committee—Walter Dodds, Tony Joern, Melinda Daniels, and Susan Sun—for their guidance and insightful and critical comments on my proposal and dissertation chapters. I thank my graduate peers for intellectual stimulation and friendship. I am particularly thankful for the fantastic group of lab mates—Nate Cathcart, Sky Hedden, Erika Martin, Josh Perkin, and James Whitney. I thank an excellent team of undergraduate technicians—Michael Denk, Jade Edmonds, Sky Hedden, Emily Johnson, Kevin Kirkbride, Dustin Shaw, Trevor Starks, Rebecca Zheng—for spending so many hours slogging through streams in search of *Pimephales*. Their enthusiasm and hard work were instrumental in the completion of my dissertation research.

I thank numerous private landowners in Marshall, Pottawatomie, Riley, and Washington counties who granted me access to study sites. I am particularly thankful for the support of Joe Gerken, Alison Gerken, James Coffman, and Sharon Coffman for extensive access to the Kansas River and Wildcat Creek for my field experiments. Daric Schneidewind provided helpful advice on rearing fish in the lab. Don Jackson, Jake Schaefer, and Adam Skibbe were excellent consultants for statistical analysis, experimental design, and IT support. I also thank Kristen Hase of the Tallgrass Prairie National Preserve and Nathan Henry of Kansas Department of Wildlife, Parks, and Tourism for providing access to streams for sampling and experimental work.

Lastly, I thank Allison Veach for her never-ending support at home and at work. I thank my mom, dad, and sister for support during my time at K-State as well as the positive and inspiring environment that they have always provided.

Preface

The contents of this dissertation represent research developed in collaboration with my major professor, Keith Gido. As such, chapters 2, 3, and 4 are presented in the first-person plural and/or third-person for the purpose of peer-reviewed publication with multiple authors. Chapter 2 is formatted for publication in the journal *Ecography* with Keith Gido as a coauthor. Chapter 3 is published with Keith Gido as a coauthor in the *Journal of Environmental Management* in volume 128 on pages 313-323. Chapter 4 has been accepted for publication in the journal *Ecosphere* with Keith Gido as a coauthor.

Chapter 1 - Environmental associations of temperate stream fishes

Freshwater fishes are the most taxonomically diverse group of vertebrates on the planet (Helfman et al. 2009). North America is home to over 700 species and represents the most diverse temperate freshwater fish fauna. However, roughly 39% of these North American species are currently imperiled due to habitat degradation, water pollution, modification of stream discharge regimes, introduction of non-native species, and overexploitation (Dudgeon et al. 2006, Jelks et al. 2008). Given the pervasive effect of anthropogenic environmental change on freshwater fish distributions, understanding the natural and anthropogenic environmental factors that constrain species' distributions is essential for conservation and management (Ebersole et al. 1997, Bond and Lake 2003). Improved prediction of species' distributions (stream fishes as well as all other taxa) is currently limited by an incomplete understanding of: (1) how functional traits influence species-environment relationships (McGill et al. 2006, Violle et al. 2007, Frimpong and Angermeier 2010), (2) how spatial scaling affects the detection of species-environment correlations (Levin 1992, Wiens 2002), (3) the generality of species-environment correlations among regions (Saupe et al. 2012, Wenger and Olden 2012), and (4) causative mechanisms that underlie correlations among species' abundances and environmental gradients (Kearney and Porter 2010, Saupe et al. 2012).

Assembly of Freshwater Fish Communities

Among freshwater fish ecologists, much debate has centered on whether communities exist as random (stochastic) or non-random (deterministic) subsets of regional species pools. For example, Grossman et al. (1982) asserted that stream fish communities are stochastic based on their observation of interannual variability in rank abundance of fishes in an Indiana stream. By contrast, Jackson et al. (1992) used null models to demonstrate that fish communities in Canadian lakes consisted of non-random subsets of regional species pools and concluded that these communities are assembled in a deterministic manner. Additional debate has focused on whether non-random community composition is determined predominantly by abiotic environmental filters or species interactions. Experiments conducted at small spatial scales and over short time periods often reveal the importance of predation and competition in constraining

community composition (e.g., He and Kitchell 1990), whereas broad-scale, long-duration observational studies point towards abiotic environmental filters as the dominant drivers of community composition (e.g., Rahel and Hubert 1991). Recent syntheses suggest that most investigators agree that stream fish communities are non-random and strongly influenced by abiotic environmental variability (Jackson et al. 2001, Grossman and Sabo 2010). Nevertheless, few studies have characterized the scale dependency of stream fish community assembly or the functional traits that are filtered during the process of assembly. In Chapter 2 of this dissertation, I use null models to test for random versus non-random patterns in functional trait dispersion (i.e., diversity) of stream fish communities across three spatial scales and along two abiotic environmental gradients. This chapter provides an explicit test of two long-debated questions in stream fish ecology and community ecology, in general. First, are communities assembled in a stochastic or deterministic manner? Second, if communities are deterministic, does abiotic environmental filtering or species interactions drive this non-random community assembly?

Spatial Scale and Fish-Environment Relationships

The spatial scale at which ecological studies are carried out can strongly influence the detection and interpretation of ecological processes and patterns (Levin 1992, Wiens 2002). Spatial scaling most generally refers to the size of the sampling unit (i.e., spatial resolution) and the area encompassed by all sampling units (i.e., spatial extent). Manipulating spatial resolutions and extents affects the partitioning of heterogeneity (environmental or taxonomic) within and among sampling units. Specifically, increasing spatial resolution should increase the within-sample heterogeneity and reduce heterogeneity among samples, whereas increasing spatial extent should increase heterogeneity among samples (Wiens 1989). These spatial scaling effects can strongly affect the mechanism identified in studies of community assembly. For example, Swenson et al. (2004) found that increasing spatial resolution lead to a shift from interspecific competition to abiotic environmental filtering driving the assembly of tropical tree communities. I address this aspect of scale dependency in Chapter 2 by quantifying functional trait composition between two spatial resolutions (mesohabitat versus reach) and two spatial extents (reach versus basin).

When studying stream fishes, spatial scaling can also refer to the spatial scale at which environmental factors are measured due to the hierarchical and branching organization of stream

networks (Frissell et al. 1986). For example, the composition of stream fish communities often depends on in-stream physicochemical conditions (i.e., local-scale environmental variables) which themselves are constrained by natural (e.g., surface geology) and anthropogenic (e.g., percent agriculture) characteristics of the watershed (i.e., catchment-scale environmental variables) (Allan 1997, Gido et al. 2006). In Chapter 3, I use multivariate statistical models to quantify the relationship between community composition of stream fishes and environmental predictor variables and address two distinct aspects of spatial scaling. First, I compare the consistency (i.e., generality) in predictive capability of environmental variables measured at the local scale and at the catchment scale among multiple regions. Second, I develop models at three spatial extents (sub-basin, basin, and the state of Kansas) to evaluate how increasing spatial extent affects model accuracy and the predictive capability of local scale and catchment scale variables.

Mechanistic Underpinnings of Fish-Environment Relationships

Environmental niche modeling has become a valuable tool for quantifying environmental niche dimensions of species (Guisan and Thuiller 2005), which can advance basic ecological and evolutionary research (e.g., Wiens et al. 2005) as well as applied conservation biology (e.g., Domínguez-Domínguez et al. 2006). Most niche models identify correlations among the abundance occupancy of a target species and environmental characteristics that may not be causally linked to individual- or population-level performance of that species. Consequently, these models are limited in their ability to accurately predict species' distributions when extrapolated to other geographic regions or novel environmental conditions (Jiménez-Valverde et al. 2009, Saupe et al. 2012). For most stream fishes, strong correlations exist between population density and longitudinal network position (i.e., stream size) (Rahel and Hubert 1991); however, many biotic and abiotic environmental gradients vary along this river continuum and little is known about which of these gradients are causally linked to population densities of stream fishes. In Chapter 2, I use a functional traits approach to test for abiotic environmental filtering of three types of functional traits (reproductive life history, body shape, and feeding morphology) that are hypothesized to respond to different environmental gradients that vary with stream size (flow regime, current velocity, and food resources, respectively). In Chapter 4, I use field mesocosms placed along a stream size gradient to quantify individual performance of two

congeneric minnows with contrasting stream size preferences to directly measure performance-environment relationships.

References

- Allan, J.D., Erickson, D.L., Fay, J. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37:149–161.
- Bond, N.R., Lake, P.S. 2003. Characterizing fish-habitat associations in streams as the first step in ecological restoration. *Austral Ecology* 28: 611–621.
- Domínguez-Domínguez, O., Martínez-Meyer, E. Zambrano, L., Pérez-Ponce de León, G. 2006. Using ecological niche modeling as a conservation tool for freshwater species: live-bearing fishes in Central Mexico. *Conservation Biology* 20:1730–1739.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Staissny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* 81:163–182.
- Ebersole, J.L., Liss W.J., Frissell C.A. 1997. Restoration of stream habitats in the western United States: Restoration as reexpression of habitat capacity. *Environmental Management* 21: 1–14.
- Frimpong, E. and Angermeier, P. 2010. Trait-based approaches in the analysis of stream fish communities. – In: Gido, K.B. and Jackson, D.A. (eds), *Community ecology of stream fishes: concepts, approaches, and techniques*. Am. Fish. Soc. Symp. 73: pp. 109–136.
- 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* 10:199–214.
- Gido, K.B., Falke, J.A., Oakes, R.M., Hase, K.J. 2006. Fish-habitat relations across spatial scales in prairie streams, in: Hughes, R.M., Wang, L.Z., Seelbach, P.W. (Eds.), *Landscape influences on stream habitats and biological assemblages*. American Fisheries Society Symposium 48, Bethesda, pp. 265–285.
- Grossman, G.D., Moyle, P.B., Whitaker, J.O. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage – a test of community theory. *American Naturalist* 120:423–454.

- Grossman, G.D. and Sabo, J.L. 2010. Structure and dynamics of stream fish assemblages in:Gido, K.B., Jackson, D.A. (Eds.), Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society Symposium 73, Bethesda, pp. 401–406.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than just simple habitat models. *Ecology Letters* 8:993–1009.
- He, X., and Kitchell, J.F. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. *Transactions of the American Fisheries Society* 119:825–835.
- Helfman, G., Collette, B.B., Facey, D.E., Bowen, B.W. 2009. The diversity of fishes: biology, evolution, and systematic. Second Edition. Wiley-Blackwell. 736 pp.
- Jackson, D.A., Somers, K.M., and Harvey, H.H. 1992. Null models and fish communities: evidence of nonrandom patterns. *American Naturalist* 139: 930–943.
- Jackson, D.A., Peres-Neto, P.R., and Olden. J.D. 2004. 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.
- Jelks, H. L., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D.A., Lyons, J., Mandrak, N.E., McCormick, F., Nelson, J.S., Platania, S.P., Porter, B.A., Renaud, C.B., Schmitter-Soto, J.J., Taylor, E.B., and Warren, M.L. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries* 33:372–407.
- Jiménez-Valverde, A., Nakazawa, Y., Lira-Noriega, A., Peterson, A.T. 2009. Environmental correlation structure and ecological niche model projections. *Biodiversity Informatics* 6:28–35.
- Kearney, M. and W.P. Porter. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Rahel, F.J. and 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* 22:341–351.

- Saupe, E.E., Barve, V., Myers, C.E., Soberon, J., Barve, N., Hensz, C.M., Peterson, A.T., Owens, H.L., Lira-Noriega, A. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. *Ecological Modelling* 237:11–22.
- Swenson, N.G., Enquist, B.J., Thompson, J., and Zimmerman, J.K. 2004. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Wenger, S. J., Olden, J.D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3, 260–267.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47:501–515.
- Wiens, J.J. and C.H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Reviews in Ecology and Systematics* 36:519–539.

Chapter 2 - Multi-trait functional strategies drive community assembly of stream fishes along environmental gradients and across spatial scales

Abstract

Trade-offs among functional traits result in multi-trait functional strategies that shape species' interactions with the abiotic and biotic environments and drive the assembly of local communities from regional species pools. The composition of stream fish communities is correlated environmental gradients associated with the river continuum and across hierarchically-organized habitat patches, but little is known about how strategy dispersion varies along these environmental gradients and across these spatial scales. We used null models to quantify the dispersion of reproductive life history, feeding, and locomotion strategies in local communities sampled at three spatial scales throughout a prairie stream network in Kansas, USA. We tested for differences in strategy dispersion along a gradient of stream size and between headwater streams draining disparate ecoregions. Null models indicated that strategies were generally underdispersed at the three spatial scales investigated. The dispersion of traits did not differ between ecoregions, but reproductive life history strategies became increasingly underdispersed when moving from downstream to upstream, suggesting that environmental filtering of reproductive life history strategies is stronger in headwater streams. This pattern was stronger at the reach resolution compared to the mesohabitat resolution, suggesting that hydrologic variability among reaches (and not among mesohabitats) acts on reproductive life history to drive community assembly. Our results affirm that the assembly of stream fish communities is driven by abiotic filtering, but the mechanisms of community assembly depend on the type of functional strategy, location along the river continuum, and the spatial scale of investigation.

Introduction

Biotic and abiotic environmental conditions influence local community structure by acting on functional traits (McGill et al. 2006, Violle et al. 2007) and the dispersion of these traits within a local community can provide insight into mechanisms of community assembly (Weiher and Keddy 1995). When the distribution of traits within a local community is more dispersed (i.e., variable) than that of communities assembled randomly from regional species

pools, competitive exclusion is invoked as the mechanism of community assembly. In contrast, a distribution of traits that is less dispersed than randomly assembled communities is taken as evidence for environmental filtering. Traits correspond to multiple aspects of a species' ecology, such as physicochemical tolerance, resource acquisition, predator avoidance, and dispersal. Whereas environmental filtering will correspond to traits associated with tolerating *environmental conditions*, traits associated with competitive interactions should correspond to the acquisition of *limiting resources*, such as food or spawning habitat (Figure 2.1A). Not surprisingly, some traits may be overdispersed while others are underdispersed in the same community as a consequence of different assembly mechanisms acting on different types of traits (Weiher et al. 1998). For example, in rockfish communities of the eastern Pacific Ocean, gill raker length, a measure of food resource use, is overdispersed due to competitive exclusion whereas eye size is associated with depth and is underdispersed due to environmental filtering along a vertical light gradient (Ingram and Shurin 2009).

Although the dispersion of single traits can provide insight into mechanisms of community assembly, traits may not interact individually with environmental factors; rather, suites of coevolved traits often convey ecological *strategies* that interact with environmental conditions during the process of community assembly (Frimpong and Angermeier 2010). Among freshwater fish species, tradeoffs in three reproductive life history traits (size at maturity, annual fecundity, and investment per progeny) form a trilateral continuum with three strategic endpoints: opportunistic (small size at maturity, low annual fecundity, and low investment per progeny), periodic (large size at maturity, high annual fecundity, and low investment per progeny), and equilibrium (moderate size at maturity and annual fecundity and high investment per progeny) (Winemiller and Rose 1992). Interannual and seasonal flow regimes act as environmental filters and constrain the reproductive life history strategies that persist in streams with different flow regimes (Olden and Kennard 2010, Mims and Olden 2012). Other examples of multi-trait strategies of freshwater fishes include feeding guilds (e.g., mouth and gut morphology; Goldstein and Simon 1999) and locomotion guilds (e.g., body shape and fin positioning; Lamouroux et al. 2002). Given the ubiquity of multi-trait strategies, evaluating the dispersion of strategies as opposed to single traits might be an informative approach to test mechanisms of community assembly.

Community assembly mechanisms also are scale dependent and the dispersion of traits or strategies associated with competitive exclusion and environmental filtering may differ across spatial resolutions and extents (Figure 2.1B, Levin 1992, Swenson et al. 2007, Weiher et al. 2011). Spatial resolution—that is, the geographic area defined as the local community—influences the amount of environmental heterogeneity *within* localities and can affect community assembly in two ways. First, different environmental gradients might filter traits at different spatial scales. For example, climatic variables operate as broader scale environmental filters than do geomorphic variables which are constrained by topographic variability within homogenous climatic regions (Tonn et al. 1990, Poff 1997). Second, processes driving trait dispersion also vary in the spatial scale at which they operate. For example, competition for resources occurs among individuals and therefore is restricted to the spatial scale of individual home ranges, which can vary greatly among species (Skalski and Gilliam 2000, Poos and Jackson 2012). On the other hand, spatial extent—that is, the geographic area defined as the regional species pool—influences the amount of environmental heterogeneity *among* localities. Environmental heterogeneity among localities should increase with spatial extent and lead to niche processes (environmental filtering or competitive exclusion) driving community assembly, whereas low environmental heterogeneity among localities apparent at narrow spatial extents should lead to neutral assembly processes (Leibold et al. 2004, Weiher et al. 2011).

Community assembly mechanisms might also vary along gradients of environmental disturbance (Figure 2.1C). In benign environments, population densities are higher leading to stronger competition for limiting resources. By contrast, in harsh environments, populations are below carrying capacity, resources limitation is reduced, and environmental filtering should be the dominant mechanism of community assembly. Given these scale and environmental dependencies, much remains to be studied to understand the role of competitive exclusion and environmental filtering among functional strategies, across spatial scales, and along disturbance gradients.

Conceptual frameworks and empirical studies suggest that the composition of stream fish communities is influenced primarily by environmental filtering, whereas interspecific competition plays a minimal role (Matthews 1998 and Jackson et al. 2001). Longitudinal position in the stream network is a strong environmental correlate of stream fish community composition (Horwitz 1978, Schlosser et al. 1987, Pease et al. 2012) and multiple abiotic

environmental gradients associated with such stream-size gradients probably filter various types of functional strategies. First, gradual changes in resource type and availability from headwaters to large rivers influence strategies associated with foraging behavior and trophic position (Vannote et al. 1980, Ibanez et al. 2009). Second, the frequency, magnitude, and timing of discharge-related disturbances vary with stream size and can filter reproductive life history strategies (Schlosser 1987, Olden and Kennard 2010, Mims and Olden 2012). Third, depth and current velocity increase with stream size resulting in the filtering of locomotion strategies associated with swimming endurance, maneuverability in complex habitats, and vertical positioning in the water column. Within stream reaches, depth and current velocity are inversely correlated—varying between pool and riffle mesohabitats—and also filter locomotion strategies at this finer spatial resolution (Lamouroux et al. 2002). Environmental gradients associated with ecoregional transitions also correlate with compositional changes in stream fishes. For example, Neff and Jackson (2013) showed that physicochemical factors and consequent taxonomic and functional composition of fish communities differed between streams draining the Canadian Shield versus those draining an adjacent glaciated region in Ontario, Canada. Although investigations of species–environment and trait–environment relationships have shed light on the abiotic factors that influence community structure, they are limited in their ability to quantify the relative roles of environmental filtering and competitive exclusion during community assembly. Null modeling approaches (e.g., Weiher et al. 1995, Webb 2000, Swenson 2006, Liu et al. 2013) allow for more explicit tests of the environmental filtering predicted by conceptual models (Schlosser 1987, Poff 1997), but have seen surprisingly limited use in empirical tests of community assembly mechanisms in stream fishes.

This study took place in the Big Blue River basin in north central Kansas, USA (Figure 2.2) where taxonomic composition of stream fish communities vary along gradients of stream size and between ecoregions (Minckley 1959, Gido et al. 2006). The southern portion of the Big Blue River basin flows through the Flint Hills EPA Level III ecoregion and is characterized by high-gradient, spring fed headwater streams. These streams have alternating pool-riffle sequences and drain catchments composed mostly of native tallgrass prairie. In contrast, headwater streams in the northern portion of the basin drain the Central Great Plains and Western Cornbelt Plains ecoregions. These streams have low gradients, are dominated by

homogenous run habitat with finer substrates, and drain catchments composed mostly of row crop agriculture.

Our first objective was to evaluate the dispersion of reproductive life history, feeding, and locomotion strategies in local stream fish communities at three spatial scales: mesohabitats within reaches, mesohabitats within the basin, and reaches within the basin. We predicted that reproductive life history and locomotion strategies would be underdispersed because these strategies convey tolerance to abiotic conditions. Because flow regimes characterize reaches rather than mesohabitats, we expected reproductive life history strategies to be underdispersed only at the reach resolution and basin extent. Current velocity varies among reaches within basins as well as among mesohabitats within reaches, so we expected locomotion strategies to be underdispersed at both spatial resolutions and extents. We predicted that feeding strategies could be over- or under-dispersed, depending on the spatial scale at which we defined the local community and regional pool. Because interspecific competition occurs at the individual level and most small-bodied stream fishes occupy small home ranges (Skalski and Gilliam 2000, Poos and Jackson 2012, Walker et al. 2013), we expected overdispersion of feeding strategies to be apparent only at the mesohabitat resolution and reach extent. In contrast, we expected feeding strategies to be underdispersed at the basin extent because changes in resource type associated with stream network position would act as environmental filters (Vannote et al. 1980, Ibanez et al. 2009). Our second objective was to test for variation in strategy dispersion along a gradient of stream size and between headwater streams draining different ecoregions. We predicted that headwater streams in the Western Cornbelt and Central Great Plains would be the most hydrologically variable and would promote the persistence of opportunistic species leading to underdispersion of reproductive life history strategies, whereas river mainstems and springfed tributaries of the Flint Hills would allow opportunistic, equilibrium, and periodic strategists to persist, leading to overdispersion of reproductive life history strategies (Figure 2.1C, Winemiller and Rose 1992, Poff and Allan 1995, Baker et al. 2003). We also predicted that feeding strategies would be underdispersed in headwater streams because the diversity of food resources is lower in relative to river mainstems (Vannote et al. 1980, Pease et al. 2012).

Methods

Fish and Environmental Sampling

Fish communities were sampled in 8 to 13 mesohabitats distributed among 40 reaches (440 mesohabitats in total) in July and August of 2012 (Figure 2.2). Reaches were 200 to 400 m in length and represented a variety of mesohabitat types (Lazorchak et al. 1998). Community and environmental sampling followed a modified version of the protocol used by Gorman and Karr (1978). Mesohabitats were selected such that the type of in-channel cover (undercut bank, log complex, bankgrass, or rootwad) if present as well as depth, velocity, and substrate, were homogenous within the mesohabitat. Mesohabitats averaged 13.1 m² in area and were selected to represent the diversity of mesohabitat types (all combinations of in-channel cover, depth, velocity, and substrate) present within a reach. This mesohabitat sampling scheme maximized the environmental heterogeneity among mesohabitats within a reach. Fish communities were sampled with a seine (5m = width, 1.5m = height, 5mm = mesh diameter). When in-channel cover was absent, seine hauls were made in the downstream direction. For samples containing in-channel cover, the seine was positioned around the perimeter of the in-channel cover which was then disturbed by the samplers to drive fish out of the cover and into the seine. Fish >200mm in total length were identified to species, measured for total length, and released. Fish <200mm were euthanized with MS-222, preserved in buffered 10% formalin, and returned to the laboratory where all specimens were identified, measured, and counted.

Functional Trait Data

Nine functional traits associated with reproduction, feeding and locomotion (sensu Frimpong and Angermeier 2010) were assembled for the 38 species collected during fish community sampling (Table 2.1). Three traits associated with each trait category (reproduction, feeding, and locomotion) were used to identify functional strategies within each of these groups. Reproductive life history traits were obtained from a database assembled from published literature and included size at maturity, annual fecundity, and investment per progeny. Investment per progeny was calculated as $(\ln[\text{egg diameter}] + \ln[\text{parental care}])$ following Olden et al. (2006). Feeding traits included the ratio of gut length to body length, mouth position, and gape width. Gut length (relative to body length) is an indicator of trophic position where species with longer guts feed at lower trophic levels (Pease et al. 2012). Mouth position was measured as

the angle formed between a line passing through the posterior-most vertebra and the eye and a line passing through the tips of the fully extended upper and lower jaws. High angles represent a terminal mouth position characteristic of a water column or surface foraging species whereas low angles represent subterminal mouth positions characteristic of benthic foraging species (Pease 2012). Gape width represents the size of prey that a species is capable of consuming.

Locomotion traits included pelvic fin position, shape factor, and swim factor. The angle between the midline and a line passing through the insertions of the pelvic and pectoral fins represent evolutionary changes in fin morphology with high angles typical of derived species (e.g., Perciformes) that use both pelvic and pectoral fins for maneuvering in structurally complex habitats, whereas low angles represent ancestral species (e.g., Cypriniformes) that use pectoral and pelvic fins for stability during sustained swimming (Moyle and Cech 2004). Shape factor is the ratio of total length to maximum body depth and high values indicate vertically compressed species capable sustained swimming in high current velocities, whereas low values indicate tall-bodied species capable of greater maneuverability in structurally complex habitats. Swim factor is the ratio of minimum caudal peduncle depth to maximum caudal fin depth, with small values indicative of strong swimmers (Webb 1984). We measured relevant morphological features (gape width, body depth, minimum caudal peduncle depth, etc.) on five individuals representing the range of body sizes present in our vouchered collections. Morphological measurements were regressed as a function of total length and the resulting regression equation was used to calculate the trait value corresponding to the mean length of each species across all mesohabitat samples.

Data Analysis

Three dissimilarity matrices were developed representing dissimilarity in the three categories of strategies (reproductive life history, feeding, locomotion). All trait values were z-score transformed prior to calculation of Euclidean distance to standardize the variance across all traits. Mantel tests were used to measure the concordance between the three trait categories to validate that each category represented a statistically independent index of ecological similarity (three Mantel tests). Mantel tests were also used to measure the concordance between phylogeny and each trait category to test for a phylogenetic signal in each trait category (three Mantel tests). Phylogenetic relatedness was inferred from taxonomic relationships between species following the method of Tedesco et al. (2008) because a complete phylogenetic hypothesis including the 38

species in the Big Blue River basin was not available. The phylogenetic dissimilarity matrix was created by assigning values of 1.0, 0.5, 0.33, or 0.25 to pairs of species in the same genus, family, order, or class, respectively.

Strategy dispersion of local communities was evaluated using an analytic approach adopted from phylogenetic dispersion analyses (Webb et al. 2002), except we replaced phylogenetic trees representing the evolutionary relationships among all species in the regional species pool with dendrograms representing dissimilarities in functional strategies among species in the regional species pool (Liu et al. 2013). Three dendrograms were developed from dissimilarity matrices from each strategy category using hierarchical clustering with the ward method. Strategy dispersion was quantified using two metrics: the mean nearest neighbor distance (MNND) and the mean pairwise distance (MPD). These metrics are widely used in studies quantifying phylogenetic and trait dispersion (Webb et al. 2002, Liu et al. 2013, Kembel et al. 2013). Mean nearest neighbor distance indicates terminal dispersion associated with the tips of the dendrogram, whereas mean pairwise distance indicates overall dispersion at the base of the dendrogram. Null models were used to test for non-random trait dispersion at each local community (40 reaches and 440 mesohabitats). Species were randomly shuffled on the dendrogram containing all species in the regional pool (i.e. all species encountered across the 40 reaches), a subset equal to the observed species richness was drawn randomly from the dendrogram, and MNND and MPD were calculated for the random subset. This process was repeated 999 times and a mean and standard deviation of MNND and MPD of the 999 random local communities were calculated. Observed dispersion metrics were compared to the null distribution of dispersion metrics and were considered significantly under- or overdispersed when observed metrics were less than the 2.5 percentile or greater than the 97.5 percentile, respectively. A standardized effect size (SES) was calculated using Equation 1 and used in subsequent analyses to (1) compare dispersion among the three types of strategies and spatial scales and (2) test for variation in functional strategy dispersion along the stream size gradient and between ecoregions.

$$SES = -1 \times \frac{obs - mean_{random}}{stdev_{random}}$$

Equation 1

Positive SES values indicate local communities in which strategies are underdispersed compared to randomly assembled communities and negative SES values indicate local

communities in which strategies are overdispersed compared to random communities. Three null models were developed for each trait category by redefining the spatial resolution (i.e., local community) and extent (i.e., regional species pool) of the metacommunity. These null models were: (1) mesohabitats as local communities and reach as the regional pool, (2) mesohabitats as local communities and basin as the regional pool, and (3) reaches as local communities and basin as the regional pool.

We tested for non-random trait dispersion for each trait category, spatial scale, and trait dispersion metric using Wilcoxon signed rank tests. Significant under- or overdispersion of functional strategies were inferred when the null hypothesis that SES is not different from zero was rejected (Ingram and Shurin 2009, Liu et al. 2013). We tested for differences in SES values from headwater reaches and mesohabitats draining the Flint Hills versus those draining the plains ecoregions using Wilcoxin rank sum tests. Headwater reaches in the western Cornbelt Plains and Central Great Plains were grouped because previous studies indicated that environmental conditions and community composition of fishes is similar between these ecoregions (Minckley 1959, Gido et al. 2006). We restricted this test of ecoregional differences to headwater streams (link magnitude ≤ 27) because the catchments of larger streams are not contained entirely within a single ecoregion (Figure 2.2). Lastly, we tested for a linear relationship between stream network position (\log_{10} -transformed link magnitude) and SES. Models were developed for SES values representing MNND and MPD for the three functional strategy types and three spatial scales (18 models in total). Statistical significance was evaluated at $\alpha < 0.003$ (adjusted for 18 equivalent tests).

All analyses were performed with the R statistical Language (R Development Core Team 2012) using the vegan (Oksanen et al. 2009), FD (Laliberte and Legendre 2010), picante (Kembel et al. 2013), ape (Paradis et al. 2004), and ade4 (Dray and Dufour 2007) packages.

Results

Functional Strategies

The dendrogram for reproductive life history strategies was composed of four major clusters of species (Figure 2.3A). The first cluster included mostly catfishes (Ictaluridae) and sunfishes (Centrarchidae) with moderate size at maturity, moderate fecundity and high investment per progeny, which is indicative of the equilibrium strategy described by Winemiller

and Rose (1992). The second cluster contained mostly sunfishes and minnows (Cyprinidae) with small to moderate size at maturity, low fecundity, and moderate to high investment per progeny, which is indicative of an intermediate strategy between equilibrium and opportunistic (Hoeinghaus et al. 2007). The third cluster also contained only minnows with small size at maturity, low fecundity, and low investment per progeny, which is indicative of the opportunistic strategy. The fourth cluster contained mostly suckers (Catostomidae) with large size at maturity, high to moderate fecundity and moderate to low investment per progeny, which are indicative of either periodic or an intermediate periodic-equilibrium strategists.

The dendrogram for feeding strategies was composed of six major clusters (strategies) of species (Figure 2.3B). The first cluster included moderately-sized omnivorous and insectivorous species from several families and exhibited low to moderate gut lengths, subterminal to ventral mouth positions and moderate gapes. The second cluster included large omnivorous suckers with moderate to high gut lengths, ventral mouth positions and moderate gapes. The third cluster included mostly algivorous minnows with high gut lengths, subterminal to terminal mouth positions, and narrow gapes. The fourth cluster included piscivorous catfishes and gar with short guts terminal mouth positions, and moderate to wide gapes. The fifth cluster included mostly piscivorous and insectivorous sunfishes and minnows with short gut lengths, terminal to dorsal mouth positions, and narrow to moderate gapes. The sixth cluster included minnows and darters (Percidae) with short gut lengths, subterminal to terminal mouth positions and narrow gapes.

The dendrogram for locomotion strategies was composed of six clusters of species (Figure 2.3C). The first cluster included mostly minnows with low pelvic fin angles characteristic of the stabilizing function of primitive teleosts, moderate to high shape factors, and low swim factors characteristic for sustained swimming in flowing water. The second cluster contained species from several families with slightly low to moderate pelvic fin angles, moderate shape factors, and moderate swim factors. The third cluster contained mostly large suckers with low pelvic fin angles, low shape factors and low swim factors. The fourth cluster contained mostly darters and gar (Lepisosteidae) with high and low pelvic fin angles, respectively, high shape factors and high swim factors. The fifth cluster contained species with moderate to low pelvic fin angles, moderate shape factors, and moderate swim factors. The sixth cluster contained mostly sunfishes with high pelvic fin angles characteristic of the maneuvering function of derived teleosts, low shape factors, and moderate swim factors.

Associations among Strategy Categories

Mantel tests indicated moderate and marginally significant correlations between pairs of dissimilarity matrices for the three trait categories. Of the three pairwise comparisons, Reproductive life history and feeding strategies were most strongly correlated (Mantel $r = 0.30$, $P = 0.04$), followed by reproductive life history and locomotion strategies (Mantel $r = 0.21$, $P = 0.07$), and feeding and locomotion strategies (Mantel $r = 0.13$, $P = 0.14$). Locomotion strategies were most strongly correlated with phylogeny (Mantel $r = 0.50$, $P = 0.001$), followed by reproductive life history strategies (Mantel $r = 0.20$, $P = 0.002$) and feeding strategies (Mantel $r = 0.20$, $P = 0.002$).

Dispersion of Functional Strategies and Environmental Correlates

Functional strategies were significantly underdispersed in 0.9 to 45.0% of the local communities, depending on the trait category, spatial scale, and dispersion metric (Table 2.2). No local communities exhibited statistically significant overdispersion of functional strategies. Locomotion strategies were underdispersed most frequently (mean = 12.5% of communities across spatial scales and dispersion metrics) followed by reproductive life history strategies (8.3%) and feeding strategies (1.3%). Functional strategies were underdispersed most frequently at the basin-reach spatial scale (mean = 18.8% of communities across functional strategy types and dispersion metrics), followed by the basin-mesohabitat (2.0%) and the reach-mesohabitat (1.3%) spatial scales. Evaluation of functional strategy dispersion using MPD produced more significantly underdispersed communities (mean = 9.5% across functional strategy types and spatial scales) than MNND (5.1%).

Wilcoxon signed-rank tests indicated that SES values were significantly greater than zero for all three types of strategies, three spatial scales, and two dispersion metrics which indicates that communities are consistently underdispersed (Table 2.3, Figures 2.4–2.5 white box plots). Wilcoxon rank sum tests indicated that SES values did not differ between on- and off-Flint Hills ecoregions, regardless of the trait category, spatial scale, or dispersion metric (Table 2.3, Figures 2.4–2.5 gray and black squares). Linear regression indicated statistically significant relationships between SES values based on mean nearest neighbor distance and stream network position (link magnitude) for four of nine models (Table 2.3, Figure 2.4 scatterplots). SES of reproductive life history strategies was negatively correlated with link magnitude at the basin-mesohabitat ($R^2 =$

0.13) and basin-reach scales ($R^2 = 0.37$), but not at the reach-mesohabitat scale suggesting that traits are strongly underdispersed in headwater reaches compared to river mainstem reaches. SES of feeding strategies was positively correlated with link magnitude at the reach-mesohabitat and basin-mesohabitat scales, although these relationships were weak ($R^2 = 0.02$ and 0.03 , respectively). Linear regression indicated statistically significant relationships between SES values based on mean pairwise distance and stream network position for six of nine models (Table 2.3, Figure 2.5 scatterplots). These relationships were stronger and qualitatively similar to those derived from SES values based on mean nearest neighbor distance. SES of reproductive life history strategies was negatively correlated with link magnitude at the basin-mesohabitat ($R^2 = 0.14$) and basin-reach scales ($R^2 = 0.42$), but not at the reach-mesohabitat. SES of feeding strategies was positively correlated with link magnitude at the reach-mesohabitat and basin-mesohabitat scales, although these relationships were also weak ($R^2 = 0.04$ and 0.04 , respectively). Additionally, SES of locomotion strategies was negatively correlated with link magnitude at the basin-mesohabitat and basin-reach scales although the former relationship was weak ($R^2 = 0.04$ and 0.19 , respectively).

Discussion

Community Assembly in Stream Fishes

Most empirical evidence suggests that temperate stream fish communities are structured by abiotic environmental filtering and to a lesser extent by competitive interactions among species (Matthews 1998, Jackson et al. 2001). Our results lend support to this paradigm in that the dispersion of reproductive life history, feeding, and locomotion strategies were underdispersed within local communities, regardless of the spatial scale of investigation. Most empirical tests of conceptual models of community assembly (Schlosser 1987, Vannote et al. 1980) test for patterns of taxonomic richness and functional diversity along stream-size gradients or geologic gradients; species- and trait-environment relationships; or community nestedness along stream-size or geologic gradients (Roberts and Hitt 2010, Pease et al. 2012, Neff and Jackson 2013). We show that null model tests of functional strategy (or trait) dispersion allow for a more explicit characterization of the roles of environmental filtering and competitive exclusion relative to tests of trait-environment relationships and community turnover and nestedness.

Individual Traits versus Multi-trait Strategies

Functional traits evolve in combination, producing multi-trait functional strategies that interact with biotic or abiotic environmental factors during the process of community assembly. Such coevolution of traits may arise from positive or negative interactions between multiple traits, which stem from synergism or fitness tradeoffs, respectively. Alternatively, traits may evolve in combination with one another not as a consequence of selection for trait combinations that are adaptive, but due to constraints imposed by physiology, biomechanics, allometry, or phylogeny (Lande and Arnold 1983, Milla and Reich 2011). When characterizing the dispersion of individual traits or multi-trait strategies in local communities, it is difficult to ascertain whether environmental filters or interspecific competition are acting holistically on multi-trait strategies or on individual traits. This was apparent in our study where we observed underdispersion of reproductive life history strategies at the mesohabitat resolution despite previous studies demonstrating that these strategies are filtered by flow regimes operating at broader spatial scales (Olden and Kennard 2010, Mims and Olden 2012). We suspect this underdispersion is a consequence of covariation between reproductive life history and body size, which was probably filtered by a depth gradient distinguishing riffle and pool mesohabitats. Large-bodied species are more susceptible to predation by terrestrial predators and occupy deep pools to avoid this predation risk, whereas small-bodied species are more susceptible to predation by pool-dwelling piscivorous fishes and thus occupy riffles and shallow pool margins (Schlosser 1987, Schlosser 1988, Martin et al. 2013). Nevertheless, our study provides insight into how multi-trait functional strategies are dispersed in local communities and how dispersion differs among three types of strategies hypothesized to interact with different aspects of the abiotic and biotic environment. Phylogenetic comparative studies examining trait evolution and intercontinental convergence (e.g., Winemiller and Rose 1992, Lamouroux et al. 2002) and functional morphology (e.g., Wainwright 1996) shed light on how traits correlate with one another and interact (both independently and in combination with other traits) with environmental factors to drive community assembly. Consideration of these studies as well as null model tests of functional strategy dispersion from additional taxa and regions will help to clarify the importance of multi-trait strategies during community assembly.

Spatial Scale

Identifying the appropriate spatial scale (both resolution and extent) is fundamental for understanding mechanisms of community assembly (Levin 1992, Swenson et al. 2006, Weiher et al. 2011). Much of the past work on scale-dependency of community assembly comes from tropical forest communities and is inferred from phylogenetic (as opposed to trait) dispersion (Webb et al. 2000). From these studies, increasing spatial resolution shifts the phylogenetic community structure from overdispersion to underdispersion, which implies that interspecific competition drives assembly between adjacent individuals whereas filtering of traits by topographic and edaphic gradients operates at broader spatial scales (Swenson et al. 2004). We did not observe this shift from competitive exclusion to environmental filtering in our study and three explanations are plausible. First, competitive exclusion will operate only when traits or strategies affect the acquisition of limiting resources. This condition is often satisfied in tropical forest communities where mineral nutrients limit growth of trees whereas food resources generally are not limiting in prairie streams where frequent hydrological disturbances maintain fish populations below carrying capacity (Dodds et al. 2004, Franssen et al. 2006). Moreover, small-bodied minnows (Teleostei: Cyprinidae) often occur in multispecies shoals to avoid predation and facilitate foraging (Gorman 1988). Such shoaling behavior often occurs among trophically-similar species and would reduce a signal of overdispersion in feeding strategies. Second, the topographic and edaphic gradients that environmentally filter tropical tree species vary at much broader spatial scales than do the species interactions driving competitive exclusion (Swenson et al. 2006). By contrast, abiotic gradients in streams (mainly depth and current velocity) occur at both fine (e.g., pool versus riffle mesohabitats) and broad (e.g., headwater versus mainstem reaches) spatial resolutions (Frissell et al. 1986). These environmental gradients filtering species' traits at multiple spatial scales might explain why we observed environmental filtering at both spatial resolutions. Third, competitive exclusion is more likely to be detected when functional redundancy within the regional pool is high and the regional pool is restricted to a narrower taxonomic group (Swenson et al. 2006). The regional pool of our temperate stream fish communities was composed of species representing nine families with low genus-to-species ratios (mean = 1.4), which might reduce the likelihood of species competitively excluding one another. Winston (1995) observed evidence of competitive exclusion in stream fish communities of the southern Great Plains; however, this study was restricted to one family (cyprinids) and

carried out in a zoogeographic region with higher regional diversity and a mean species-to-genus ratio of 3.0. Competitive exclusion might be more likely in areas with higher regional diversity, but this hypothesis would need to be validated across a greater number of regions (Hugueny et al. 2010).

When spatial extent is reduced, community assembly may appear increasingly neutral (i.e., traits are neither under- nor over-dispersed) because a combination of low environmental heterogeneity among localities and small regional species pools precludes species sorting by environmental gradients (Leibold et al. 2004, Weiher et al. 2011). We did not observe such a decrease in underdispersion when narrowing the spatial extent from basin to reach. Again, this is probably a consequence of equally-high environmental heterogeneity among mesohabitats within a reach compared to mesohabitats within the basin.

Environmental Gradients

Mechanisms of community assembly should also vary along gradients of abiotic harshness (Weiher and Keddy 1995, Chase 2007, Yan et al. 2012). Competitive exclusion is predicted to decrease in importance, whereas environmental filtering is expected to increase in importance with increasing environmental harshness or disturbance frequency. For example, Graham et al. (2009) observed an increase in ecological similarity (inferred from phylogenetic relatedness) with altitude in Ecuadorian hummingbird communities, suggesting that environmental filtering becomes stronger in seasonally harsh, high-elevation environments compared to seasonally stable, tropical lowlands. In temperate freshwater fish communities, this is apparent in hydrologically-stable natural lakes where species interactions have strong influences on species composition (e.g., Helmus et al. 2007), whereas frequent hydrologic disturbances in streams often have overriding influences on species composition (e.g., Grossman et al. 1982). Such gradients of environmental harshness also exist within individual stream networks, where hydrological regimes are more severe in headwater streams compared to river mainstems (Dodds et al. 2004). We showed that reproductive life history strategies are more strongly filtered in headwater streams compared to river mainstems. Indeed, fish communities in headwater streams of the Big Blue River basin are limited mostly to opportunistic life history strategists (e.g., minnows and darters), whereas river mainstem communities are composed of a more diverse group of life history strategists including periodic (e.g., suckers) and equilibrium

(e.g., catfishes and sunfishes) strategists (Gido et al. 2006). In contrast, trophic and fluvial morphological strategies were consistently underdispersed along the gradient of stream size. Food resource type turns over along gradients of stream size and feeding strategies should also turn over and be consistently underdispersed provided that resources are not limiting and instead operate as an environmental filter (Vannote et al. 1980, Ibanez et al. 2009).

Although taxonomic composition of headwater communities differs between ecoregions in our study area (Minckley 1959, Gido et al. 2006), we did not observe a difference in the dispersion of functional strategies, which is contrary to our prediction that environmental filters would be weaker in springfed headwater streams draining the Flint Hills ecoregion. Perhaps hydrologic regimes are driven by the broader regional climate and were equally severe in all three ecoregions. The taxonomic differences in community composition probably stem from functional traits that we did not characterize. Several species characteristic of headwater streams in the Flint Hills are cool-water adapted (*Chrosomus erythrogaster*, *Luxilus cornutus*, *Semotilus atromaculatus*) and populations in the Flint Hills are at the southern periphery of their geographic range (Pflieger 1997). As such, we suspect that warm and variable thermal regimes in streams draining the Western Cornbelt Plains and Central Great Plains would act as an environmental filter limiting the abundance of these cool-water species, whereas cool and stable thermal regimes in the Flint Hills would not filter thermal traits.

Conclusions

This study illustrates that the use of null models to characterize trait dispersion is an effective, yet unexploited approach to objectively test alternate mechanisms (environmental filtering versus competitive exclusion) of community assembly in stream fish communities. We show that functional strategies of stream fishes are underdispersed, lending support for the paradigm of environmental filtering in stream fish communities. Whereas testing the dispersion of multi-trait functional strategies provided a broad understanding of community assembly, it may be difficult to separate the importance of single traits. Finally, effects of scaling on the perceived importance of environmental filtering versus competitive exclusion in our study differed from studies in other regions and taxonomic groups. These differences probably stem from a combination of taxon-specific differences in community assembly (i.e., competitive

exclusion is rare in stream fish communities) and differences in environmental variability (i.e., abiotic gradients are hierarchically structured in stream networks).

References

- Burrough, P.A., 1983. Multiscale sources of spatial variation in soil, 1. The Application of fractal concepts to nested levels of soil variation. *J. Soil Sci.* 34: 577–597.
- Chase, J.M. 2007. Drought mediates the importance of stochastic community assembly. – *Proc. Nat. Acad. Sci.* 104:17430–17434.
- Dray, S. and Legendre, P. 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. – *Ecology* 89: 3400–3412.
- Dodds, W.K. et al. Life on the edge: the ecology of Great Plains prairie streams. – *Bioscience* 54: 205–216.
- Doledec S. et al. 1996. Matching species traits to environmental variables: a new three-table ordination method. – *Environ. Ecol. Stat.* 3: 143–166.
- Dray, S. and Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. – *J. Stat. Softw.* 22: 1–20.
- Fausch, K.D. et al. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. – *Bioscience* 52:1–16.
- Franssen, N.R. and Gido, K.B. 2006. Use of stable isotopes to test literature-based trophic classifications of small-bodied stream fishes. – *Am. Midl. Nat.* 156: 1–10.
- Frimpong, E. and Angermeier, P. 2010. Trait-based approaches in the analysis of stream fish communities. – In: Gido, K.B. and Jackson, D.A. (eds), *Community ecology of stream fishes: concepts, approaches, and techniques*. *Am. Fish. Soc. Symp.* 73: pp. 109–136.
- Frissell, C.A. et al. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. – *Environ. Manage.* 10: 199–214.
- Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123–202 in T. P. Simon, editor. *Assessing the sustainability and biological integrity of water resources using fish communities*. CRC Press, Boca Raton, Florida
- Gorman, O.T. 1988. The dynamics of habitat use in a guild of Ozark minnows. – *Ecol. Monogr.* 58: 1–18.

- Graham, C.H., et al. 2009. Phylogenetic structure in tropical hummingbird communities. – *Proc. Nat. Acad. Sci.* 106: 19673–19678
- Grossman, G.D. et al. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage – a test of community theory. – *Am. Nat.* 120: 423–454.
- Helmus, M.R. et al. 2007. Separating the determinants of phylogenetic community structure. – *Ecology Letters* 10:917-925.
- Hoeinghaus, D.J. et al. 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. – *Journal of Biogeography* 34: 324-338.
- Horwitz, , R.J. 1978. Temporal variability patterns and distributional patterns of stream fishes. – *Ecol. Monogr.* 48: 307–321.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography.* – Princeton Univ. Press.
- Hugueny, B. et al. 2010. Community ecology of river fishes: a large-scale perspective. – In: Gido, K.B. and Jackson, D.A. (eds), *Community ecology of stream fishes: concepts, approaches, and techniques.* *Am. Fish. Soc. Symp.* 73: pp. 29–62.
- Huryn, A. D. and Wallace, J.B. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. – *Ecology* 68: 1932–1942.
- Ibanez, C. et al. 2009. Convergence of temperate and tropical stream fish assemblages. – *Ecography* 32: 658–670.
- Ingram, T. and Shurin, J.B. 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. – *Ecology* 90: 2444–2453.
- Jackson, D.A. et al. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. – *Can. J. Fish. Aquat. Sci.* 58: 157–170.
- Kembel, S.W. et al. 2013. R tools for integrating phylogenies and ecology. – <<http://cran.r-project.org/web/packages/picante/picante.pdf>>.
- Laliberte, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – *Ecology* 91: 299–305.
- Lamouroux, N. et al. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. – *Ecology* 83: 1792–1807.

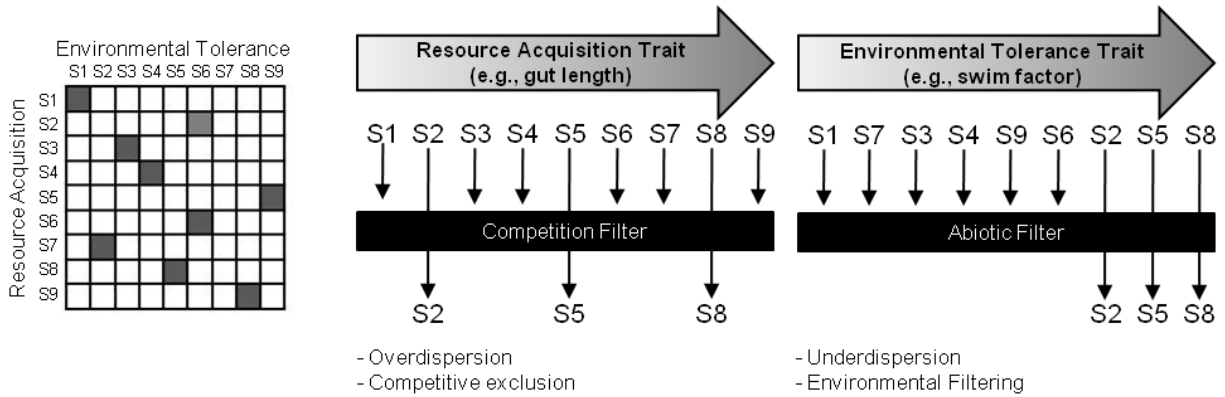
- Lande R. and Arnold S.J. 1983. The measurement of selection on correlated characters. – *Evolution* 37: 1210–1226.
- Lazorchak, J.M. et al. 1998. Environmental monitoring and assessment program-surface waters: field operations and methods for measuring ecological condition of wadeable streams. – U.S. Environmental Protection Agency.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*. – Elsevier Scientific.
- Leibold, M.A. et al. 2004. The metacommunity concept: a framework for multiscale community ecology. – *Ecol. Lett.* 7: 601–613.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. – *Ecology* 73: 1943–1967.
- Liu, X. et al. 2013. The environment and space, not phylogeny, determine trait dispersion in a subtropical forest. – *Funct. Ecol.* 27: 264–272.
- Martin, E.C. et al. 2013. Habitat associations of stream fishes in protected tallgrass prairie streams. – *Am. Midl. Nat.* 170: 39–51.
- McGill, B.J. et al. 2006. Rebuilding community ecology from functional traits. – *Trends. Ecol. Evol.* 21: 178–185.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. – *Ecol. Monogr.* 46:355–393.
- Milla, R. and Reich, P.B. 2011. Multi-trait interactions, not phylogeny, fine-tune leaf size reduction with increasing latitude. – *Annals of Botany* 107: 455–465.
- Mims, M.C. and Olden, J.D. 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history traits. – *Freshwater Biol.* 58: 50–62.
- Minckley, W.L., 1959. *Fishes of the Big Blue River Basin, Kansas*. University of Kansas Publications of the Museum of Natural History. – 11: 401–422.
- Moyle, P.B. and Cech, J.J. 2004. *Fishes: An Introduction to Ichthyology*. – Prentice-Hall, Inc.
- Oksanen, J. et al. 2011. *Vegan: community ecology package*. – <cran.rproject.org/package=vegan>.
- Olden, J.D., Poff, N.L., Bestgen, K.R. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado river basin. *Ecol. Monogr.* 76: 25–40.
- Olden, J.D. and Kennard, M. 2010. Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. – In: Gido, K.B. and Jackson D.A. (eds),

- Community ecology of stream fishes: concepts, approaches, and techniques. *Am. Fish. Soc. Symp.* 73: pp. 83–107.
- Paradis, E. et al. APE: analysis of phylogenetics and evolution in R language. – *Bioinformatics* 20: 289–290.
- Pease, A.A. et al. 2012. Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. – *Freshwater Biol.* 57: 1060–1075.
- Peres-Neto, P.R. et al. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. – *Ecology* 87: 2614–2625.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. – *J. N. Am. Benthol. Soc.* 16: 391–409.
- Poff, N.L. and Allan, J.D. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. – *Ecology* 76: 606–627.
- Poos, M.S. and Jackson, D.A. 2012. Impact of species-specific dispersal and regional stochasticity on estimates of population viability in stream populations. – *Landscape Ecol.* 27: 405–416
- R Development Core Team. 2012. R: A language and environment for statistical computing. – R Foundation for Statistical Computing.
- Resetarits, W.J. 1997. Interspecific competition and qualitative competitive asymmetry between two benthic stream fishes. – *Oikos* 78: 428–439.
- Skalski, G.T. and Gilliam, J.F. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. – *Ecology* 81: 1685–1700.
- Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. – In: Matthews, W. J. and Heins, D. C. (eds), *Community and evolutionary ecology of North American stream fishes*. Oklahoma Univ. Press: pp. 17–24.
- Schlosser, I. J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. – *Oikos* 52: 36–40.
- Swenson, N.G. et al. 2004. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. – *Ecology* 88: 1770–1780.
- Swenson, N.G. et al. 2006 The problem and promise of scale dependency in community phylogenetics. – *Ecology* 87: 2418–2424.

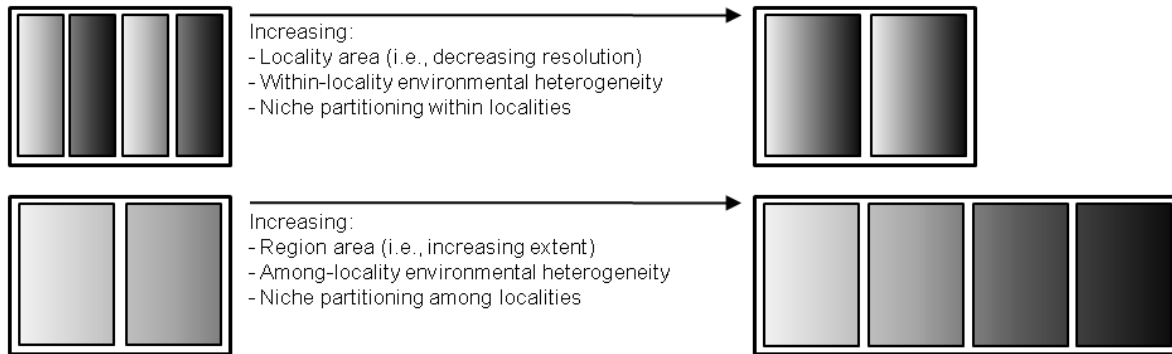
- Tedesco, P.A., Hugueny, B., Oberdorff, T., Durr, H.H., Merigoux, S., de Merona, B. 2008. River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia* 156: 691–702.
- Tonn, W.M. et al. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. – *Am. Nat.* 136: 345–375.
- Taylor, C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. – *Freshwater Biol.* 36: 385–396.
- Townsend, C.R. and Hildrew, A.G. 1994. Species traits in relation to a habitat template for river systems. – *Freshwater Biol.* 31: 265–275.
- Vannote, R.L. et al. 1980. The river continuum concept. – *Can. J. Fish. Aquat. Sci.* 37: 130–137.
- Violle, C. et al. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Wainwright, P.C. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. – *Ecology* 77: 882–892.
- Walker, R.H. et al. 2013. Movement patterns of southern redbelly dace, *Chrosomus erythrogaster*, in a headwater reach of an Ozark stream. – *Ecol. Freshwater Fish.* 22: 216–227.
- Webb, C.O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – *Am. Nat.* 156: 145–155
- Webb, C.O. et al. 2002. Phylogenies and community ecology. – *Annu. Rev. Ecol. Syst.* 33: 475–505.
- Webb, P. W. 1984. Form and function in fish swimming. – *Sci. Am.* 251: 58–68.
- Weiher, E. and Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. – *Oikos*. 74: 159–164.
- Weiher, E., et al. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. – *Oikos*. 81: 309–322.
- Weiher, E. et al. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. – *Philos. T. R. Soc. B.* 366: 2403–2413.
- Winston, M.R. 1995. Co-occurrence of morphologically similar species of stream fishes. – *The Am. Nat.* 145: 527–545.
- Yan, B., et al. 2012. Trait assembly of woody plants in communities across sub-alpine gradients: Identifying the role of limiting similarity. – *J. Veg. Sci.* 23: 698–708.

Figure 2.1 Conceptual diagram outlining three types of context dependency in community assembly. (A) Abiotic environmental filtering and competitive exclusion operate on different types of traits which may or may not be correlated among species. S1, S2, S3, etc. denote hypothetical species. (B) Increasing the spatial extent of the regional pool or local community can influence the amount environmental heterogeneity within and among local communities and shift the perceived mechanism of community assembly. Grey scaling represents a continuous environmental gradient. (C) Increasing severity and frequency of abiotic disturbance can maintain populations below carrying capacity, reduce resource limitation and decrease competitive.

(A) Trait Correlation and Dispersion



(B) Spatial Scaling



(C) Environmental Gradients

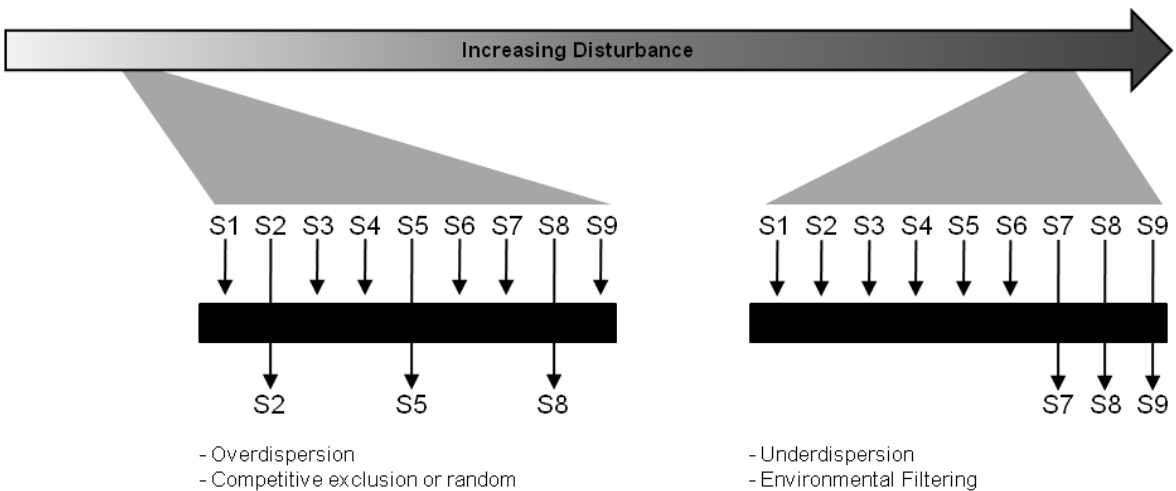


Figure 2.2 Study area in the Big Blue River basin showing locations of 40 reaches (Upper Panel). The dashed lines represent EPA Level III ecoregion boundaries and circles represent five headwater reaches on the Flint Hills (black), nine headwater reaches off the Flint Hills (white), and twenty six mainstem sites (gray). Mesohabitats sampled from a reach on the Little Blue River (Lower Panel). Black lines represent stream margins, light gray areas are sandbars, dark gray areas are log complexes, and open rectangles represent sampled mesohabitats.

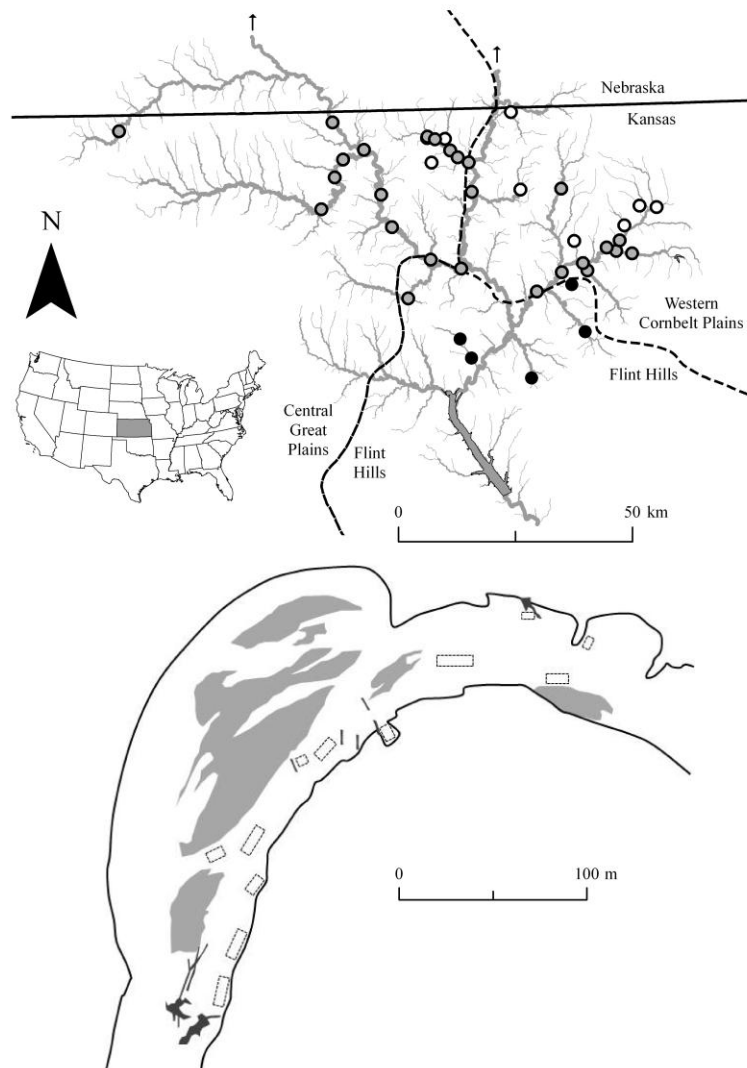
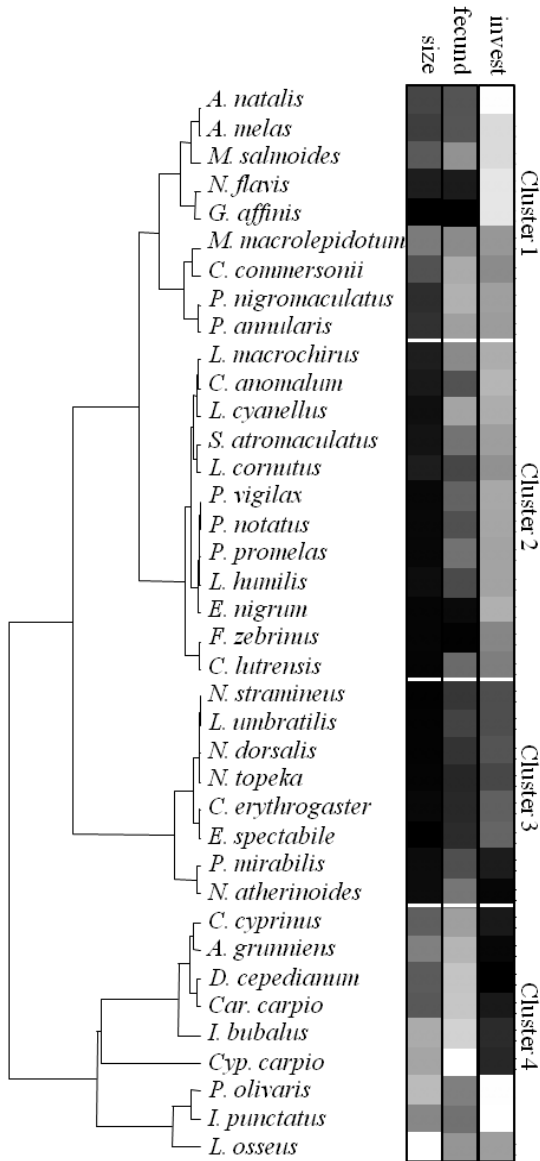
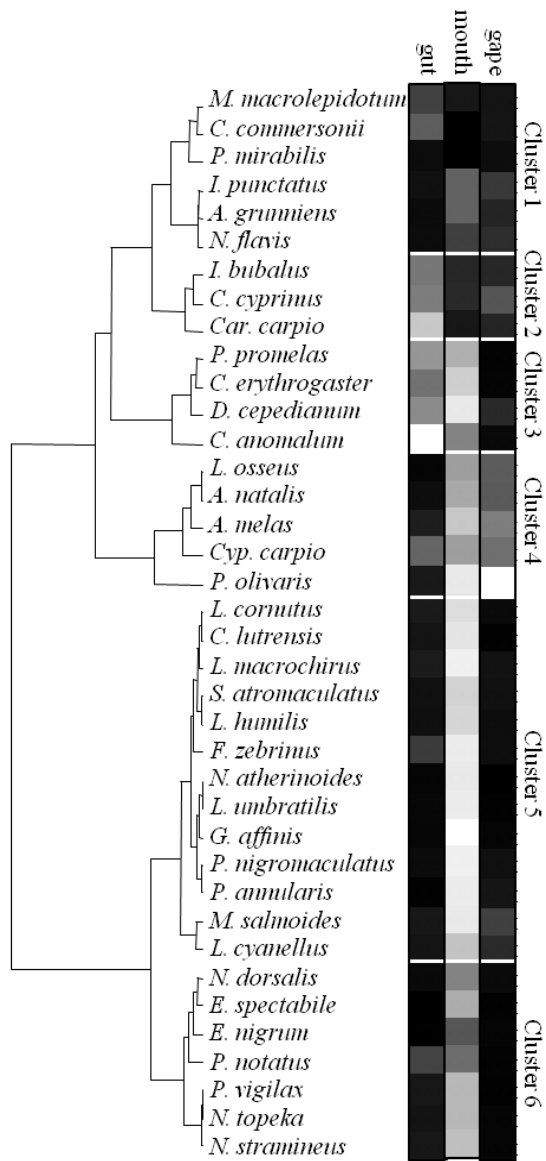


Figure 2.3 Multi-trait dendrograms for reproductive life history, feeding, and locomotion strategies. Shaded boxes indicate low (black) to high (white) values of individual traits representing each functional strategy type for each species. See Appendix A for trait abbreviations and numerical trait values area in the Big Blue River basin showing locations of 40 reaches (Upper Panel).

(A) Reproduction



(B) Feeding



(C) Locomotion

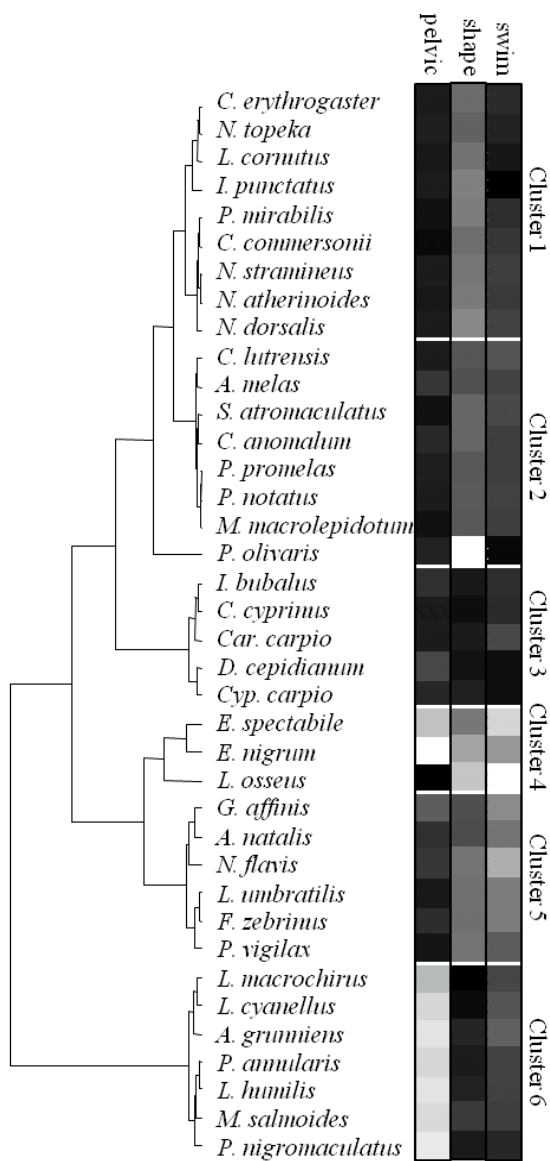


Figure 2.4 Dispersion of reproductive life history (A–C), feeding (D–F), and locomotion (G–I) strategies at three spatial scales: mesohabitat within reach (A, D, G), mesohabitat within basin (B, E, H), reach within basin (C, F, I). Functional strategy dispersion was calculated as the standardized effect size (SES) of the mean nearest neighbor distance (MNND). Boxplots show the distribution of SES values and asterisks indicate statistically significant underdispersion (i.e., SES values significantly greater than zero) at $\alpha < 0.003$ based on Wilcoxon signed-rank tests. Squares show mean (\pm 95% confidence intervals) SES for headwater reaches/mesohabitats on Flint Hills (black) and off Flint Hills (white) and different letters denote statistically significant differences based on Wilcoxon rank sum tests. Scatterplots show the relationship between stream network position (link magnitude) and SES values for headwater reaches/mesohabitats on Flint Hills (black) and off Flint Hills (white) and mainstem reaches/mesohabitats (gray). Best fit lines are shown for linear relationships with $R^2_{\text{adj}} > 0.10$. See Table 2.3 for summary of statistical tests.-trait dendrograms.

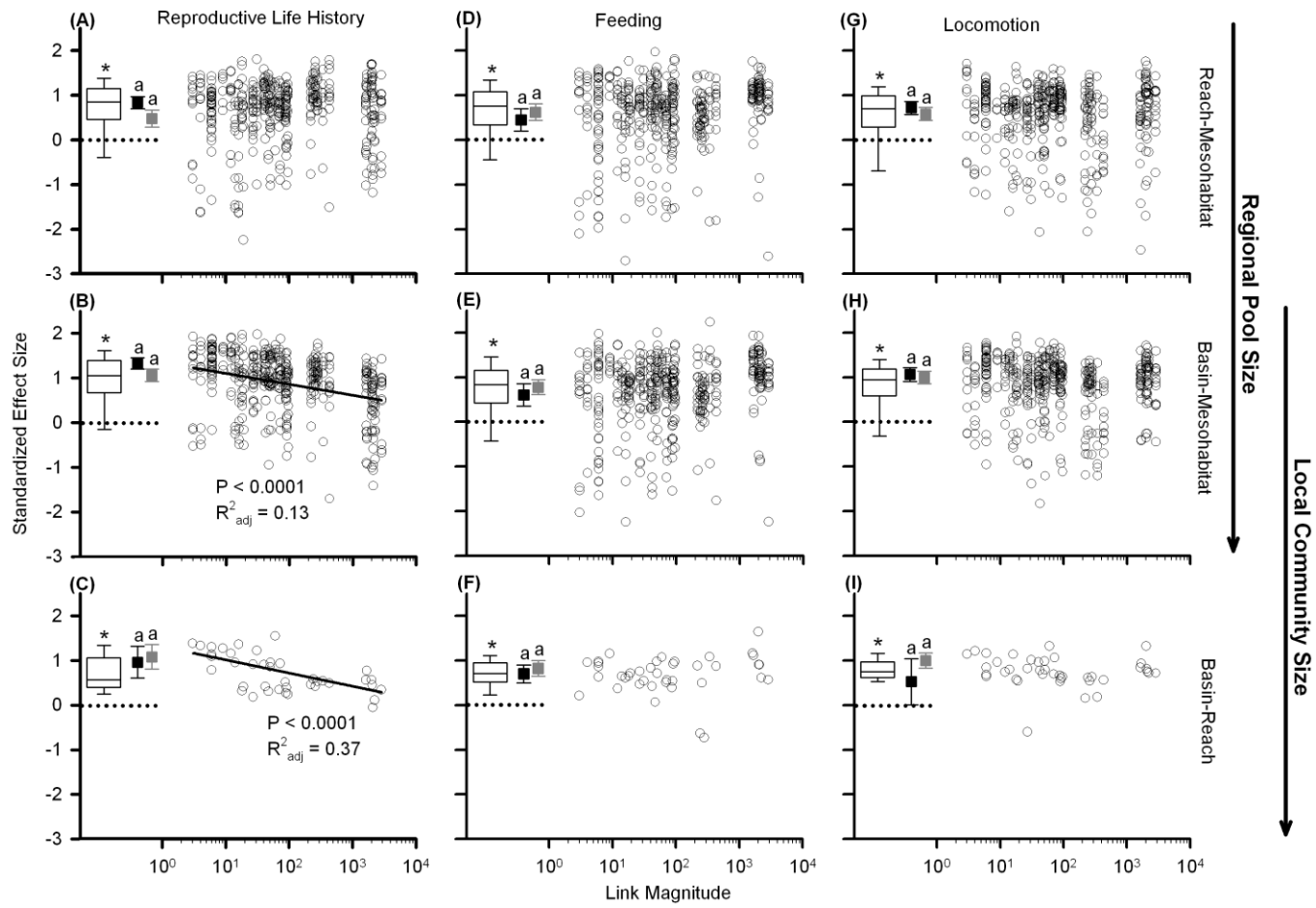


Figure 2.5 As in Figure 2.4, except standardized effect size (SES) is calculated from mean pairwise distance (MPD).

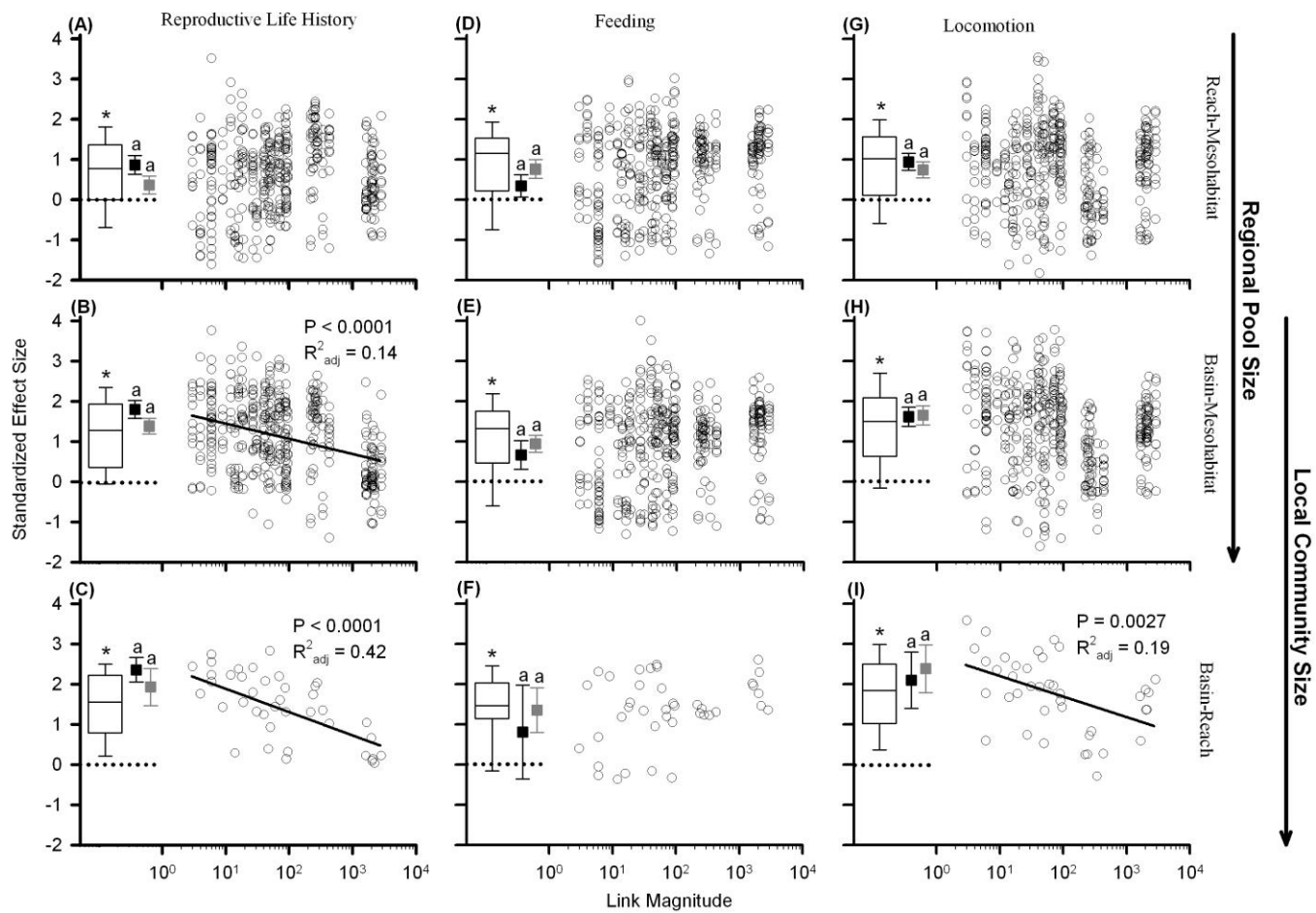


Table 2.1 Trait values for 38 fish species collected in the Big Blue River basin.

Species	Reproductive Life History			Feeding Ecology			Fluvial Morphology		
	Size at Maturity	Annual Fecundity	Investment/ Progeny	Gut Length	Mouth Position	Gape Width	Pelvic fin Position	Shape Factor	Swim Factor
<i>Ameiurus melas</i> (Rafinesque, 1820)	180	3069	2.93	0.80	82	23.90	18	4.88	0.44
<i>Ameiurus natalis</i> (Lesueur, 1819)	200	2961	2.93	0.59	74	17.70	16	4.75	0.57
<i>Aplodinotus grunniens</i> (Rafinesque, 1819)	342	85800	0.63	0.56	55	8.30	68	3.77	0.52
<i>Campostoma anomalum</i> (Rafinesque, 1820)	91	2800	2.26	3.55	64	3.70	14	5.39	0.43
<i>Carpionodes carpio</i> (Rafinesque, 1820)	245	157854	0.79	2.88	35	8.40	10	3.52	0.46
<i>Carpionodes cyprinus</i> (Lesueur, 1817)	260	40000	0.79	1.96	40	16.70	8	3.21	0.38
<i>Catostomus commersonii</i> (Lacepede, 1803)	230	60325	1.86	1.57	29	5.70	5	5.60	0.41
<i>Chrosomus erythrogaster</i> (Rafinesque, 1820)	50	632	1.46	1.83	84	2.80	10	5.55	0.38
<i>Cyprinus carpio</i> (Linnaeus, 1758)	432	1125000	0.92	1.67	71	21.20	13	3.66	0.31
<i>Cyprinella lutrensis</i> (Baird & Girard, 1853)	40	6435	1.74	0.67	90	2.50	10	5.00	0.49
<i>Dorosoma cepedianum</i> (Lesueur, 1818)	251	144000	0.56	2.13	91	9.10	23	3.31	0.31
<i>Etheostoma nigrum</i> (Rafinesque, 1820)	42.5	230	2.2	0.44	52	3.00	76	6.93	0.66
<i>Etheostoma spectabile</i> (Agassiz, 1854)	30	705	1.5	0.43	75	2.50	58	5.84	0.82
<i>Fundulus zebrinus</i> (Jordan & Gilbert, 1883)	41	172	1.81	1.15	92	4.50	15	5.64	0.59
<i>Gambusia affinis</i> (Baird & Girard, 1853)	30	160	2.71	0.50	97	3.00	29	4.83	0.63
<i>Ictiobus bubalus</i> (Rafinesque, 1818)	445	233031	0.96	1.88	39	8.90	16	3.44	0.39
<i>Ictalurus punctatus</i> (Rafinesque, 1818)	358	7977	2.94	0.62	55	11.90	10	6.03	0.27
<i>Lepomis cyanellus</i> (Rafinesque, 1819)	66	48000	2.17	0.68	81	9.30	64	3.13	0.49
<i>Lepomis humilis</i> (Girard, 1858)	61	2077.5	2.08	0.61	86	4.40	68	3.71	0.44
<i>Lepomis macrochirus</i> (Rafinesque, 1819)	102	19225	2.17	0.76	93	5.20	56	2.85	0.45
<i>Lepisosteus osseus</i> (Linnaeus, 1758)	650	27830	2.03	0.49	71	17.90	2	7.76	0.93
<i>Luxilus cornutus</i> (Mitchill, 1817)	101	1800	1.91	0.75	88	3.80	9	5.72	0.33
<i>Lythrurus umbratilis</i> (Girard, 1856)	38	1659	1.29	0.51	92	2.40	9	5.68	0.59
<i>Micropterus salmoides</i> (Lacepede, 1802)	250	25544	2.59	0.71	91	13.10	65	4.29	0.43
<i>Moxostoma macrolepidotum</i> (Lesueur, 1817)	330	20325	1.97	1.23	35	5.50	7	5.05	0.43
<i>Notropis atherinoides</i> (Rafinesque, 1818)	60	9600	0.62	0.49	91	2.10	9	5.90	0.42

<i>Notropis dorsalis</i> (Agassiz, 1854)	38	950	1.34	0.54	64	3.90	10	6.23	0.44
<i>Noturus flavis</i> (Rafinesque, 1818)	100	410	2.71	0.58	46	9.80	18	5.75	0.72
<i>Notropis stramineus</i> (Cope, 1865)	36	1050	1.29	0.71	80	3.00	10	5.79	0.43
<i>Notropis topeka</i> (Gilbert, 1884)	40	600	1.22	0.66	78	2.90	11	5.29	0.36
<i>Phenacobius mirabilis</i> (Girard, 1856)	60	2470	0.82	0.58	29	4.40	7	5.96	0.39
<i>Pimephales notatus</i> (Rafinesque, 1820)	50.5	2544	2.11	1.25	58	2.70	10	5.10	0.44
<i>Pimephales promelas</i> (Rafinesque, 1820)	48	8280	2.08	2.26	76	2.60	11	5.04	0.43
<i>Pimephales vigilax</i> (Baird & Girard, 1853)	47	5008	2.13	0.71	78	2.50	8	5.74	0.51
<i>Pomoxis annularis</i> (Rafinesque, 1818)	150	39922	2.02	0.46	92	5.80	64	3.54	0.44
<i>Pomoxis nigromaculatus</i> (Lesueur, 1829)	140	75590	2.04	0.57	93	4.80	70	3.51	0.37
<i>Pylodictis olivaris</i> (Rafinesque, 1818)	485	13250	2.93	0.74	91	46.10	12	9.21	0.29
<i>Semotilus atromaculatus</i> (Mitchill, 1818)	76	8684	2.03	0.63	85	5.10	7	5.43	0.46

Table 2.2 Percent of local communities that were significantly underdispersed ($\alpha < 0.025$) or overdispersed ($\alpha > 0.975$) based on reproductive life history, feeding, and locomotion traits at three spatial scales: reach-mesohabitat (n = 440), basin-mesohabitat (n=440), and basin-reach (n = 40). Trait dispersion metrics were mean nearest neighbor distance (MNND) and mean pairwise distance (MPD).

Dispersion Metric	Extent-Resolution	Functional strategy type					
		Rep. Life Hist.		Feeding		Locomotion	
		under	over	under	over	under	over
MNND	Reach-Mesohabitat	1.4	0.0	0.7	0.0	1.4	0.0
	Basin-Mesohabitat	2.7	0.0	0.2	0.0	2.3	0.0
	Basin-Reach	15.0	0.0	2.5	0.0	20.0	0.0
MPD	Reach-Mesohabitat	0.9	0.0	0.5	0.0	2.7	0.0
	Basin-Mesohabitat	2.0	0.0	1.1	0.0	3.6	0.0
	Basin-Reach	27.5	0.0	2.5	0.0	45.0	0.0

Table 2.3 Summary of statistical tests presented in Figures 2.4 and 2.5. Statistically significant P-values at $\alpha < 0.003$ are bolded.

Metric	Region-Locality	Functional Strategy Type	Underdispersion		Ecoregion		Stream Network Position		
			V	P	W	P	P	R ² _{adj}	Est.
MNND	Reach-Mesohabitat	Reproductive Life History	85900	<0.0001	2829	0.06	0.283	0.00	n/a
		Feeding	83335	<0.0001	2091	0.24	0.002	0.02	0.14
		Locomotion	82901	<0.0001	2576	0.40	0.59	0.00	n/a
	Basin-Mesohabitat	Reproductive Life History	92848	<0.0001	2808	0.07	<0.0001	0.13	-0.28
		Feeding	86488	<0.0001	2191	0.44	0.0002	0.03	0.16
		Locomotion	91728	<0.0001	2362	0.96	0.084	0.01	n/a
	Basin-Reach	Reproductive Life History	819	<0.0001	15	0.36	<0.0001	0.37	-0.30
		Feeding	784	<0.0001	15	0.36	0.523	-0.02	n/a
		Locomotion	811	<0.0001	9	0.08	0.473	-0.01	n/a
MPD	Reach-Mesohabitat	Reproductive Life History	79710	<0.0001	2981	0.012	0.19	0.00	n/a
		Feeding	85437	<0.0001	1874	0.037	<0.0001	0.04	0.24
		Locomotion	84448	<0.0001	2666	0.227	0.23	0.00	n/a
	Basin-Mesohabitat	Reproductive Life History	91907	<0.0001	3067	0.004	<0.0001	0.14	-0.42
		Feeding	89205	<0.0001	1989	0.108	<0.0001	0.04	0.24
		Locomotion	92512	<0.0001	2198	0.462	<0.0001	0.04	-0.25
	Basin-Reach	Reproductive Life History	820	<0.0001	32	0.24	<0.0001	0.42	-0.64
		Feeding	799	<0.0001	17	0.52	0.033	0.09	n/a
		Locomotion	816	<0.0001	21	0.90	0.003	0.19	-0.50

Chapter 3 - Predicting community-environment relationships of stream fishes across multiple drainage basins: Insights into model generality and the effect of spatial extent

Abstract

Resource managers increasingly rely on predictive models to understand species-environment relationships. Stream fish communities are influenced by longitudinal position within the stream network as well local environmental characteristics that are constrained by catchment characteristics. Despite an abundance of studies quantifying species-environment relationships, few studies have evaluated the generality of these relationships among basins and spatial extents. We modeled community composition of stream fishes in thirteen sub-basins, nested within three basins in Kansas, USA using constrained ordination and environmental predictor variables representing (1) longitudinal network position, (2) local habitat, and (3) catchment characteristics. We tested the generality of species-environment relationships by quantifying the variation in model performance and the importance of environmental variables among the thirteen sub-basins and among three spatial extents (sub-basin, basin, state). Model performance was variable across the thirteen sub-basins, with adjusted constrained inertia ranging from 0.13 to 0.36. The importance of environmental variables was also variable among sub-basins, but longitudinal network position consistently predicted more variation in community composition than local or catchment variables. Model performance did not differ among spatial extents, but the importance of longitudinal network position decreased at broader spatial extents whereas local and catchment variables increased in importance. Results of this study support the longstanding frameworks of the river continuum and hierarchically-structured habitat. We show that (1) the relative importance of longitudinal network position, local conditions, and catchment conditions can vary from one region to another and (2) the spatial extent at which predictive habitat models are developed can influence the perceived importance of different environmental predictor variables. Resource managers should consider physiographic context and spatial extent when developing predictive habitat models for management and conservation purposes.

Introduction

Understanding species-environment relationships is a fundamental step in the conservation of aquatic biodiversity. Resource managers increasingly rely on predictive models to assess impacts of habitat alteration (Oberdorff et al. 2001), evaluate the spatial hierarchical nature of stream habitat (Allan et al. 1997), estimate habitat suitability for native species reintroductions (Harig and Fausch 2002), forecast non-native species invasions (Vander Zanden et al. 2004), and predict impacts of climate change on species distributions (Lyons et al. 2010). Additionally, natural resources agencies use species distribution models to make informed management decisions and identify priority areas of conservation. Such predictive modeling tools are particularly important in regions that are highly modified by human activities and harbor endemic and imperiled species such as the Great Plains of the central United States (Dodds et al. 2004; Gido et al. 2010; Hoagstrom et al. 2011).

Early conceptual models provided a framework for understanding stream communities based on the hierarchical structure of stream habitats (Frissell et al. 1986; Allan et al. 1997). That is, natural and anthropogenic characteristics of the catchment influence habitat characteristics at the spatial resolution of the stream reach, mesohabitat, and microhabitat. For example, models of stream fish community composition in the Great Plains found environmental predictor variables measured at the catchment-, reach-, and site-resolutions to be correlated with one another (Gido et al. 2006). In these streams, soil erodibility in the catchment was correlated with channel gradient, a reach-scale variable, and turbidity, a site-scale variable. Although environmental variables measured at the catchment resolution may be adequate predictors of community composition, it is through the hierarchical structure of lotic habitat that these variables are causatively linked to population vital rates (i.e., birth, death, emigration, and immigration) and consequent spatial variation in the distribution and abundance of species (Frissell et al. 1986). Consequently, the relationship between community composition and catchment characteristics may vary among drainage basins, depending on the interactions among environmental conditions at different levels of the hierarchy. Understanding how these hierarchical relationships may differ among basins poses a challenge to resource managers in interpreting and applying predictive habitat models.

Few studies have evaluated the generality of species-environment relationships among drainage basins (but see Wang et al. 2003; Wenger and Olden 2012), resulting in limited understanding of how the relative importance of local and catchment variables differs among drainage basins. Regardless, inferences of among-basin differences have been made by comparing the results of multiple, independent studies. For example, Wang et al. (2006) asserted that fish communities responded most strongly to catchment variables in basins with extensive anthropogenic land cover changes (e.g., Roth et al. 1996; Allan et al. 1997; Wang et al. 1997; 2001) whereas assemblages in more pristine basins responded more strongly to local variables (e.g., Lammert and Allan 1999; Wang et al. 2003). Natural catchment characteristics such as geology and soil properties can also scale down and constrain local habitat and stream communities (Frissell et al. 1986; Gido et al. 2006; Neff and Jackson 2011), but the consistency of multi-scale linkages of these natural catchment characteristics among basins is also poorly understood.

Several factors may lead to inconsistent species-environment relationships among basins. First, consistent importance of local or catchment variables between regions (e.g., drainage basins) may change if their correlation with causative environmental variables differs in strength or direction between two regions. For example, water temperature may be a proximal variable that varies with stream size, but the strength of the relationship between these two variables may depend on riparian canopy cover which may differ among regions. This relationship between such distal and proximal predictor variables is referred to as environmental correlation structure (Jiménez-Valverde et al. 2009; Saupe et al. 2012). It is likely that catchment variables are distal to population vital rates of stream fishes and constrain proximal variables such as disturbance regime, water chemistry, temperature, or local habitat that directly affect population vital rates (Poff and Allan 1995; Poff 1997). Second, differences in the length of an environmental gradient between regions may affect the importance of that environmental variable between those regions. For example, Sundblad et al. (2009) showed that niche models for estuarine fishes transferred inaccurately between two regions when the range of values for a key environmental variable (salinity) observed within each region differed between those regions. Similarly, in a study of stream macroinvertebrate communities, Mykra et al. (2007) demonstrated that the importance of environmental variables was positively correlated with their range of variation (i.e., gradient length) within the study region. Lastly, the spatial extent at which predictive habitat models are

developed may also affect the importance of environmental variables by altering environmental correlation structure or the length of environmental gradients (Ohmann and Spies 1998).

Longitudinal network position is a ubiquitous predictor of community composition of stream fishes. Changes in the type and diversity of local habitat as well as increased colonization and decreased extinction rates are factors that may contribute to the observed change in community composition from headwaters to large rivers (Schlosser 1987; Taylor and Warren 2001; Roberts and Hitt 2010). Previous studies assessing the relative importance of local and catchment variables on community composition frequently included measures of network position at several spatial resolutions. For example, investigators often include channel width and catchment area as measures of network position representing local and catchment categories, respectively (e.g., Gido et al. 2006; Esselman and Allan 2010; Saly et al. 2011). Given the ubiquitous importance of network position in predicting community composition, it is likely that network position directly (via colonization and extinction dynamics) or indirectly (via strong correlation with important abiotic variables such as local habitat) increases the perceived importance of local or catchment variables assessed in these studies. Thus, assessing the relative roles of local and catchment variables, independent of network position, may improve understanding of the hierarchical nature of stream habitat as well as the generality of species-environment relationships.

Objectives and Hypotheses

In this study, we used constrained ordination to relate environmental variables to community composition of stream fishes in thirteen sub-basins and across three spatial extents of the Central Great Plains, USA. Our first objective was to assess variation in model performance and the importance of network position, local, and catchment predictor variables among thirteen sub-basins. We hypothesized that the importance of network position would be consistently greater than the importance of catchment and local variables across the thirteen sub-basins, given the thoroughly documented change in community composition along the river continuum (Schlosser 1987; Taylor and Warren 2001; Roberts and Hitt 2010). By contrast, we hypothesized that correlation structure between catchment predictors and the causative environmental variables that drive variation in population vital rates would differ among the thirteen sub-basins, resulting in reduced concordance of these environmental variables among sub-basins. Because

sub-basins differ in physiography associated with ecoregions and annual precipitation associated with an east-west aridity gradient, we expected inconsistent environmental correlation structure among sub-basins. Second, we hypothesized that models would perform better in sub-basins draining multiple ecoregions that have longer environmental gradients. Greater environmental variation within a sub-basin that drives variation in community composition will likely improve model performance.

Our second objective was to compare model performance and the importance of local, catchment, and network position across three spatial extents (sub-basins, basins, and the state of Kansas). We predicted that broadening the spatial extent would increase the length of environmental gradients, but the rate of increase in gradient length would differ among network position, local, and catchment variables. Specifically, we predicted that all stream sizes would be represented at all three spatial extents (i.e., sub-basins, basins, and state), whereas variation in local and catchment variables associated with ecoregional transitions and an east-west precipitation gradient would be apparent only at broader spatial extents (i.e., basins and state). Accordingly, we hypothesized that network position would decrease in importance whereas local and catchment variables would increase in importance at broader spatial extents.

Methods

Study Area and Datasets

We modeled community composition within the Great Plains of the central United States at three nested spatial extents: thirteen sub-basins, three basins, and the state of Kansas (hereafter referred to as ‘modeling units’). This study area spanned six EPA level III ecoregions: Western Corn Belt Plains in northeastern Kansas, Central Irregular Plains in southeastern Kansas, Flint Hills in east central Kansas, Central Great Plains in central Kansas, Southwestern Tablelands in south central Kansas, and High Plains in western Kansas. Mean annual precipitation decreases from 102 cm in the east to 43 cm in the west. Basins and sub-basins varied in area, number of sites sampled, and species richness (Table 3.1). We delineated sub-basins within the state of Kansas to maximize the number of sub-basins, while maintaining adequate sample size (i.e., number of fish collection sites) to develop robust community models. Sub-basin delineations approximately followed four digit USGS Hydrologic Unit Codes (HUC 4s) and we used terminal HUC 4s (i.e., HUC 4s that are complete drainage basins without upstream HUC 4s) when

possible to compare species-environment relationships in isolated and independent sub-basins (Figure 3.1).

We used fish community data from collections made by the Kansas Department of Wildlife, Parks, and Tourism (KDWPT) Stream Monitoring Program conducted between May and August from 1995 to 2008. The KDWPT sampling protocol followed that of Lazorchak et al. (1998). Site lengths were 40 times the mean wetted width, with lower and upper limits of 150 m and 300 m, respectively. A combination of straight and bag seines (4.7-mm mesh) and DC-pulsed backpack or tote-barge electrofishing were used to capture fish. Equal effort among gear types was used at all sites to facilitate comparison of community composition among sites.

Twenty nine environmental variables representing three predictor datasets (hereafter referred to as ‘local’, ‘network position’, and ‘catchment’) were compiled and screened for use as predictors of community composition (Table 3.2). For the local dataset, we used thirteen variables measured by the KDWPT Stream Monitoring Program at the time of fish sampling that summarized depth, substrate, riparian characteristics, over-channel cover, and in-channel cover. Bank angle and canopy cover were measured at eleven equally-spaced transects (positioned perpendicular to flow) within each site. In-stream cover (i.e., filamentous algae, macrophytes, boulders, small wood (<0.3m), and large wood (>0.3m)) and over-channel cover (i.e., overhanging vegetation and undercut bank) were estimated at each transect using a five category system (0 = 0% coverage, 1 = 0-10% coverage, 2 = 10-40% coverage, 3 = 40-75% coverage, and 4 = 75-100% coverage) and averaged for the site, resulting in a score between 0 and 4 for each cover type at each site. Depth, substrate diameter, and substrate embeddedness were measured at five equally spaced points along each transect. The presence of four additional substrate classes that could not be quantified by diameter (i.e., bedrock, boulder, wood, clay) was determined at the aforementioned points and percent coverage for each class was calculated for each site. Although discharge and current velocity may be important correlates of community composition, we did not include these variables as local predictors because both vary among seasons and years within sites. Substrate diameter and embeddedness are more temporally-stable local predictors that correlate with current velocity and discharge in prairie streams (Gido et al. 2006) and indirectly represent discharge and current velocity gradients, regardless of the year or season during which sampling occurred.

We quantified network position as link magnitude, which we obtained from the National Hydrography Dataset (USGS 1997). Link magnitude was defined as the number of stream segments upstream of the site, where a segment is a first order stream or a section of stream between consecutive tributary confluences (Table 3.2). For the catchment dataset, we used fifteen variables from a geographic information system assembled for the Kansas Aquatic Gap analysis project characterizing land cover, soil, and geology in the catchment upstream of each site (Table 3.2; described in Gido et al. 2006). Land cover data were obtained from the National Land Cover Database (USGS 1992) and soil and geology characteristics were obtained from the State Soil Geographic Database (STATSGO), which provides seven soil and geological variables relevant to hydrology and in-stream habitat (NRCS 1994).

Statistical Analysis

Environmental Variation among Sub-basins

Prior to analyses, environmental variables were checked for normality and \log_{10} -transformed or arcsine-square root transformed (for proportional variables (e.g., land cover)) if non-normally distributed. We generated Principal Components Analysis (PCA) biplots to characterize variation in local characteristics and catchment characteristics among the thirteen sub-basins. We performed separate PCAs for these two predictor categories at the extent of the entire state, grouped site scores for PC axes 1 and 2 by sub-basin, calculated the mean and standard error of site scores for each sub-basin, and plotted these values in bivariate space. For network position, we calculated the mean and standard error of link magnitude for each sub-basin and plotted these values in univariate space.

Preparation of Environmental Predictor Variables for Community Models

We performed PCA to summarize the main gradients in local and catchment predictor categories for each modeling unit. Separate PCAs were performed on each modeling unit (17 modeling units) and predictor category (2 predictor categories) for a total of thirty four PCAs. We retained only interpretable PCA axes, determined using broken stick models (Borcard et al. 2011), and used the axis scores as derived environmental predictor variables to summarize these complex environmental gradients (e.g., Taylor 2010; Neff and Jackson 2011). We did not

perform a PCA on the network position predictor category because it contained only one variable, link magnitude, which was used as a predictor of network position.

Community Modeling

We used Canonical Correspondence Analysis (CCA) to relate patterns in fish community composition to environmental conditions in each of the seventeen modeling units. CCA is a constrained ordination technique that uses multiple predictor variables to predict multiple response variables (e.g., ordination axes that summarize species' abundances). We chose to use CCA as opposed to linear-based ordination methods after a preliminary analysis using Detrended Correspondence Analysis (DCA) indicated relatively high turnover in community composition among sites within modeling units (i.e., standard deviation of the first DCA axis was greater than 2; Legendre and Legendre 1998).

For each modeling unit, we developed a model containing all predictor variables (hereafter referred to as 'global models') and used permutation tests ($n = 1000$) to determine model significance. We calculated total inertia and proportion of total inertia constrained by environmental predictor variables. Because the number of environmental predictor variables and sites may influence constrained inertia, we calculated an adjusted redundancy statistic using Ezekiel's formula (Peres-Neto et al. 2006; Borcard et al. 2011) to facilitate comparison of model performance among sub-basins and spatial extents that differed in sample size.

We were interested in the importance of the three predictor categories as well as differences in their importance among modeling units. For each modeling unit, we quantified the importance of the predictor categories by excluding each environmental predictor variable, in turn, from the CCA and quantifying the percent reduction in constrained inertia with each predictor variable removed using Equation 1.

$$PctRed_i = 100 \times (CI_{glob} - CI_i / CI_{glob}) \quad \text{Equation 1}$$

$PctRed_i$ is the percent reduction in constrained inertia with predictor variable i removed from the CCA model and is a measure of variable importance. CI_{glob} is the constrained inertia of the global model containing all predictor variables and CI_i is the constrained inertia with predictor variable i removed from the CCA model. We reasoned that a large percent reduction in constrained inertia with a predictor variable removed indicated high importance of that predictor variable. We included the removed predictor variable (i) as a covariate in the reduced models to partition out the shared variation between the removed predictor variable and the predictor

variables that remained in the model. This method provided an estimation of the pure effect of each predictor variable (Borcard et al. 2011). Statistical analyses were performed with the vegan package (Oksanen et al. 2009) in R (version 2.13.1; R Development Core Team, Vienna, Austria).

Results

Environmental Variation among Sub-basins

The east-west aridity gradient influenced environmental conditions in the three environmental predictor categories among the thirteen sub-basins. Environmental conditions of sites represented by network position, local habitat, and catchment characteristics differed between eastern and western sub-basins (Figure 3.2). Mean link magnitude (network position) of sites was greater in the more arid western sub-basins, where fewer perennial headwater streams occur per unit of catchment area (Figure 3.2a). These western sub-basins also had finer substrates than eastern sub-basins (Figure 3.2b) and soils in the catchments of sites had lower organic matter in western sub-basins compared to eastern sub-basins (Figure 3.2c).

Derived Environmental Predictor Variables

The first two axes of the Principal Components Analyses of each modeling unit captured 31 to 62% and 46 to 70% of the variation in environmental variables from the local and catchment predictor categories, respectively. Site scores from these axes were retained as environmental predictors in community models (hereafter referred to as ‘Local 1’, ‘Local 2’, ‘Catchment 1’, and ‘Catchment 2’). For the local dataset, substrate diameter loaded most strongly on the PC axis 1 for 10 of 17 modeling units, whereas depth, in-channel cover, and bank angle loaded strongly on PC axis 2. For the catchment dataset, soil permeability and organic matter loaded most strongly on the PC axis 1 for most modeling units, whereas available water capacity, an indicator of groundwater flow potential, loaded most strongly on PC axis 2 for most modeling units (Table 3.3). A complete list of variable loadings is provided in Appendices A and B.

Model Performance

We detected significant community-environment relationships for all modeling units ($P < 0.01$). Model performance (i.e., adjusted proportion of constrained inertia) averaged 0.21 and ranged from 0.13 in the Ninnescah sub-basin to 0.36 in the Big Blue basin (Figure 3.3). Total inertia averaged 6.64, 7.84, and 8.44 at the sub-basin, basin, and state extents, respectively, indicating that community turnover across sites increased slightly with extent. Adjusted constrained inertia was 0.20, 0.19, and 0.20 for the sub-basin, basin, and state extents, respectively, indicating that model performance did not differ across extents after controlling for the number of predictor variables and sample sites included in the model.

Importance of Environmental Variables

Network position was the best predictor of community composition (56% mean reduction in model performance with that variable removed from the global model), followed by Local 1 (28% reduction), Catchment 1 (25% reduction), Local 2 (17% reduction), and Catchment 2 (15% reduction). Local 1 and Catchment 2 were the least variable among sub-basins (range = 33% and 40%, respectively) and Local 2 and Catchment 1 were the most variable among sub-basins (range = 53% and 47%, respectively) (Figure 3.4). The importance of network position decreased at broader spatial extents. By contrast, the importance of Local 1 and Catchment 1 increased at broader spatial extents (Figure 3.5).

Species-Environment Relationships

Network position distinguished downstream communities dominated by predatory catfishes (*Ictalurus sp.* and *Pylodictis sp.*), shovelnose sturgeon (*Scaphirhynchus platorhynchus*) and freshwater drum (*Aplodinotus grunniens*) from headwater communities dominated by longear sunfish (*Lepomis megalotis*), creek chubs (*Semotilus atromaculatus*), and central stonerollers (*Campostoma anomalum*). Species' responses to local and catchment variables were variable among sub-basins, but generally distinguished communities dominated by bullhead catfishes (*Ameiurus sp.*), fathead minnows (*Pimephales promelas*), and bluntnose minnows (*Pimephales notatus*) from communities dominated by Common shiner (*Luxilus cornuttus*), Cardinal shiner (*Luxilus cardinalis*), and Southern redbelly dace (*Chrosomus erythrogaster*).

Discussion

We show that stream fishes responded to environmental variables represented by network position, local conditions, and catchment conditions, which supports the longstanding frameworks of the river continuum and hierarchically structured stream habitats (Vannote et al. 1980; Frissell et al. 1986; Allan et al. 1997). Despite this, substantial variation existed in the strength of community-environment relationships (i.e., model performance) and the importance of environmental variables among sub-basins. Quantifying species-environment relationships and understanding the generality of such relationships across multiple spatial extents is a fundamental step in the conservation of stream fishes. Specifically, if species' responses to environmental gradients vary across geographic space, it will be important to adjust habitat management plans to accommodate for these differences.

Variation in model performance among sub-basins was likely influenced by the amount of environmental variation within a sub-basin. For example, model performance was highest in the Big Blue sub-basin which contained a long stream size gradient and a catchment geology gradient distinguishing high-gradient, headwater streams of the Flint Hills ecoregion from low-gradient, headwater streams draining the Western Corn Belt Plains and Central Great Plains ecoregions. Given the well documented community turnover along these two environmental gradients in the Big Blue basin (Minckley 1959; Gido et al. 2002; Gido et al. 2006), it is not surprising that our model was able to identify a strong community-environment relationship in this sub-basin. In particular, high-gradient headwater streams in the Flint Hills were dominated by Common shiner and Southern redbelly dace, whereas low-gradient headwater streams of the Western Corn Belt Plains and Central Great Plains were dominated by bullhead catfishes, fathead minnows, and bluntnose minnows. By contrast, our poorest model came from the Ninescah sub-basin, which contained two river mainstems and few perennial, headwater streams. This resulted in a short stream size gradient and minimal change in community composition among sites arrayed along this short environmental gradient. Moreover, the Ninescah sub-basin drains a single ecoregion—the Central Great Plains—resulting in minimal variation in local and catchment conditions among sites.

Network position was a consistently better predictor of community composition than either local or catchment variables for all sub-basins. The importance of stream size in predicting stream fish community composition in all of the sub-basins of our study system was not

surprising given the propensity for stream fish communities to change along the river continuum (Vannote et al. 1980; Schlosser 1987; Roberts and Hitt 2010). In particular, downstream communities were dominated by generalist and predatory species (e.g., red shiners and channel catfish), whereas upstream communities were dominated by benthic-foraging herbivorous and invertivorous species (e.g., central stonerollers and orangethroat darters) (Gido et al. 2006). Still, the importance of network position was variable among sub-basins which may also be a consequence of gradient length. The importance of network position was highest in highly dendritic sub-basins with high drainage densities in eastern Kansas (including the Big Blue, Little Osage, and Marais des Cygnes) where sites were arrayed along a range of stream sizes. By contrast, network position was a poor predictor of community composition in narrow sub-basins with low drainage densities in the arid western High Plains and Central Great Plains ecoregions (including the Upper Arkansas and Republican) that are composed of long river mainstems with few perennial, headwater streams. Network position was also a poor predictor of community composition in the lower Kansas sub-basin, despite a range of stream sizes present in this sub-basin. However, this long gradient was not represented in the dataset because no samples were taken from the non-wadeable Kansas River mainstem where sampling protocols used by the KDWPT were unfeasible. The variation in importance of network position among sub-basins in our study was likely a consequence of the east-west aridity gradient affecting drainage density and stream network topology and, in one case (lower Kansas), an artifact of sampling design, where a long stream size gradient existed but sampling was biased toward the headwater end of this gradient.

We hypothesized that catchment variables (e.g., geology or land cover) would be the least consistent in importance among sub-basins because correlation with the causative environmental variables that directly influence population vital rates may change in strength or direction from one sub-basin to another (Jiménez-Valverde et al. 2009; Saupe et al. 2012). By contrast, we expected local variables (e.g., depth or substrate size) to be causatively linked to population vital rates and therefore more consistent in their importance from one sub-basin to another. Our results provide some evidence in support of this hypothesis. For example, Catchment 1, which represented soil permeability and organic matter content, was the least consistent in importance across sub-basins and Local 1, which represented substrate diameter, was the most consistent in importance across sub-basins. Substrate characteristics are key environmental factors affecting

resource quantity and quality as well as spawning success in many stream fishes (Berkman and Rabeni 1987, Lamberti and Berg 1995) that influence population vital rates and consequent spatial variation in the distribution and abundance of species. By contrast, soil characteristics influence substrate characteristics in prairie streams (Gido et al. 2006) and therefore are indirectly related to resource availability, spawning success, and population vital rates. We suspect that variability in the strength of correlation between soil characteristics and substrate diameter among sub-basins resulted in the observed differences in predictive consistency between these two environmental predictors. Other environmental variables such as flow regime, current velocity, temperature, and resource quantity and quality are important environmental correlates of stream fish communities (Rahel and Hubert 1991; Poff and Allan 1995), but were not directly represented by the environmental variables available in our dataset. We expect these environmental variables that are directly linked to population vital rates would be most consistent in predicting the distribution and abundance of species among sub-basins. Future efforts to develop broad-scale datasets with these proximal variables or modeled predictions of these proximal variables would be useful for testing their causative link with population vital rates and their consistency in importance among sub-basins.

Spatial extent can be an important consideration when evaluating species-environment relationships (Wiens 1989; Cooper et al. 1998; Sundblad et al. 2009). We hypothesized that the importance of network position, local habitat, and catchment characteristics would change with spatial extent—a pattern documented in several studies (Ohmann and Spies 1998, Mykra et al. 2007). Indeed, the importance of network position decreased at broader spatial extents, whereas the main local and catchment variables (i.e., Local 1 and Catchment 1) were better predictors at broader spatial extents. This result was expected because long stream size gradients are represented at all spatial extents, whereas among-site variation in local and catchment variables became apparent at broader spatial extents that spanned multiple ecoregions and/or a greater portion of the east-west aridity gradient.

Conclusions

This study highlights several important considerations when developing predictive models for management and conservation purposes. First, model performance is influenced by environmental variation within the study region, but extent does not seem to influence model

performance. Second, perceived importance of environmental variables can change from one region to another, depending on network topology, drainage density, and ecoregional transitions within the study region. Moreover, the causative proximity of an environmental variable to population vital rates may influence the consistency in importance of that environmental variable among regions. Third, spatial extent can affect the perceived importance of environmental variables because network position, local conditions, and catchment conditions vary at different spatial scales. Future efforts to quantify species-environment relationships should carefully consider physiographic context and spatial extent as well as the causative proximity of environmental predictors to population vital rates, particularly when extrapolating species-environment relationships from one region to another.

References

- Allan, J.D., Erickson, D.L., Fay, J. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37, 149–161.
- Berkman, H.E., Rabeni, C.F. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18, 285–294.
- Borcard, D., Gillet, F., Legendre, P. 2011. *Numerical Ecology with R*. Springer, New York
- Cooper, S.D., Diehl, S., Kratz, K., Sarnelle, O. 1998. Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* 23, 27–40.
- Dodds, W.K., Gido, K.B., Whiles, M.R., Fritz, K.M., Matthews, W.J. 2004. Life on the edge: the ecology of Great Plains prairie streams. *BioScience* 54, 306–216.
- Esselman, P.C., Freeman, M.C., Pringle, C.M. 2006. Fish-assemblage variation between geologically defined regions and across a longitudinal gradient in the Monkey River Basin, Belize. *Journal of the North American Benthological Society* 19, 439–454.
- Esselman, P.C., Allan, J.D. 2010. Relative influences of catchment- and reach-scale abiotic factors on freshwater fish communities in rivers of northeastern Mesoamerica. *Ecology of Freshwater Fish* 19, 439–454.
- 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, 199–214.

- Gido, K.B., Guy, C.S., Strakosh, T.R., Bernot, R.J., Hase, K.J., Shaw, M.A. 2002. Long-term changes in the fish assemblages of the Big Blue river basin 40 years after the construction of Tuttle Creek reservoir. *Transactions of the Kansas Academy of Science* 105, 193–208.
- Gido, K.B., Falke, J.A., Oakes, R.M., Hase, K.J. 2006. Fish-habitat relations across spatial scales in prairie streams, in: Hughes, R.M., Wang, L.Z., Seelbach, P.W. (Eds.), *Landscape influences on stream habitats and biological assemblages*. American Fisheries Society Symposium 48, Bethesda, pp. 265–285.
- Gido, K.B., Dodds, W.K., Eberle, M.E. 2010. Retrospective analysis of fish community change during a half-century of landuse and streamflow changes. *Journal of the North American Benthological Society* 29, 970–987.
- Harig, A.L., Fausch, K.D. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12, 535–551
- Hoagstrom, C.W., Brooks, J.E., Davenport, S.R. 2011. A large-scale conservation perspective considering endemic fishes of the North American Plains. *Biological Conservation* 144, 21–34.
- Jiménez-Valverde, A., Nakazawa, Y., Lira-Noriega, A., Peterson, A.T. 2009. Environmental correlation structure and ecological niche model projections. *Biodiversity Informatics* 6, 28–35.
- Lamberti, G.A., Berg, M.B. 1995. Invertebrates and other benthic features as indicators of environmental change in Juday Creek, Indiana. *Natural Areas Journal* 15, 249–258.
- Lammert, M., Allan, J.D. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. *Environmental Management* 12, 198–203.
- Lazorchak, J.M., Klemm, D.J., Peck, D.V., editors. 1998. *Environmental monitoring and assessment program-surface waters: field operations and methods for measuring ecological condition of wadeable streams*. U.S. Environmental Protection Agency, EPA/620/R-94/004F, Washington, D.C.
- Legendre, P., Legendre, L. 1998. *Numerical Ecology*, Second English edition. Elsevier Science BV, Amsterdam, The Netherlands.
- Lyons, J., Stewart, J.S., Mitro, M. 2010. Predicting effects of climate warming on the distribution of 50 stream fishes in Wisconsin, U.S.A. *Journal of Fish Biology* 77, 1867–1898.

- Minckley, W.L. 1959. Fishes of the Big Blue River basin, Kansas. University of Kansas Publications of the Museum of Natural History 11, 401–422.
- Mykra, H., Heino, J., Muotka, T. 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* 16, 1449–159.
- Neff, M.R., Jackson, D.A. 2011. Effects of broad-scale geological changes on patterns in macroinvertebrate assemblages. *Journal of the North American Benthological Society* 30, 459–473.
- NRCS (Natural Resources Conservation Service). 1994. State soil geographic (STATSGO) database for Kansas. NRCS, Fort Worth, Texas.
- Oberdorff, T., Pont, D., Hugueny, B., Chessel, D. 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. *Freshwater Biology* 46, 399–415
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O’Hara, R.G., Simpson, G.L., Solymos, P., Henry, M., Stevens, H.H., Wagner, J. 2009. *Vegan: community ecology package*. R library. R Project for Statistical Computing, Vienna, Austria.
- Ohmann, J.L., Spies, T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68, 151–182.
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- Poff, N.L. 1997. Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16, 391–409.
- Poff, N.L., Allan, J.D. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* 76, 606–627.
- R Development Core Team. 2010. *R 2.10.1: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- 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, 319–332.

- Roberts, J.H., Hitt, N.P. 2010. Longitudinal structure in temperate stream fish communities: evaluating conceptual models with temporal data, in: Gido, K.B. Jackson, D.A. (Eds.), Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society Symposium 73, Bethesda, pp. 281–299.
- Roth, N.E., Allan, J.D., Erickson, D.L. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11, 141–156.
- Saly, P., Takacs, P., Kiss, I., Biro, P. Eros, T. 2011. The relative influence of spatial context and catchment- and site-scale environmental factors on stream fish assemblages in a human-modified landscape. *Ecology of Freshwater Fish* 20, 251–262.
- Saupe, E.E., Barve, V., Myers, C.E., Soberon, J., Barve, N., Hensz, C.M., Peterson, A.T., Owens, H.L., Lira-Noriega, A. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. *Ecological Modelling* 237, 11–22.
- Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams, in: Matthews, W.J., Heins, D.C. (Eds.), Community and Evolutionary Ecology of North American Freshwater Fishes. University of Oklahoma Press, Norman, pp. 17–28.
- Sundblad, G., Härmä, M., Lappalainen, A., Urho, L., Bergström, U. 2009. Transferability of predictive fish distribution models in two coastal systems. *Estuarine, Coastal and Shelf Science* 83, 90–96.
- Taylor, C.M. 2010. Covariation among plains fish assemblages, flow regimes, and patterns of water use, in Gido, K.B., Jackson, D.A. (Eds.), Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society Symposium 73, Bethesda, pp. 447–459.
- Taylor, C.M., Warren, M.L. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* 82, 2320–2330.
- USGS (U.S. Geological Survey). 1992. National land cover data (NLCD). USGS, Reston, Virginia.
- USGS (U.S. Geological Survey). 1997. National hydrography dataset (NHD). USGS, Reston, Virginia.

- Vander Zanden, M.J., Olden, J.D., Thorne, J.H., Mandrak, N.E. 2004. Predicting the occurrence and impact of bass introductions on temperate lake food webs. *Ecological Applications* 14, 132–148.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 130–137.
- Wang, L.Z., Lyons, J., Kanehl, P., Gatti, R. 1997. Influence of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22, 340–347.
- Wang, L.Z., Lyons, J., Kanehl, P., Bannerman, R. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management* 28, 255–266.
- Wang, L.Z., Lyons, J., Rasmussen, P., Seelbach, P., Simon, T., Wildey, M., Kanehl, P., Baker, E., Niemela, S., Stewart, P.M. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 60, 491–505.
- Wang, L.Z., Seelbach, P.W., Lyons, J. 2006. Effects of levels of human disturbance on the influence of catchment, riparian, and reach-scale factors on fish assemblages, in: Hughes, R.M., Wang, L.Z., Seelbach, P.W. (Eds), *Landscape influences on stream habitats and biological assemblages*. American Fisheries Society Symposium 48, Bethesda, pp. 199–219.
- Wenger, S. J., Olden, J.D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3, 260–267.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385–397.

Figure 3.1 Study area in Kansas located in the central United States showing the seventeen modeling units: State of Kansas, three basins, and thirteen sub-basins. See Table 3.1 for sub-basin codes. River mainstems are 4th order or larger streams.

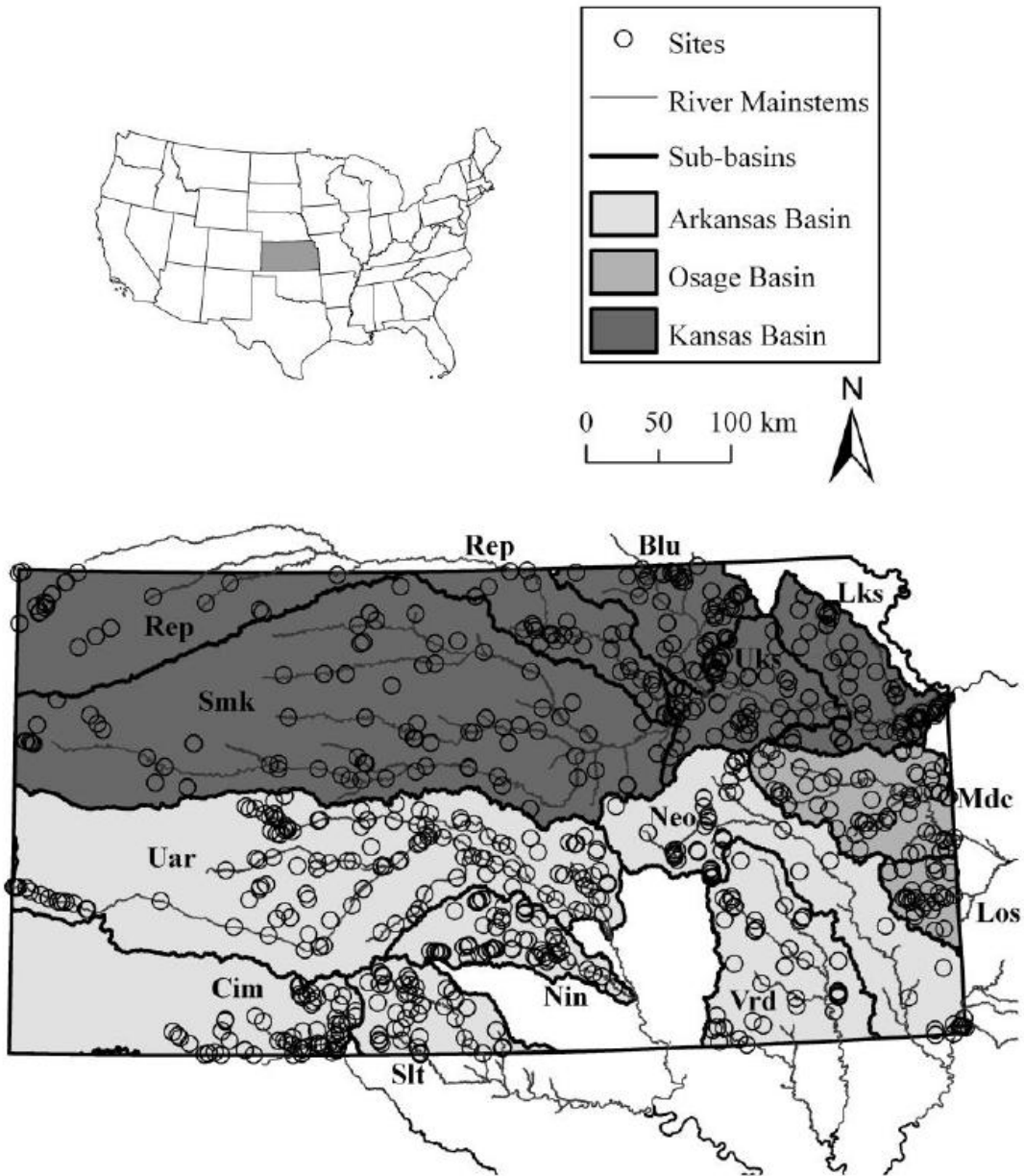


Figure 3.2 Variation in (a) network position, (b) local characteristics, and (c) catchment characteristics among 13 sub-basins. Points represent mean link magnitude (a) or mean PC axis scores (b and c) for all sample sites within a sub-basin (± 1 standard error). Horizontal and vertical axes represent 1st and 2nd PC axes, respectively for b and c. See Table 3.1 for sub-basin codes and sub-basin sample sizes.

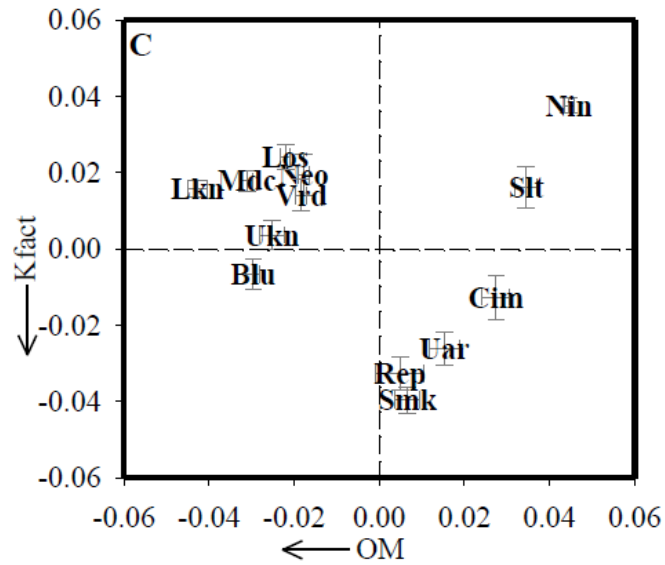
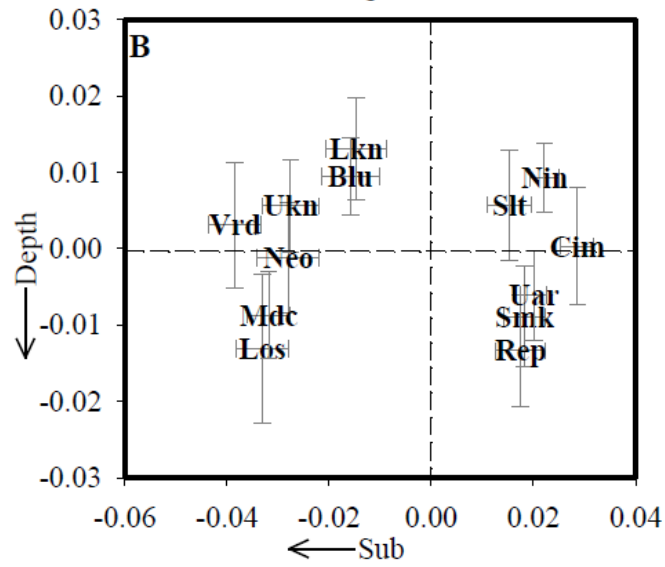
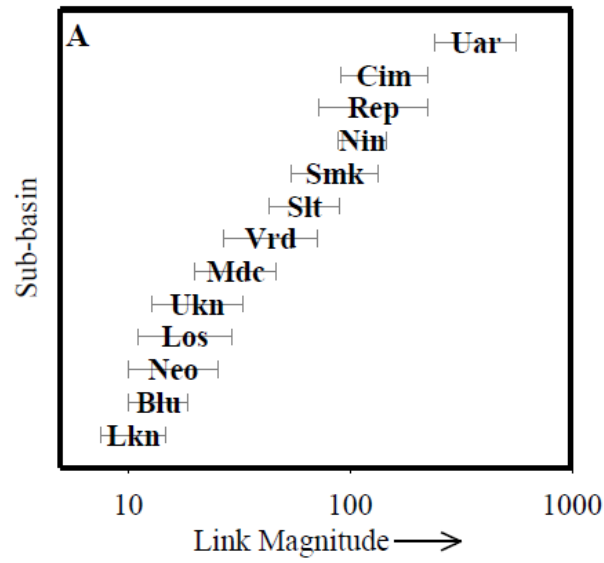


Figure 3.3 Model performance among thirteen sub-basins. Bars represent adjusted proportion of inertia constrained by all five environmental variables in a canonical correspondence analysis. All models were statistically significant based on randomization tests ($P < 0.01$).

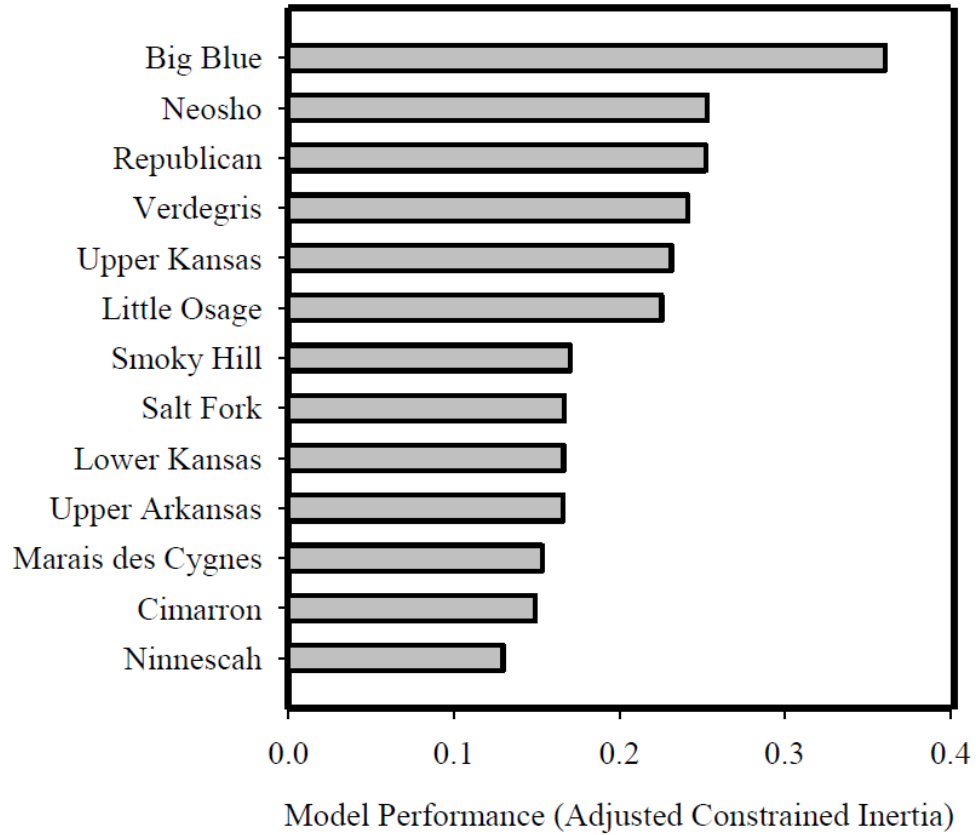


Figure 3.4 Predictive capability of five environmental predictor variables among thirteen sub-basins. Values indicate percent reduction in constrained inertia with that variable removed as an environmental constraint in a canonical correspondence analysis.

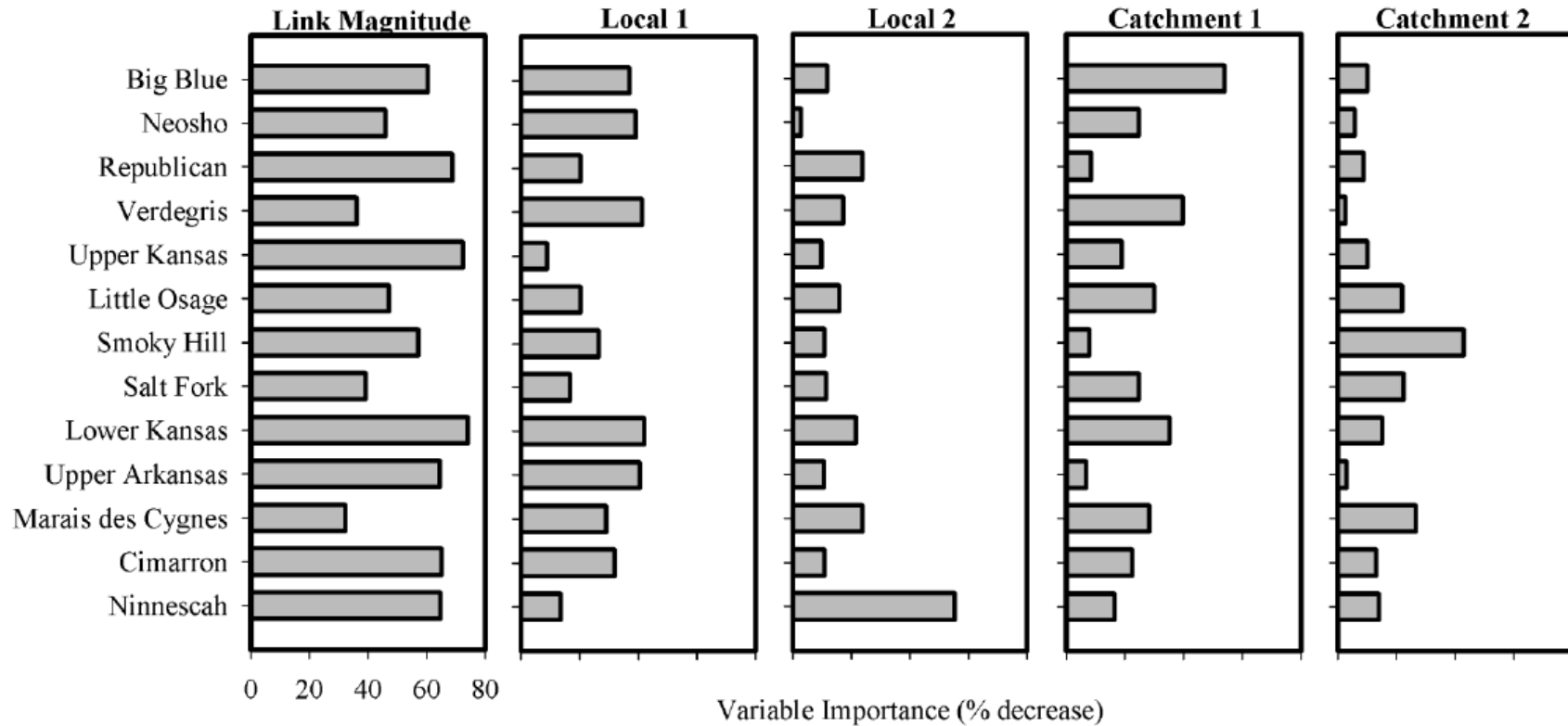


Figure 3.5 Predictive capability of environmental variables at three spatial extents: Entire state (white), three basins (light gray), and thirteen sub-basins (dark gray). Values represent percent reduction in constrained inertia with that variable removed as an environmental constraint in a canonical correspondence analysis. Error bars represent ± 1 standard error for basin (n = 3) and sub-basin (n = 13) extents.

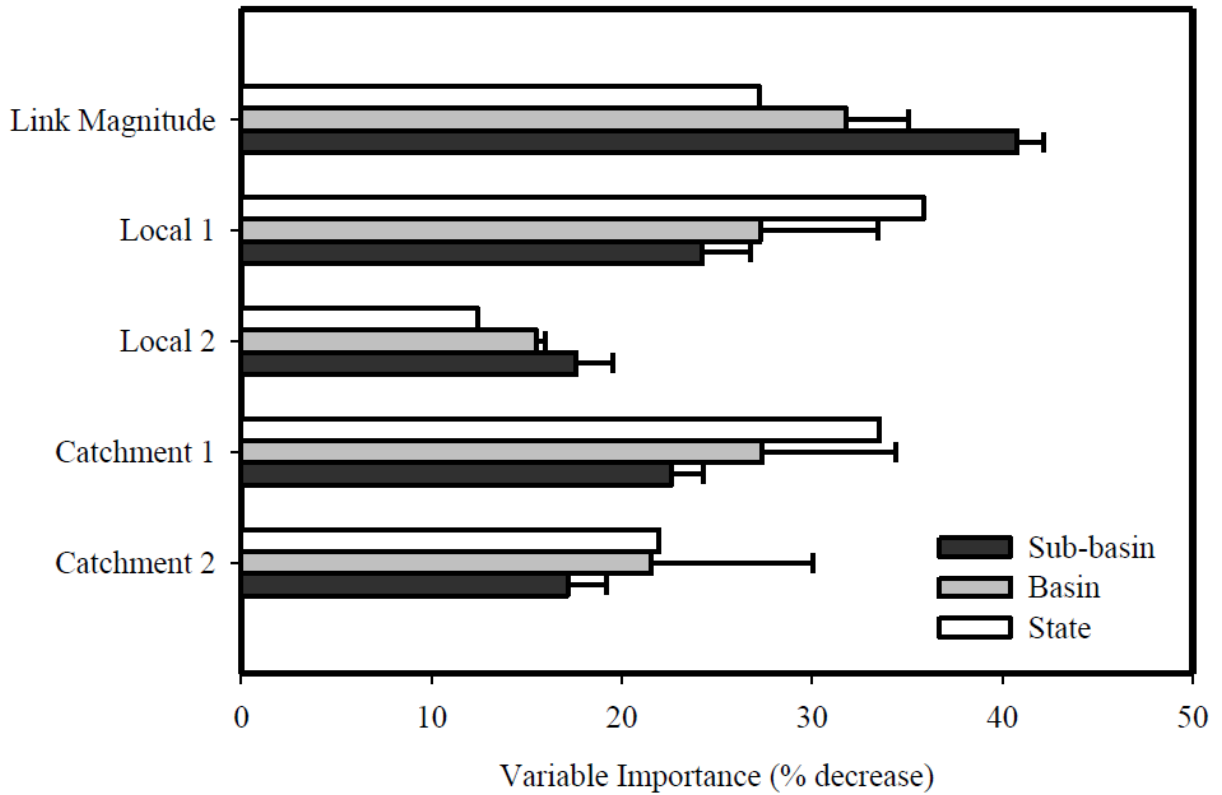


Table 3.1 Abiotic and biotic characteristics of 13 sub-basins, 3 basins, and the state of Kansas in which the fish community composition was modeled. Catchment area is only the area within the state of Kansas, does not include sub-basins removed from the analysis for the basin and state extents, and represents the spatial extent of each modeling unit.

State Basin Sub-basin	Code	Catchment Area (km ²)	Sites Sampled	Species Richness
State	Sta	195461	1038	110
Kansas	Kan	89223	398	61
Republican	Rep	19550	67	49
Smoky Hill	Smk	49027	93	47
Big Blue	Blu	6307	91	40
Upper Kansas	Ukn	7043	67	54
Lower Kansas	Lkn	7296	80	43
Osage	Osg	11086	113	66
Marais des Cygnes	Mdc	8566	77	63
Little Osage	Los	2520	36	52
Arkansas	Ark	95152	527	99
Upper Arkansas	Uar	38662	149	38
Cimarron	Cim	17133	76	27
Salt Fork	Slt	5754	68	41
Ninnescah	Nin	5910	121	55
Verdigris	Vrd	11332	46	57
Neosho	Neo	16361	67	83

Table 3.2 Twenty nine environmental predictor variables representing three categories: local characteristics, network position, and catchment characteristics.

Variable Code	Description (unit)
Local	Local
Sub	Mean substrate diameter (mm)
BL	Boulder (% of stream bed)
R	Bedrock (% of stream bed)
WD	Wood (% of stream bed)
CL	Clay (% of stream bed)
Embed	Substrate embeddedness (% coverage)
Depth	Mean depth (m)
InCov	In-channel cover (score 0-4) ^a
OverCov	Over-channel cover (score 0-4) ^b
Can	Canopy cover (% Site length)
Bank	Bank angle (°)
Slope	Segment slope (m · m ⁻¹)
WDrat	Width to depth ratio (unitless)
Network Position	Position within stream network
Link	Number of upstream segments
Catchment	Geology, soil, and land cover in upstream catchment
WTdep	Mean water table depth (m)
Kfact	Soil erodeability factor (tons · unit of rainfall erosion index ⁻¹)
Perm	Soil permeability (cm · h ⁻¹)
AWC	Soil available water capacity (%)
BD	Soil bulk density (g · cm ⁻³)
OM	Soil organic matter (% by weight)
Tfact	Soil loss tolerance factor (tons · acre ⁻¹ · year ⁻¹)
WEG	Soil wind erosion group (wind erosion)
Water	Percent of upstream catchment open water (%)
Urban	Percent of upstream catchment urban (%)
Forest	Percent of upstream catchment forest (%)
Shrub	Percent of upstream catchment shrubland (%)
Grass	Percent of upstream catchment grassland (%)
Agr	Percent of upstream catchment agriculture (%)
Wetland	Percent of upstream catchment wetland (%)

^a Filamentous algae, macrophytes, boulders, brush/ small wood (<0.3m), and large wood (>0.3m). ^b Overhanging vegetation and undercut bank.

Table 3.3 Summary of principal component analysis for the state of Kansas, three basins, and thirteen sub-basins.

Variables with strongest loading are listed for PC axis 1 and PC axis 2 for local and catchment variable sets. Proportion of total variance explained by PC axis 1 and PC axis 2 are listed.

Extent	Code	Local				Catchment			
		PC 1		PC 2		PC 1		PC 2	
		Variable	Variance	Variable	Variance	Variable	Variance	Variable	Variance
State	St	Sub	21.4	Depth	12.6	WEG	29.9	AWC	21.3
Basin	Ark	Sub	20.9	WDrat	13.3	Perm	32.2	Water	25.4
	Kan	Sub	21.3	Depth	13.7	Perm	38.6	Shrub	17.4
	Osg	Sub	20.1	Bank	15.0	WTdep	28.1	OM	22.9
Sub-basin	Blue	Sub	26.1	Depth	13.4	OM	38.5	WTdep	21.2
	Cim	WDrat	22.0	Sub	17.5	AWC	39.2	Agr	25.3
	Lkan	Sub	23.4	InCov	38.3	Perm	26.9	Tfact	18.8
	Losg	OverCov	24.7	Depth	19.6	WTdep	51.1	Grass	13.8
	MdC	Embed	22.8	Slope	16.0	Agr	28.1	WEG	24.1
	Neo	Sub	21.6	InCov	15.0	OM	40.3	Kfact	29.9
	Nin	Sub	18.1	OverCov	13.3	WEG	43.3	Agr	22.4
	Rep	Sub	19.5	InCov	16.2	Perm	43.1	AWC	22.3
	Salt	OverCov	18.9	Embed	16.8	Water	30.4	Kfact	27.5
	Smk	Sub	20.4	Can	16.5	OM	28.3	WTdep	24.2
	Uark	WDrat	18.1	Bank	14.8	Perm	32.2	BD	31.0
	Ukan	Sub	24.9	Bank	17.0	Grass	34.1	BD	23.7
	Verd	Sub	23.0	Slope	15.2	Forest	53.4	AWC	15.1

Table 3.4 Loadings of local variables on the first two principal component axes for 17 modeling units. See Tables 3.1 and 3.2 for modeling unit codes and local variable codes, respectively. Bolded values indicate highest positive and negative loadings.

Modeling Unit	PC Axis	Sub	BL	R	WD	CL	Embed	Depth	InCov	OverCov	Can	Bank	Slope	WDrat
Sta	1	-0.88	-0.20	-0.32	0.02	-0.01	-0.05	-0.02	0.15	0.01	0.00	0.12	-0.22	0.04
	2	0.22	0.04	0.06	-0.13	0.00	-0.10	0.05	0.00	-0.05	0.00	0.03	-0.94	0.20
Kan	1	-0.90	-0.23	-0.22	0.02	0.00	0.03	0.02	0.14	0.00	0.02	0.10	-0.26	0.00
	2	0.21	0.12	0.15	-0.10	0.00	0.02	0.06	-0.04	-0.10	0.11	0.09	-0.93	0.08
Rep	1	0.96	0.11	0.00	0.04	0.00	-0.07	-0.01	-0.08	0.01	0.00	-0.15	0.17	0.08
	2	0.17	0.08	0.00	-0.11	0.01	0.01	-0.05	-0.01	-0.05	0.16	0.20	-0.91	0.22
Smk	1	-0.33	-0.03	0.04	-0.04	0.00	0.00	0.01	0.02	-0.12	0.08	0.12	-0.92	-0.01
	2	0.91	0.07	0.09	-0.10	0.00	-0.05	0.00	-0.06	-0.05	-0.07	-0.10	-0.34	0.13
Blu	1	-0.77	-0.38	-0.41	0.04	0.00	-0.07	-0.02	0.20	-0.03	-0.13	-0.09	-0.12	0.06
	2	0.33	0.11	-0.87	0.05	-0.01	0.01	0.03	-0.18	0.01	-0.03	0.07	0.03	-0.27
Ukn	1	-0.56	-0.51	-0.58	0.03	0.01	0.01	-0.11	0.15	-0.01	-0.19	-0.09	-0.08	0.05
	2	0.41	0.04	-0.64	-0.09	0.01	0.14	0.29	-0.14	0.09	0.06	0.11	0.20	-0.48
Lkn	1	-0.80	-0.33	-0.40	0.06	-0.01	-0.04	-0.16	0.17	0.01	-0.02	-0.07	-0.07	0.17
	2	-0.22	-0.27	0.79	-0.04	0.01	-0.20	-0.18	0.10	-0.05	-0.35	-0.19	0.05	-0.09
Osg	1	-0.33	-0.13	-0.90	0.05	-0.01	0.04	-0.03	0.16	0.00	-0.03	-0.13	0.08	-0.14
	2	0.56	0.63	-0.34	0.15	0.01	-0.09	0.30	-0.05	-0.08	0.14	0.11	-0.09	0.04
Mdc	1	0.40	0.15	0.86	-0.13	0.00	-0.04	0.01	-0.18	0.00	-0.02	0.06	-0.09	0.14
	2	0.36	0.79	-0.29	0.14	0.00	0.00	0.31	0.03	-0.03	0.20	-0.01	-0.11	0.03
Los	1	-0.14	-0.07	-0.87	-0.18	0.00	-0.01	-0.10	0.08	-0.02	-0.19	-0.32	0.11	-0.14
	2	-0.73	0.12	0.31	-0.15	0.00	0.32	-0.27	0.15	0.20	-0.07	-0.26	-0.02	-0.14
Ark	1	0.89	0.17	0.36	-0.04	0.02	0.07	0.08	-0.15	-0.01	0.00	-0.11	0.07	-0.01
	2	0.12	-0.01	-0.10	-0.14	-0.01	-0.14	0.02	0.04	-0.03	-0.07	-0.07	-0.94	0.21
Uar	1	-0.95	-0.07	-0.03	0.13	0.00	0.01	-0.04	0.05	-0.04	0.05	0.06	0.18	-0.15
	2	0.25	0.05	0.00	0.31	0.00	0.27	-0.06	-0.02	0.11	0.08	-0.02	0.80	-0.33
Cim	1	0.23	-0.05	-0.04	-0.03	0.00	0.02	0.01	-0.01	0.00	-0.08	-0.24	-0.93	0.09
	2	-0.89	-0.13	-0.13	0.02	0.00	-0.12	-0.13	0.11	-0.12	-0.03	0.01	-0.19	0.27
Slt	1	0.59	0.10	0.59	-0.10	0.00	-0.04	0.00	-0.09	0.00	-0.07	-0.43	0.01	0.30
	2	0.46	0.01	0.00	0.14	0.00	0.04	0.06	-0.14	-0.01	0.26	0.29	0.62	-0.45
Nin	1	-0.43	0.00	-0.81	0.02	0.00	-0.08	0.02	0.07	0.01	-0.05	-0.01	-0.24	0.29
	2	-0.03	0.06	-0.25	0.07	0.00	0.02	-0.10	-0.02	0.04	0.07	0.16	0.94	0.07
Vrd	1	-0.19	-0.37	-0.21	0.02	0.08	0.24	-0.11	0.05	0.05	-0.08	0.10	0.83	-0.05
	2	-0.19	0.08	-0.90	-0.06	-0.09	-0.17	0.09	-0.03	0.03	0.01	0.18	-0.20	-0.18
Neo	1	-0.76	-0.19	-0.55	0.03	-0.02	0.02	0.11	0.15	0.06	0.01	0.08	-0.02	-0.18
	2	-0.25	-0.14	0.37	0.10	0.02	0.09	-0.07	-0.01	0.07	0.02	-0.01	0.87	-0.01

Table 3.6 Number of sub-basins occupied and correlation of log₁₀ abundance with environmental predictor variables for all species. Values represent Pearson correlation coefficients averaged across occupied sub-basins. See Appendices A and B for environmental variable loadings on derived local and catchment variables.

Species	Sub-basins Occupied	Link Magnitude	Local 1	Local 2	Catch 1	Catch 2
<i>Ambloplites rupestris</i>	1	0.15	-0.02	-0.03	0.15	-0.23
<i>Ameiurus melas</i>	13	-0.21	-0.03	0.06	-0.06	0.04
<i>Ameiurus natalis</i>	13	-0.19	0.00	0.02	0.06	0.00
<i>Aplodinotus grunniens</i>	12	0.23	-0.05	0.01	0.02	0.05
<i>Campostoma anomalum</i>	13	-0.24	-0.12	0.03	0.04	-0.12
<i>Carassius auratus</i>	4	-0.05	-0.01	-0.03	0.01	0.03
<i>Carpionodes carpio</i>	12	0.13	-0.01	-0.06	0.04	0.06
<i>Carpionodes cyprinus</i>	8	0.18	0.03	-0.04	-0.04	0.07
<i>Catostomus commersonii</i>	9	-0.10	-0.03	-0.02	-0.05	-0.07
<i>Cottus carolinae</i>	1	-0.06	-0.08	0.08	0.03	-0.13
<i>Ctenopharyngodon idella</i>	2	-0.08	0.01	0.01	-0.03	-0.22
<i>Cycleptus elongatus</i>	2	0.10	-0.01	0.02	-0.01	0.01
<i>Cyprinella camura</i>	3	0.31	0.07	-0.04	-0.05	0.28
<i>Cyprinus carpio</i>	13	0.09	0.08	0.05	0.02	-0.10
<i>Cyprinella lutrensis</i>	13	0.12	0.03	-0.02	0.04	0.07
<i>Cyprinodon rubrofluviatilis</i>	1	0.13	-0.02	-0.04	0.12	-0.20
<i>Cyprinella spiloptera</i>	1	0.20	0.00	0.07	-0.02	0.06
<i>Dorosoma cepedianum</i>	13	0.02	0.01	0.01	-0.03	0.03
<i>Erimystax x-punctatus</i>	1	0.07	-0.03	0.00	0.02	0.02
<i>Esox lucius</i>	1	0.11	0.00	-0.02	0.10	-0.15
<i>Etheostoma blennioides</i>	2	-0.02	-0.05	0.01	-0.03	-0.01
<i>Etheostoma cragini</i>	5	0.17	-0.11	-0.02	0.11	-0.11
<i>Etheostoma flabellare</i>	3	-0.05	-0.04	0.04	0.05	-0.02
<i>Etheostoma gracile</i>	1	-0.01	-0.03	-0.02	0.12	0.02
<i>Etheostoma nigrum</i>	7	-0.07	0.12	0.03	0.05	0.07
<i>Etheostoma punctulatum</i>	1	-0.11	0.02	-0.06	0.08	-0.03
<i>Etheostoma spectabile</i>	11	0.05	-0.02	0.04	0.06	-0.17
<i>Etheostoma stigmaeum</i>	1	-0.30	-0.09	0.11	0.07	-0.14
<i>Etheostoma whipplei</i>	2	0.14	-0.01	-0.05	0.13	-0.21
<i>Etheostoma zonale</i>	2	-0.01	-0.07	0.05	0.06	0.10
<i>Fundulus zebrinus</i>	7	0.15	0.00	0.04	0.07	-0.08
<i>Fundulus notatus</i>	4	-0.15	0.10	0.09	0.11	0.02
<i>Gambusia affinis</i>	13	0.01	0.05	-0.06	-0.08	0.01
<i>Hiodon alosoides</i>	1	-0.07	0.00	0.00	0.03	-0.02
<i>Hybognathus hankinsoni</i>	2	0.02	-0.11	-0.08	0.02	0.09
<i>Hybognathus placitus</i>	5	0.06	0.05	0.06	-0.12	-0.10
<i>Hypentelium nigricans</i>	1	0.21	0.07	0.03	-0.12	-0.02
<i>Ictiobus bubalus</i>	11	0.13	-0.04	0.00	0.12	-0.19
<i>Ictiobus cyprinellus</i>	9	0.24	0.09	-0.09	-0.01	0.18
<i>Ictalurus furcatus</i>	2	0.22	-0.06	-0.04	0.03	0.04
<i>Ictiobus niger</i>	9	0.10	-0.05	0.04	0.06	-0.01
<i>Ictalurus punctatus</i>	13	-0.05	-0.04	0.05	0.01	0.13
<i>Labidesthes sicculus</i>	7	0.18	0.02	0.03	0.05	0.05
<i>Lepomis cyanellus</i>	13	-0.05	0.05	0.05	-0.01	0.05
<i>Lepomis gulosus</i>	5	0.13	-0.03	-0.07	0.08	-0.03
<i>Lepomis humilis</i>	13	0.16	0.03	0.08	0.04	0.01
<i>Lepomis macrochirus</i>	13	0.10	-0.02	0.01	0.03	0.05

<i>Lepomis megalotis</i>	12	-0.28	-0.08	0.06	0.01	-0.04
<i>Lepomis microlophus</i>	5	-0.03	-0.07	-0.01	-0.03	-0.02
<i>Lepisosteus oculatus</i>	2	-0.04	0.04	0.02	0.00	0.04
<i>Lepisosteus osseus</i>	11	-0.15	-0.04	0.11	0.03	0.02
<i>Lepisosteus platostomus</i>	9	-0.03	-0.09	0.01	0.03	0.02
<i>Luxilus cardinalis</i>	1	0.02	-0.07	0.00	0.11	-0.04
<i>Luxilus cornutus</i>	8	0.01	-0.11	0.02	-0.03	-0.12
<i>Lythrurus umbratilus</i>	8	-0.14	-0.03	0.04	-0.05	-0.18
<i>Macrhybopsis hyostoma</i>	3	-0.10	0.03	0.01	0.02	0.01
<i>Macrhybopsis storeriana</i>	1	0.23	0.06	-0.03	-0.10	0.06
<i>Macrhybopsis tetranema</i>	1	0.13	-0.02	-0.03	-0.03	0.02
<i>Menidia beryllina</i>	2	0.10	0.03	0.01	-0.07	-0.02
<i>Micropterus dolomieu</i>	4	0.11	-0.03	-0.13	-0.03	-0.01
<i>Micropterus punctulatus</i>	7	0.04	0.01	0.08	0.08	-0.14
<i>Micropterus salmoides</i>	13	0.06	-0.03	0.07	0.03	0.00
<i>Minytrema melanops</i>	3	-0.22	0.01	-0.02	0.04	-0.08
<i>Morone americana</i>	1	0.06	0.07	0.07	-0.05	0.02
<i>Morone chrysops</i>	11	0.03	-0.16	-0.02	0.07	0.10
<i>Morone saxatilis</i>	1	0.10	-0.01	-0.02	0.09	-0.15
<i>Morone carinatum</i>	1	0.21	0.01	0.00	0.02	0.05
<i>Moxostoma erythrurum</i>	10	0.11	-0.11	0.02	0.07	-0.07
<i>Moxostoma macrolepidotum</i>	6	-0.04	-0.06	0.02	-0.01	0.07
<i>Moxostoma pisolabrum</i>	7	0.08	-0.01	0.09	0.00	-0.03
<i>Nocomis asper</i>	1	0.18	0.02	0.01	0.03	0.00
<i>Nocomis biguttatus</i>	2	0.11	0.00	-0.04	0.11	-0.17
<i>Notropis atherinoides</i>	9	0.08	0.07	-0.08	-0.04	0.00
<i>Notropis bairdi</i>	1	-0.13	-0.01	0.02	0.05	0.07
<i>Notropis boops</i>	2	0.22	0.03	-0.01	-0.07	0.07
<i>Notropis buccula</i>	3	0.12	-0.01	0.07	-0.01	-0.04
<i>Notemigonus crysoleucas</i>	13	0.00	-0.02	-0.09	0.13	-0.04
<i>Notropis dorsalis</i>	2	0.27	-0.07	-0.02	0.02	0.00
<i>Noturus exilis</i>	6	0.02	0.13	0.03	-0.11	0.02
<i>Noturus flavus</i>	9	0.12	-0.01	-0.03	0.12	-0.19
<i>Noturus miurus</i>	1	0.07	-0.01	0.03	0.03	-0.09
<i>Noturus nocturnus</i>	5	0.01	0.06	-0.04	-0.02	0.01
<i>Notropis nubilus</i>	1	-0.11	-0.03	-0.03	-0.02	-0.06
<i>Notropis percobromus</i>	6	0.03	0.04	0.00	0.09	-0.04
<i>Noturus placidus</i>	1	-0.10	-0.10	0.01	0.05	-0.09
<i>Notropis stramineus</i>	12	0.12	-0.01	0.00	0.05	0.00
<i>Notropis topeka</i>	4	0.00	-0.08	0.05	-0.08	0.06
<i>Notropis volucellus</i>	3	0.17	0.01	0.04	0.05	0.01
<i>Percina caprodes</i>	4	0.18	-0.10	0.00	0.07	-0.05
<i>Percina copelandi</i>	2	-0.02	0.01	0.05	0.08	0.00
<i>Perca flavescens</i>	1	-0.01	-0.08	-0.03	0.00	-0.02
<i>Percina fulvitaenia</i>	9	0.12	0.02	0.01	0.06	0.02
<i>Percina maculata</i>	1	0.06	0.01	0.02	0.03	-0.04
<i>Percina phoxocephala</i>	9	0.06	-0.06	0.13	-0.06	-0.01
<i>Percina shumardi</i>	1	0.18	0.02	0.00	0.03	0.04
<i>Phenacobius mirabilis</i>	13	0.12	-0.04	0.00	0.10	-0.08
<i>Chrosomus erythrogaster</i>	5	0.08	-0.02	-0.01	0.01	0.02
<i>Pimephales notatus</i>	12	-0.11	-0.01	0.01	-0.01	-0.01
<i>Pimephales promelas</i>	13	-0.12	0.07	0.01	0.00	-0.07
<i>Pimephales tenellus</i>	2	0.07	-0.07	-0.03	0.03	0.03
<i>Pimephales vigilax</i>	11	0.10	0.00	0.01	0.01	0.04
<i>Platygobio gracilis</i>	1	0.09	-0.04	-0.04	-0.08	0.01
<i>Polydon spathula</i>	1	-0.05	-0.02	0.20	0.04	0.02
<i>Pomoxis annularis</i>	13	0.01	0.00	0.03	0.03	0.03

<i>Pomoxis nigromaculatus</i>	10	0.09	0.00	0.01	0.01	0.02
<i>Pylodictis olivaris</i>	12	0.32	-0.01	-0.02	0.02	0.01
<i>Sander vitreus</i>	2	0.02	-0.06	0.05	0.08	-0.01
<i>Sander canadensis</i>	9	0.06	-0.04	0.03	0.02	-0.02
<i>Scaphirhynchus platorynchus</i>	2	0.32	0.14	-0.19	-0.07	0.39
<i>Semotilus atromaculatus</i>	9	-0.26	-0.02	0.01	0.03	-0.09

Chapter 4 - Towards a mechanistic understanding of fish species niche divergence along a river continuum

Abstract

Environmental niche modeling is a valuable tool but it often fails to identify causal links between environmental gradients and the individual performance currencies that drive species' distributions. Correlation between the abundances of stream fish species and longitudinal position in stream networks is well documented and is hypothesized to occur through differential environmental filtering of trophic traits. Still, trophically-similar congeners often exhibit complementary distributions along stream-size gradients, suggesting that other mechanisms are important. We present niche models to test the hypothesis that four congeneric pairs (Teleostei: Cyprinidae) exhibit complementary distributions along a gradient of stream size in the central Great Plains of Kansas, USA. Stream size was the strongest predictor of abundance compared to five other environmental variables tested and three of the four species pairs exhibited complementary distributions along a stream-size gradient. We carried out field experiments to quantify potentially causal environmental gradients (food resources, temperature, and turbidity) and four individual performance currencies (adult spawning success and juvenile survival, condition, and growth) along a stream-size gradient for one congeneric pair: *Pimephales notatus*, a tributary species and *P. vigilax*, a river mainstem species. These experiments revealed an increase in temperature and food resources with stream size, along with a corresponding increase in adult spawning success, juvenile condition, and juvenile growth for both species. We conclude that these congeners respond similarly to abiotic gradients associated with the river continuum and that complementary distributions are a consequence of biotic interactions, differential environmental filtering evident in an unmeasured performance currency, or differential environmental filtering by a direct environmental gradient operating at longer timescales.

Introduction

Environmental niche modeling offers a quantitative and objective means to identify environmental associations of species (Guisan and Thuiller 2005) and compare environmental niche differences among species (Kozak et al. 2008). The recent development of broad-scale environmental datasets (e.g., Hijmans et al. 2005), advancement of geographic information systems, and refinement of modeling algorithms (e.g., Phillips et al. 2006, Fitzpatrick et al. 2013) has accelerated the use of environmental niche models to address a variety of ecological and evolutionary questions. Most environmental niche models are correlative in that environmental predictor variables and the abundance of target species are not necessarily causally linked. For example, elevation may be an informative predictor of a species' distribution, but it is only indirectly linked to population dynamics through a correlation with temperature that directly affects individual performance. Inconsistent correlation between such direct and indirect environmental variables in time and space can reduce the transferability of niche models (Jiménez-Valverde et al. 2009). Thus, identification of direct environmental variables is necessary to understand mechanistic underpinnings of species–environment relationships and generalize prediction of species' distributions to different geographic regions or future environmental conditions. Moreover, because correlative niche models are developed from observed species' distributions that are potentially influenced by biotic interactions, environmental niche dimensions are more representative of the realized niche rather than the fundamental niche (Guisan and Thuiller 2005).

Functional traits and associated performance currencies (measured at the individual or population level) underlie the mechanisms that shape fundamental niche dimensions (McGill et al. 2006). Mechanistic (i.e., process-based) environmental niche models characterize the fundamental niche and improve upon correlative models by explicitly incorporating measures of performance along direct environmental gradients in the absence of biotic interactions (Kearney and Porter 2009). Investigators have used a variety of performance currencies to elucidate causal relationships between environmental gradients and the abundance of a species including water and energy balance, daily duration of activity, foraging energetics, and reproductive success (Kearney and Porter 2004, Crozier and Dwyer 2006, Kearney et al. 2010, Buckley et al. 2010, Thomas et al. 2012). Additionally, identifying interspecific variation in functional traits and the

shape of performance curves along direct environmental gradients may be an informative approach to identify mechanisms underlying distributional differences between species (Cooper et al. 2010, Weber and Agrawal 2012).

Complementary (i.e., opposing) distributions of closely-related congeners along environmental gradients can result from differential environmental filtering (e.g., Culumber et al. 2012) or condition-specific competitive exclusion along an environmental gradient (e.g., Taniguchi and Nakano 2000, Torres-Dowdall 2013). Because correlative niche models do not distinguish between these two mechanisms, elucidating the true drivers of interspecific niche differences can be difficult. Comparing performance–environment relationships of congeneric pairs in the absence of biotic interactions offers an informative approach to test various performance currencies as drivers of fundamental niche differences between species and may aid in the development of mechanistic niche models. Moreover, niche similarity often is correlated with evolutionary relatedness (Wiens and Graham 2005) and environmental niche divergence between congeners is often driven by the divergence of only one or several functional traits (Lai et al. 2005, Broennimann et al. 2007). As such, congeneric pairs may provide useful and relatively simple study systems for identifying the key functional traits and performance currencies driving spatial distributions.

The composition of stream fish communities is structured primarily by abiotic environmental filtering (Jackson et al. 2001) and many species vary in abundance along gradients of stream size (Horwitz 1978). Mechanistic hypotheses linking community structure to stream-size gradients for wadeable streams (i.e., 1st to 5th order streams) have generally focused on species additions, rather than species turnover, with increasing stream size. These hypotheses invoke decreasing dispersal limitation and increasing habitat area and stability downstream as causal factors for species additions (Schlosser 1987, Roberts and Hitt 2010). Decreasing species richness upstream might also result from greater resistance to upstream dispersal against the current in high-gradient streams (Grossman et al. 2010). When considering longer stream-size gradients (i.e., 1st to 9th order streams), species replacements become more common (Matthews 1986, Rahel and Hubert 1991) and two mechanistic hypotheses might explain this turnover. First, in streams draining high elevations or arising from springs, strong temperature gradients result in turnover from cold-water assemblages at high elevations or in headwater springs, to cool-water assemblages in mid-order streams, and finally to warm-water assemblages in river mainstems

that are at low elevations or are far from headwater springs (Rahel and Hubert 1991, Lyons et al. 2009). Secondly, gradual changes in resource type and origin (Vannote et al. 1980) promotes turnover in the trophic composition of fish communities from benthic invertivores and herbivores in headwater streams to detritivores and planktivores in river mainstems. Ibañez et al. (2009) provided empirical support this hypothesis and demonstrated its global generality, showing that invertivorous fishes decreased and detritivorous fishes increased in relative abundance from upstream to downstream across four continents. Despite the empirical evidence of resource and temperature gradients driving species turnover, many investigators have noted cases of trophically-similar warm-water congeners occupying complementary stream-size niches. For example, congeneric topminnow species (Teleostei: Fundulidae) *Fundulus notatus* and *F. olivaceus*, occupy tributaries and river mainstems, respectively, in the Mississippi River basin (Braasch and Smith 1965, Schaefer et al. 2011). Similarly, Taylor and Lienesch (1996) described the tributary and river mainstem preferences of *Lythrurus snelsoni* and *L. umbratilis* (Teleostei: Cyprinidae), respectively, in the Ouachita Mountains of southeastern Oklahoma, USA. These observations suggest that turnover in warm-water stream fish communities is a consequence of direct environmental gradients (other than resources and temperature) differentially filtering congeners or condition-specific competitive exclusion by competitors.

The Flint Hills ecoregion of the central Great Plains in Kansas, USA are drained by streams with abiotic gradients that strongly influence the distribution of stream organisms (Dodds et al. 2004, Gido et al. 2006). Cross (1967) provided a qualitative description of stream-size preferences of four congeneric pairs of minnows (Cyprinidae) in the Flint Hills, noting that each pair exhibited a complementary distribution along a stream-size gradient. In particular, *Cyprinella camura*, *Notropis percobromus*, *Notropis topeka*, and *Pimephales notatus* prefer tributaries, whereas their respective congeners, *Cyprinella lutrensis*, *Notropis atherinoides*, *Notropis stramineus*, and *Pimephales vigilax*, prefer river mainstems. Although two of these pairs are both in the genus *Notropis*, they reside in divergent phylogenetic clades that differ morphologically (Schmidt and Gold 1995, Bielawski and Gold 2001). We developed environmental niche models for these eight species to quantify environmental correlates of their distributions and test for complementary distributions between congeners along a stream-size gradient. We predicted that stream size would be the strongest environmental correlate of abundance compared to other environmental gradients and that congeners would exhibit

complementary relationships. To test for differential environmental filtering as a mechanism for one congeneric pair, we used field experiments to quantify four individual performance currencies (adult spawning success and juvenile survival, condition and growth) along a stream-size gradient. *Pimephales notatus* was the hypothesized tributary species and *P. vigilax* the hypothesized river mainstem species. We predicted that one or more of these individual performance currencies would decrease with stream size for *P. notatus* and increase for *P. vigilax*.

Methods

Environmental Niche Models

Environmental niche models for eight species (four congeneric pairs) were developed at the extent of the Flint Hills EPA Level III ecoregion, Kansas, USA (Figure 4.1). The Flint Hills are drained by the Kansas River in the north and the Arkansas River in the south and historical distributions of the eight study species are well documented in this region (Gido et al. 2010). Six of the species (*C. lutrensis*, *N. percobromus*, *N. atherinoides*, *N. topeka*, *N. stramineus*, and *P. notatus*) are native to both river basins and one species (*Cyprinella camura*) is native only to the Arkansas River basin. *Pimephales vigilax* is native only to the Arkansas River basin but also occurs in the Kansas River basin, having been introduced between 1967 and 1995 (Cross and Collins 1995). Densities (number per m²) of these species were based on collections from 221 different sites sampled one time each by the Kansas Department of Wildlife, Parks, and Tourism (KDWPT) Stream Monitoring Program between 1995 and 2008. Site lengths were 40 times the mean wetted width, with lower and upper limits of 150m and 300m, respectively. A combination of straight and bag seines (4.7-mm mesh) and DC-pulsed backpack or tote-barge electrofishing were used to capture fish and effort was standardized (i.e., one pass for each gear type) across all sites. Bertrand et al. (2006) compared estimates of relative abundance of minnows in prairie streams based on one- and three-pass electrofishing and showed that one-pass estimates of relative abundance were highly concordant with three-pass estimates.

Twenty three environmental variables were screened for use as predictors of species abundance including: ten site-scale variables measured at the time of fish sampling, two GIS-derived segment-scale variables, and eleven GIS-derived catchment-scale variables (Appendix A). Previous studies have demonstrated the utility of these environmental variables for predicting

stream fish distributions in the Great Plains (Gido et al. 2006, Troia and Gido 2013). Environmental variables were checked for normality and \log_{10} -transformed prior to analysis if necessary to reduce heterogeneous variances. To identify the predominant, non-covarying environmental gradients within the study area we selected environmental variables that loaded most strongly (i.e., greatest absolute value) on interpretable (based on broken stick models; Borcard et al. 2011) Principal Components Analysis (PCA) axes. This approach ensured that main environmental gradients in the study area were included as potential predictors and allowed us to evaluate the predictive capability of stream size relative to other potential predictors (Borcard et al. 2011). We included basin as a nominal predictor variable in the niche models for the seven species that occur in both the Kansas and Arkansas River basins to account for disparate biogeographic histories of the populations in these basins. For the *Cyprinella camura* model, we used only sites from the Arkansas River basin (101 sites) and basin was not used as a predictor variable.

We used generalized additive models (GAM) to quantify relationships between species' densities and the reduced set of environmental variables described above. GAM uses a link function to establish a relationship between the mean of the response variable and a 'smoothed' function of the explanatory variable(s) allowing for the detection of non-linear relationships between predictor variables and a response variable (Guisan et al. 2002). We fit separate models for each species using all five or six environmental predictors. We assessed (1) model performance using percent of deviance explained and (2) predictive capability of each environmental variable by measuring the percent reduction in deviance explained with that variable removed from the model relative to a model containing all predictor variables (see Troia and Gido 2013). Non-linear relationships between species' densities and link magnitude (a measure of stream size) were visualized with cubic regression splines and 95% confidence bands (Zuur et al. 2009). Niche modeling was performed in R (version 2.13.1; R Development Core Team, Vienna, Austria) using the *vegan* (Oksanen et al. 2009) and *mgcv* (Wood 2006) libraries.

Field Experiments

We carried out two field experiments to test for variation in adult spawn success (Experiment 1) and juvenile survival, condition, and growth (Experiment 2) along a stream-size gradient for *P. notatus* and *P. vigilax*. We selected this congeneric pair because they attach

adhesive eggs to the bottom side of crevices (Pflieger 1997), making assessment of spawning success in field enclosures feasible (Figure 4.2A–B). Treatments crossed species (*P. notatus* or *P. vigilax*) and stream size (2nd, 4th, or 8th order stream; hereafter referred to as small, medium, and large streams) in a 2 x 3 factorial design. Experiments were carried out in enclosures (91cm length x 61cm width x 76cm height) constructed of a pine wood frame and hardware cloth (3mm mesh) on the sides and bottom, and secured to the streambed with steel rebar (Figure 4.2C). Enclosures were placed in Kings Creek, a 2nd order tributary of the Kansas River, Wildcat Creek, a 4th order tributary of the Kansas River, and the Kansas River proper, an 8th order river mainstem in the Flint Hills, Riley County, Kansas, USA (Figure 4.1). This gradient spanned two and four orders of magnitude in mean annual discharge and catchment area, respectively (see Table 4.1 for site characteristics). Enclosures were placed in streams 5 to 10 days prior to the start of the experiments to facilitate algae accrual, organic matter accumulation, and macroinvertebrate colonization. Enclosures were placed in mesohabitats with depths (18.5–30.0 cm) and current velocities (0.0 m/s) similar to those used by reproductively active adults in early summer and juveniles in late summer (Troia and Gido, unpublished data).

Experiment 1 – Spawning Success

Experiment 1 consisted of two 10 day runs starting on 5 June 2012 and 20 June 2012. For each run five or six enclosures per treatment were stocked with one age-1 male and three age-1 females. Only reproductively active individuals, determined from the presence of breeding tubercles on males and an exterior ovipositor on females (Flickinger 1969), were used. Mean eviscerated male wet mass was 3.5g and 3.7g for *P. notatus* and *P. vigilax*, respectively and did not differ significantly between species or among stream sizes (Table 4.2). Eviscerated female mass was significantly lower for *P. vigilax* (mean = 1.3g) compared to *P. notatus* (mean = 1.4g) but did not differ significantly among stream sizes for either species. *Pimephales notatus* were collected using DC-pulsed backpack electrofishing from Deep Creek, a 4th order tributary of the Kansas River in Riley County, Kansas. *Pimephales vigilax* were collected using the same gear from the Kansas River proper also in Riley County. At the time of enclosure deployment, one artificial spawning crevice was placed in each enclosure. Spawning crevices were constructed from unglazed ceramic tiles (15cm length x 15cm width) suspended 4.5cm above the enclosure bottom with pine board sides (1.5cm width x 4.5cm height x 15cm length) (Figure 4.2A).

Enclosures were observed daily and spawning crevices were checked for eggs, photographed if present, and returned to the enclosure (Figure 4.2B). After 10 days, fish were removed from each enclosure, euthanized with a lethal dose of MS-222 (tricane methanesulfonate), and fixed in buffered 10% formalin. In the laboratory, standard length and eviscerated wet mass of each individual was measured. Maximum egg count over the duration of each run for each enclosure was determined by counting eggs in photographs and spawn success was calculated as maximum egg count \cdot g of wet eviscerated female mass⁻¹ \cdot d⁻¹. Water temperature was recorded hourly at each site for the full duration of each run with a Hobo temperature logger (Onset Computer Corporation, Bourne, MA, USA) and turbidity was recorded hourly from 12 to 14 June and 28 to 30 June with a YSI turbidity probe (Yellow Springs Instruments, Yellow Springs, Ohio, USA).

Experiment 2 – Juvenile Survival, Growth, and Condition

Experiment 2 started on 30 August 2012 and lasted 30 days. Five or six enclosures per treatment were stocked with five age-0 *P. notatus* or *P. vigilax*. This density is lower than ambient densities observed for both species in Flint Hills streams and was chosen to limit the effect of density-dependent survival, condition and growth (Troia and Gido, unpublished data). *Pimephales notatus* and *P. vigilax* were collected with a seine from Deep Creek and the Kansas River proper, respectively. Length-frequency histograms were used to identify cohorts for each species and individuals nearest to the mean standard length of the age-0 cohort were selected for the experiment. All fish were photographed from above for measurement of standard length at the start of the experiment. Starting length was significantly higher for *P. notatus* (mean = 38.7mm standard length) compared to *P. vigilax* (mean = 30.5mm standard length). *Pimephales vigilax* did not differ significantly in starting length among stream sizes but mean starting length of *P. notatus* was approximately 3 mm lower in the large stream (mean = 37.3mm standard length) compared to the small stream (mean = 40.2mm standard length) (Table 4.2). Three plastic baskets (10cm length x 10cm width x 10cm height, 2cm x 1.25cm mesh size) filled with streambed substrate were placed in each enclosure at the time of enclosure deployment to facilitate algae growth, retention of organic matter, and colonization by macroinvertebrates. Substrates were harvested from the streambed within 2 m of enclosures to match the substrate diameter representative of each stream size.

Enclosures were observed daily and dead individuals were removed and photographed for measurement. Because mortality was low throughout the experiment (two or fewer deaths per enclosure) and stocked density was lower than natural densities, we assumed density-dependent survival, growth, and condition did not decrease in enclosures with mortality and therefore did not replace dead individuals. After 30 days, all individuals were removed from each enclosure, photographed for measurement, euthanized, and fixed in formalin. Survival was quantified for each enclosure as the proportion of the five individuals surviving to day 30 and daily survival rate was quantified as the 30th root of the proportion of individuals surviving to day 30. Standard length of all individuals at the start and end of the experiment was measured to the nearest 0.1mm using the overhead photographs and the polyline measuring tool in ImageJ software (National Institute of Health, Bethesda, Maryland, USA) Daily growth rate was measured as the difference in standard length between the start and end of the experiment divided by thirty days. To quantify condition, we extracted storage lipids and measured content (% of eviscerated body mass). Each individual was eviscerated, dried in an oven for at 40°C for 72 hours, and weighed to the nearest 0.1mg. To extract storage lipids, each individual was rinsed four times for 3 days in 20mL of petroleum ether. Lipid-extracted individuals were dried again at 40°C for 72 hours and weighed. Lipid content was calculated as the percent decrease in mass from the initial dry mass to the lipid-extracted dry mass (Heulett et al. 1995). Daily growth rate and lipid content were averaged for all individuals from the same enclosure and means from each enclosure were used as sample replicates in statistical analyses.

To evaluate if abundance of food resources varied among treatments, benthic algal biomass (chlorophyll-*a*), percent coverage of filamentous algae, benthic organic matter (BOM), benthic macroinvertebrate abundance, and pelagic zooplankton abundance were measured at the end of the experiment. Percent of the enclosure bottom covered by filamentous algae was visually estimated by calculating the percent of fifty-four 10 x 10cm grid cells overlaid on the enclosure bottom that contained filamentous algae. Chlorophyll-*a* was measured by collecting three rocks from each plastic basket. Rocks were placed in an autoclavable bag, submerged in 95% ethanol, heated in a water bath to 78°C for five minutes, and incubated in complete darkness for twelve hours to extract chlorophyll-*a*. Concentration of chlorophyll-*a* was measured with a spectrophotometer (Hitachi, Tokyo, Japan) and standardized by surface area of the three rocks (Steinman et al. 2006). The substrate remaining in the baskets was placed in a bucket

containing 6L of water and agitated to suspend and homogenize organic matter after which a 0.5L water sample was collected and preserved in 10% formalin for measurement of BOM. The remaining material in the bucket was elutriated 3-6 times and passed through a 250 μ m mesh sieve to capture macroinvertebrates, which were preserved in 10% formalin. To quantify zooplankton density, twelve liters of water from each enclosure was passed through a 47 μ m-mesh sieve to capture zooplankton, which were preserved in 10% formalin. In the laboratory, BOM was quantified as ash-free dry mass of the 0.5L sample retained after filtering through a glass fiber filter (Gelman A/E) (Lamberti and Gregory 2006). Zooplankton and benthic macroinvertebrates were identified to order, measured for length, and counted (Merritt et al. 2008). Only benthic macroinvertebrates <4mm were counted because gape limitation prevented consumption of larger prey items in both species. Water temperature was recorded hourly for the entire duration of Experiment 2 and turbidity was recorded hourly from 26 to 28 September at each experimental site.

Experimental Data Analysis

We used two-way analysis of variance (ANOVA) to test for differences in male and female eviscerated wet mass between species (*P. notatus* and *P. vigilax*) and among stream sizes (small, medium, and large) in Experiment 1 and length of juveniles at the start of Experiment 2. We used one-way ANOVA to test for differences in substrate diameter, benthic organic matter, chlorophyll-*a*, filamentous algae, benthic macroinvertebrate density, and zooplankton density in Experiment 2. Two-way ANOVA was used to test interspecific and site differences in the four main response variables: spawning success in Experiment 1 and juvenile survival, condition, and growth in Experiment 2. Because spawning success and juvenile survival did not meet the assumption of normality, we used generalized linear models (GLM) with Poisson distributions in addition to two-way ANOVA (Zuur et al. 2009). Interpretation of results for GLMs and two-way ANOVAs did not differ so we presented the parameters from the two-way ANOVAs for all four response variables for consistency. Pair-wise differences among treatments were assessed with Tukey's Honestly Significant differences post-hoc tests. All experimental statistical analyses were performed in R (version 2.10.1; R Development Core Team, Vienna, Austria).

Results

Environmental Niche Models

The first five principal component axes were interpretable based on broken stick models and explained 73.4% of the variance in the environmental dataset. The reduced set of environmental predictor variables taken from the PCA included algae, macrophyte, and large wood cover; link magnitude (a measure of stream size); and percent agriculture in the catchment (Appendix A). Pearson correlation coefficients between pairs of predictors were ≤ 0.3 indicating low correlation among these predictors.

All niche models but one (*N. topeka*) revealed statistically significant ($P < 0.05$) relationships between fish density and environmental gradients in the Flint Hills. Model performance (% deviance explained) ranged from 17.9% for *N. topeka* to 43.9% for *P. vigilax* and link magnitude was a statistically significant predictor of density for all species (Table 4.3). Predictive capability (% reduction in model performance) averaged across all species was highest for link magnitude, followed by percent agriculture, macrophytes, large wood, algae, and basin (Figure 4.3). The low predictive capability of basin indicates that any inter-basin differences in stream size niche dimensions are negligible for the seven species that occur in both basins. Estimated smoothing curves revealed strong complementary relationships between density and stream-size for congeneric pairs (Figure 4.4). *Cyprinella camura* peaked in density in medium-sized streams (link magnitude of 100), whereas density of *C. lutrensis* was low in small streams and peaked in medium- to large-sized streams (link magnitude 100 to 1000). Density of *N. percobromus* peaked in medium-sized streams (link magnitudes 50 to 100), whereas *N. atherinoides* was absent in small to medium-sized streams and increased in density linearly at link magnitudes greater than 100, peaking in density in the largest rivers (e.g., Kansas River). *Notropis stramineus* density increased linearly with stream size, and peaked in the largest rivers. Density of *P. notatus* peaked in small to medium-sized streams (link magnitudes 50 to 100), whereas density of *P. vigilax* increased linearly with stream size and peaked in the largest rivers in the Flint Hills.

Field Experiments

Experiment 1 –Spawning Success

Mean water temperature and turbidity increased with stream size (Table 4.1). Spawning success did not differ between the first and second experimental run (ANOVA, $F_{1,62} = 0.04$, $P = 0.85$). Spawning success ranged from 0 to 72.7 ova · gram of somatic female mass⁻¹ · d⁻¹ and was higher for *P. vigilax* (mean = 14.1) than for *P. notatus* (mean = 1.6). There was a significant stream size and species effect. Spawning success did not differ among stream sizes for *P. notatus*, but was significantly higher in the large stream compared to the small stream for *P. vigilax* (Table 4.4, Figure 4.5A), as predicted from the niche model.

Experiment 2 – Juvenile Survival, Growth, and Condition

In general, resource availability (benthic organic matter and macroinvertebrate density) and temperature increased with stream size; however, zooplankton density decreased with stream size and filamentous algae cover was higher in the medium-sized stream compared to the small and large streams. Chlorophyll-*a* did not differ among stream sizes (Table 4.1). Contrary to expectations and attributed to drought conditions, turbidity was highest in the small stream. Substrate diameter was lowest in the large stream, but larger in the medium-sized stream than the small stream (Table 4.1).

Daily survival of juveniles was high, ranging from 0.97 to 1.00, and did not differ significantly between species or among stream sizes (Table 4.4, Figure 4.5B). Daily growth rate ranged from 0% to 1.27% and was higher in the large stream than other sites but was not different between species (Table 4.4, Figure 4.5C). Storage lipid content of juveniles ranged from 0.006% to 0.278% of eviscerated dry somatic mass and differed significantly among stream sizes and between species. Lipid content of *P. notatus* was greater in the large stream compared to the small stream. For *P. vigilax*, lipid content did not differ significantly between the small and medium-sized streams, but was greater in the large stream compared to small and medium-sized streams (Table 4.4, Figure 4.5D).

Discussion

Complementary Distributions of Congeners

Our environmental niche models and field experiments confirmed that stream size is a strong environmental correlate of species abundances' and individual performance throughout the Flint Hills. This result is consistent with conceptual models (Vannote et al. 1980, Schlosser

1987) and empirical studies (Horwitz 1978, Rahel and Hubert 1991, Ibañez et al. 2009, Roberts and Hitt 2010). Although a large proportion of the variance in abundance of these species remained unexplained by environmental predictors (56.1 to 82.1%), all but one of these relationships were highly significant and the unexplained variation was likely due to sampling error and our inability to control for the temporal stochasticity in fish abundance that is common in prairie streams (Franssen et al. 2006), given the thirteen year time span during which surveys were conducted. The weakest response to stream size by *N. topeka*, was likely because the rarity of this species in our study area (11% of sites occupied) reduced the power of analysis.

Nevertheless, recently published niche models for *N. topeka* have documented a decrease in site occupancy with stream size (Wall et al. 2004, Gerken and Paukert 2013), supporting the stream-size preference described by Cross (1967) and our hypothesis that *N. topeka* exhibits a complementary distribution with its congener, *N. stramineus*. This repeated pattern of stream-size niche complementarity between congeners shown in the current study and for other congeners in eastern North America (e.g., Braasch and Smith 1965, Taylor and Lienesch 1996) suggests that a general, yet poorly understood mechanism underlies the distribution of fishes in stream networks.

Complementary stream size niches of congeners may be a consequence of differential environmental filtering or condition-specific competitive exclusion. Our field experiments did not support the hypothesis of differential environmental filtering because individual performance was consistently higher in river mainstems compared to headwaters for both species. Several potentially direct environmental gradients probably contributed to this positive relationship between performance and stream size. Temperature increased with stream size in both of our field experiments as expected (Vannote et al. 1980) and is causally linked to juvenile growth and condition (Schultz and Bonar 2009) as well as adult spawning success (Dorts et al. 2012). Detritus and benthic macroinvertebrates also increased with stream size during the juvenile performance experiments. Because *P. notatus* and *P. vigilax* forage on benthic resources (Pflieger 1997), this may also have contributed to greater growth rates and body conditions in both of these species in the river mainstem (Heulett et al. 1995). Turbidity generally increases with stream size (Vannote et al. 1980) and we observed this in the adult reproduction experiment. Turbidity was probably not directly related to adult spawning success because both species spawned more successfully in the more turbid river mainstem, yet both species of

Pimephales rely on visual courtship displays (Pflieger 1987). Increasing turbidity has been shown to reduce spawning success in other cyprinids that use visual courtship displays (Burkhead and Jelks 2001).

Whereas our field experiments do not support the hypothesis of differential environmental filtering, we cannot reject this as a mechanism for stream-size niche complementarity. Two additional environmental gradients, which could not be evaluated with our field experiments, may differentially filter *P. notatus* and *P. vigilax*. First, hydrologic stability increases with stream size and results in the filtering of poor colonizers from headwaters (Schlosser et al. 1987). This filter operates at seasonal and interannual timescales and did not affect performance currencies measured over the ten and thirty day durations of our field experiments. Nevertheless, this mechanism of community assembly predicts species additions moving downstream, which is not supported by our correlative niche models that show tributary species declining in abundance with stream size. Second, predator density tends to increase with stream size (Goldstein and Meador 2004), but our results represent performance in the absence of predation. Predation can strongly and directly affect survival through consumption (Schlosser 1988). Indirect effects of predation include reduced foraging and changes in microhabitat use which may reduce spawning success and growth rates in prey species (Fraser and Gilliam 1992). Such lethal and nonlethal effects of predation can strongly influence the distribution of prey species along gradients of stream size (Gilliam et al. 1993) and are highly variable among prey and predator species (Hoeinghaus and Pelicice 2010). Previous experiments did not detect differences in susceptibility to predation by largemouth bass (*Micropterus salmoides*) between two tributary species (*P. notatus* and *N. topeka*) and a mainstem species (*C. lutrensis*) (Knight and Gido 2005). Prey response might differ when subjected to other predator species that are more common in river mainstems of the Flint Hills (e.g., Ictalurid catfishes), thus we cannot eliminate predation as a possible filtering mechanism. Lastly, although these species are trophically-similar (Franssen and Gido 2006), other aspects of resource acquisition could differ between *P. notatus* and *P. vigilax* (and the other congeneric pairs). Morphologically-similar congeners often exploit the same resources but acquire these resources using distinct behavioral adaptations that differ in efficiency between environments (Knickle and Rose 2013).

Condition-specific competitive exclusion, in which competitive dominance between two species differs depending on one or more environmental factors, could also create

complementary distributions. This mechanism has been demonstrated in congeneric charrs (*Salvelinus species*) in Japan where a temperature gradient associated with shifts competitive superiority such that the high elevation species performs better at lower temperatures and the low elevation species performs better at higher temperatures (Taniguchi and Nakano 2000). Our experimental results represent performance in the absence of interspecific competition and would not detect this mechanism. Manipulative or natural (if possible) experiments testing for condition-specific competition of our study species, particularly along gradients of temperature and turbidity, would elucidate the importance of this mechanism in driving the complementary distributions of these species. Overall, our study eliminates several potential environmental filtering mechanisms driving complementary distributions and has isolated several other environmental filters and biotic interactions that merit further investigation.

An Analytic Framework for Mechanistic Niche Modeling

Our study demonstrates the utility of a three step analytic framework to develop mechanistically-based environmental niche models (Figure 4.6). First, correlative environmental niche models offer a quantitative and objective approach to identify congeners with complementary distributions and candidate environmental gradients which can be tested as direct environmental predictors. We demonstrate this first step with stream fishes and show that congeneric pairs exhibit complementary distributions along an indirect and very complex gradient of stream size. Second, experimental evaluations can be used to quantify performance currencies along direct environmental gradients to identify which performance currencies are informative with regard to characterizing fundamental niche dimensions. Using reciprocal transplant field experiments, we demonstrate that several performance currencies differ in their response to environmental gradients. Juvenile survival did not vary with stream size whereas juvenile growth rate, condition, and adult spawn success increased with stream size. These findings indicate that some performance currencies are informative whereas others are not, which demonstrates the necessity of evaluating multiple performance currencies representing a variety behaviors (e.g., mate courtship, foraging) and physiological processes (e.g., gonadogenesis, somatic growth) associated with multiple life history events (e.g., reproduction, juvenile recruitment). Our experiments suggested that two stream fish species have similar fundamental niches and point toward further experiments to test for other abiotic filters,

condition-specific competition, or predation susceptibility. Our experiments eliminated resources availability, temperature and turbidity as factors driving complementary distributions, and suggest future investigations should focus on condition-specific competition along these gradients or other environmental filters (e.g., predation) that might differentially limit abundances of these species.

Developing mechanistically-based environmental niche models is an essential task for basic ecology and biodiversity conservation (Guisan and Thuiller 2005, Kearney and Porter 2009), yet natural environmental gradients (e.g., stream-size gradients) are often complex. By combining niche modeling with mechanistic experiments, we have begun to untangle some of the complex drivers of a frequently-observed pattern of turnover in species composition across a stream-size gradient. Building upon these experiments and refining mechanistic models will help to generalize prediction of species' distributions to different geographic regions or future environmental conditions.

References

- Bertrand, K.N., K.B. Gido, and C.S. Guy. 2006. An evaluation of single-pass versus multiple-pass backpack electrofishing to estimate trends in species abundance and richness in prairie streams. *Transactions of the Kansas Academy of Science* 109:131d–138.
- Bielawski, J.P. and J.R. Gold. 2001. Phylogenetic relationships of cyprinid fishes in subgenus *Notropis* inferred from nucleotide sequences of the mitochondrially encoded cytochrome *b* gene. *Copeia* 2001:656–667.
- Borcard, D., F. Gillet, and P. Legendre. 2011. *Numerical Ecology with R*. Springer, New York.
- Braasch, M.E. and P.W. Smith. 1965. Relationships of the topminnows *Fundulus notatus* and *Fundulus olivaceus* in the Upper Mississippi River Valley. *Copeia* 1965:46–53.
- Broennimann, O., U.A. Treier, H. Muller-Scharer, W. Thuiller, A.T. Peterson, and A. Guisan. 2007. Evidence of climate niche shift during biological invasion. *Ecology Letters* 10:701–709.
- Buckley, L.B., M.C. Urban, M.J. Angilletta, L.G. Crozier, L.J. Rissler, and M.W. Sears. 2010. Can mechanism inform species distribution models? *Ecology Letters* 13:1041–1054.

- Burkhead, N.M. and H.L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. *Transactions of the American Fisheries Society* 130: 959–968.
- Carlander, K. D. 1977. *Handbook of freshwater fishery biology*. The Iowa State University Press, Ames.
- Cooper, N., W. Jetz, and R.P. Freckleton. 2010. Phylogenetic comparative approaches for studying niche conservatism. *Journal of Evolutionary Biology* 23:2529–2539.
- Cross, F.B. 1967. *Handbook of the Fishes of Kansas*. University of Kansas, Lawrence Kansas, USA.
- Cross, F.B. and J.T. Collins. 1995. *Fishes in Kansas, Second Edition*. University Press of Kansas, Lawrence, Kansas.
- Crozier, L. and G. Dwyer. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist* 167:853–866.
- Culumber, Z.W., D.B. Shepard, S.W. Coleman, G.G. Rosenthal, and M. Tobler. 2012. Physiological adaptation along environmental gradients and replicated hybrid zone structure in swordtails (Teleostei: Xiphophorus). *Journal of Evolutionary Biology* 25:1800–1814.
- Dodds, W.K., K.B. Gido, M.R. Whiles, K.M. Fritz, and W.J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54:205–216.
- Dorts, J., G. Grenouillet, J. Douxfils, S.N.M. Mandiki, S. Milla, F. Silvestre, and P. Kestemont. 2012. Evidence that elevated water temperature affects the reproductive physiology of the European bullhead *Cottus gobio*. *Fish Physiology and Biochemistry* 38:389–399.
- Fitzpatrick, M.C., N.J. Gotelli, and A.M. Ellison. 2013. MaxEnt versus MaxLike: empirical comparisons with ant species distributions. *Ecosphere* 4:1–15.
- Flickinger, S.A. 1969. Determination of sexes in the Fathead Minnow. *Transactions of the American Fisheries Society* 98:526–527.
- Franssen, N.R., and K.B. Gido. 2006. Use of stable isotopes to test literature-based trophic classifications of small-bodied stream fishes. *American Midland Naturalist* 156:1–10.
- Franssen, N.R., K.B. Gido, C.S. Guy, J.A. Tripe, S.J. Shrank, T.R. Strakosh, K.N. Bertrand, C.M. Franssen, K.L. Pitts, and C.P. Paukert. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. *Freshwater Biology* 51:2072–2086.

- Fraser, D.F. and J.F. Gilliam. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73:959–970.
- Gerken, J.E., and C.P. Paukert. 2013. Fish assemblage and habitat factors associated with the distribution of Topeka shiner (*Notropis topeka*) in Kansas streams. *Journal of Freshwater Ecology* 28:503–516.
- Gido, K.B., J.A. Falke, R.M. Oakes, and K.J. Hase. 2006. Fish-habitat relations across spatial scales in prairie streams. Pages 265-285 in R.M. Hughes, L.Z. Wang, and P.W. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society Symposium 48, Bethesda, Maryland, USA.
- Gido, K.B., W.K. Dodds, and M.E. Eberle. 2010. Retrospective analysis of fish community change during a half-century of land use and streamflow changes. *Journal of the North American Benthological Society* 29:970–987.
- Gilliam, J.F., D.F. Fraser, and M. Alkins-Koo. Structure of a tropical stream fish community: a role for biotic interactions. *Ecology* 74:1856–1870.
- Goldstein, R.M., and M.R. Meador. 2004. Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society* 133:971–983.
- Grossman, G.D., R.E. Ratajczak, M.D. Farr, C.M. Wagner, and J.T. Petty. 2010. Why are there fewer fish upstream. Pages 63–81 in K.B. Gido, and D.A. Jackson, editors. Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society Symposium 73, Bethesda, Maryland, USA.
- Guisan, A., T.C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157:89–100.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than just simple habitat models. *Ecology Letters* 8:993–1009.
- Heulett, S.T., S.C. Weeks, and G.K. Meffe. 1995. Lipid dynamics and growth relative to resource level in juvenile eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae). *Copeia* 1995:97–104.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.

- Hoeninghaus, D.J. and F.M. Pelicice. 2010. Lethal and nonlethal effects of predators on stream fish species and assemblages: a synthesis of predation experiments. Pages 619–648 in K.B. Gido, and D.A. Jackson, editors. *Community ecology of stream fishes: concepts, approaches, and techniques*. American Fisheries Society Symposium 73, Bethesda, Maryland, USA.
- Horwitz, R.J. 1978. Temporal variability patterns and distributional patterns of stream fishes. *Ecological Monographs* 48:307–321.
- Ibañez, C., J. Belliard, R.M. Hughes, P. Irz, A. Kamdem-Toham, N. Lamouroux, P.A. Tedesco, and T. Oberdorff. 2009. Convergence of temperate and tropical stream fish assemblages. *Ecography* 32:658–670.
- 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.
- Jiménez-Valverde, A., Y. Nakazawa, A. Lira-Noriega, and A.T. Peterson. 2009. Environmental correlation structure and ecological niche model projections. *Biodiversity Informatics* 6:28–35.
- Kearney, M. and W.P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Kearney, M. and W.P. Porter. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- Kearney, M.R., B.A. Wintle, and W.P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* 3:203–213.
- Knickle, D.C., and G.A. Rose. 2013. Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes. *Environmental Biology of Fishes*. DOI: 10.1007/s10641-013-0156-0.
- Knight, G.L. and K.B. Gido. 2005. Habitat use and susceptibility to predation of four prairie stream fishes: implications for conservation of the endangered Topeka shiner. *Copeia* 2005:38–47.
- Kozak, K.H., C.H. Graham, and J.J. Wiens. 2008. Integrating GIS-based environmental data into evolutionary biology. *Trends in Ecology and Evolution* 23:141–148.

- Lai, I.L., H. Scharr, A. Chavarria-Krauser, R. Justers, J.T. Wu, C.H. Chou, U. Schurr, and A. Walter. 2005. Leaf growth dynamics of two congener gymnosperm tree species reflect the heterogeneity of light intensities given in their natural ecological niche. *Plant, Cell and Environment* 28:1496–1505.
- Lyons, J., T.Zorn, J. Stewart, P. Seelbach, K. Wehrly, and L. Wang. 2009. Defining and Characterizing Coolwater Streams and Their Fish Assemblages in Michigan and Wisconsin, USA. *North American Journal of Fisheries Management* 29:1130–1151.
- Lamberti, G.A. and S.V. Gregory. 2006. CPOM transport, retention, and measurement. Pages 273-289 in F.R. Hauer and G.A. Lambert, editors. *Methods in stream ecology*. Second edition. Academic Press, San Diego, California, USA.
- Matthews, W.J. 1986. Fish faunal ‘breaks’ and stream order in the eastern and central United States. *Environmental Biology of Fishes* 17:81–92.
- McGill, B.J., B.J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- Merritt, R.W., K.W. Cummins, and M.B. Berg. 2008. *An introduction to the aquatic insects of North America*. Fourth edition. Kendall/Hunt, Dubuque, Iowa, USA.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, R.G. O’Hara, G.L. Simpson, P. Solymos, M. Henry, H.H. Stevens, and J. Wagner. 2009. *Vegan: Community Ecology Package*. R Library. R Project for Statistical Computing, Vienna, Austria.
- Pflieger, W.L. 1997. *The Fishes of Missouri*. Revised Edition, Missouri Department of Conservation, Jefferson City, Missouri, USA.
- Phillips, S.J., Anderson, R.P., and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- 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* 22:341–351.
- Roberts, J.H. and N.P. Hitt. 2010. Longitudinal structure in temperate stream fish communities: evaluating conceptual models with temporal data. Pages 281–299 in K.B. Gido, and D.A.

- Jackson, editors. Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society Symposium 73, Bethesda, Maryland, USA.
- Schaefer, J., D. Duvernell and B. Kreiser. 2011. Shape variability in topminnows (*Fundulus notatus* species complex) along the river continuum. *Biological Journal of the Linnean Society* 103: 612–621.
- Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-28 in W.J. Matthews and D.C. Heins, editors. *Community and Evolutionary Ecology of North American Freshwater Fishes*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Schlosser, I.J. 1988. Predation rates and the behavioral response of adult brassy minnows (*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. *Copeia* 1988:691–697.
- Schmidt, T.R. and J.R. Gold. 1995. Systematic affinities of *Notropis topeka* (Topeka shiner) inferred from sequences of the cytochrome *b* gene. *Copeia* 1995:199–204.
- Schultz, A.A. and S.A. Bonar. 2009. Growth and survival of larval and juvenile Gila chub at different temperatures. *North American Journal of Aquaculture* 71:1–5.
- Steinman, A.D., G.A. Lamberti, and P.R. Leavitt. 2006. Biomass and pigments of benthic algae. Pages 357-379 in F.R. Hauer and G.A. Lambert, editors. *Methods in stream ecology*. Second edition. Academic Press, San Diego, California, USA.
- Taniguchi, Y. and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027–2039.
- Torres-Dowdall, J., F. Dargent, C.A. Handelsman, I.W. Ramnarine, and C.K. Ghalambor. 2013. Ecological correlates of the distribution limits of two poeciliid species along a salinity gradient. *Biological Journal of the Linnean Society* 108:790–805.
- Taylor, C.M., and P.W. Lienesch. 1996. Regional parapatry of the congeneric cyprinids *Lythrurus snelsoni* and *L. umbratilis*: species replacement along a complex environmental gradient. *Copeia* 1996:493–497.
- Thomas, M.K. C.T. Kremer, C.A. Klausmeier, and E. Litchman. 2012. A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085–1088.

- Troia, M.J., and Gido, K.B. 2013. Predicting Community–Environment Relationships of Stream Fishes across Multiple Drainage Basins: Insights into Model Generality and the Effect of Spatial Extent. *Journal of Environmental Management* 123:313–323.
- 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.
- Wall, S.S., C.R. Berry, C.M. Blausey, J.A. Jenks, and C.J. Kopplin. 2004. Fish-habitat modeling for gap analysis to conserve the endangered Topeka shiner (*Notropis topeka*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:954–973.
- Weber, M.G. and A.A. Agrawal. 2012. Phylogeny, ecology, and the coupling of comparative and experimental approaches. *Trends in Ecology and Evolution* 27:394–403.
- Wiens, J.J. and C.H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Reviews in Ecology and Systematics* 36:519–539.
- Wood, S.N. 2006. Generalized additive models: an introduction with R. *Journal of the American Statistical Association* 99:673–686.
- Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer. New York, NY.

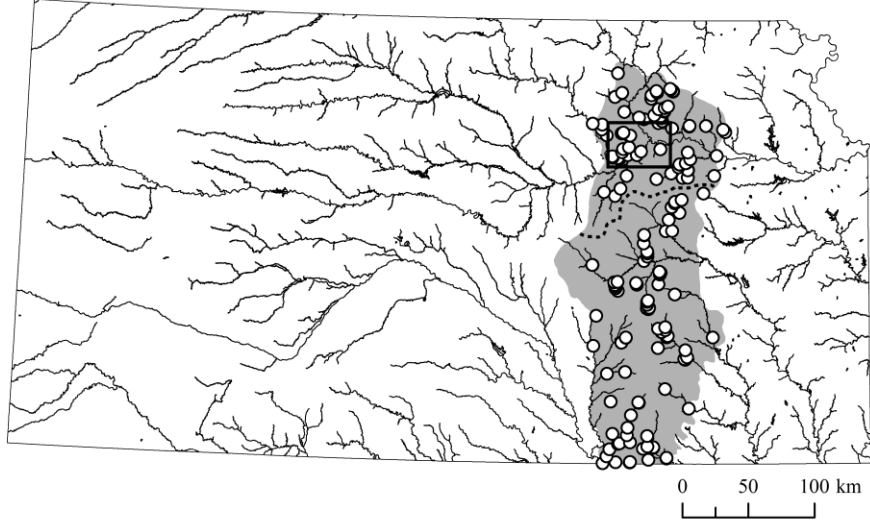
Figure 4.1 (A) Study area in Kansas, USA, (B) locations of 221 KDWPT stream surveys sites in the Flint Hills EPA Level III ecoregion used for niche models, and (C) locations of small, medium, and large streams (Kings Creek, Wildcat Creek, and Kansas River, respectively) in northern Flint Hills where field experiments were conducted. Dashed line indicates the drainage divide separating the Kansas River basin from the Arkansas River basin.

A



- Niche Model Sites
- ⊕ Experiment Sites
- Flint Hills

B



C

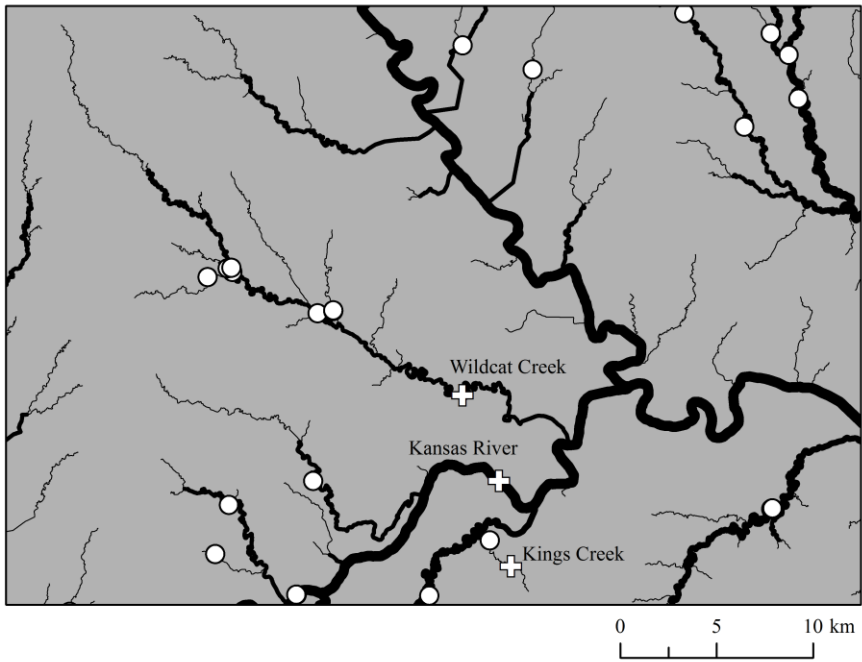


Figure 4.2 (A) Male *P. notatus* under a spawning tile. (B) *P. notatus* eggs on the underside of a spawning tile. (C) Experimental enclosures in the Kansas River, Riley County, Kansas.

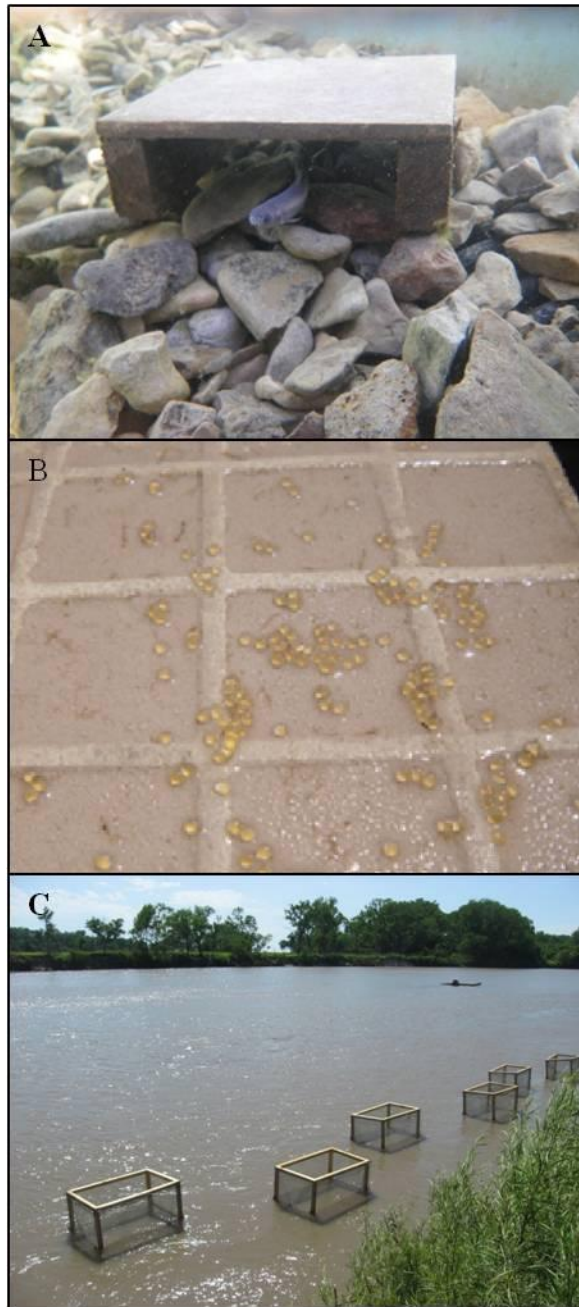


Figure 4.3 Mean (\pm 95% confidence intervals) predictive capability of environmental variables included in niche models of eight species. Predictive capability was calculated as the reduction in deviance explained by a model without a predictor variable relative to a global model containing all predictor variables.

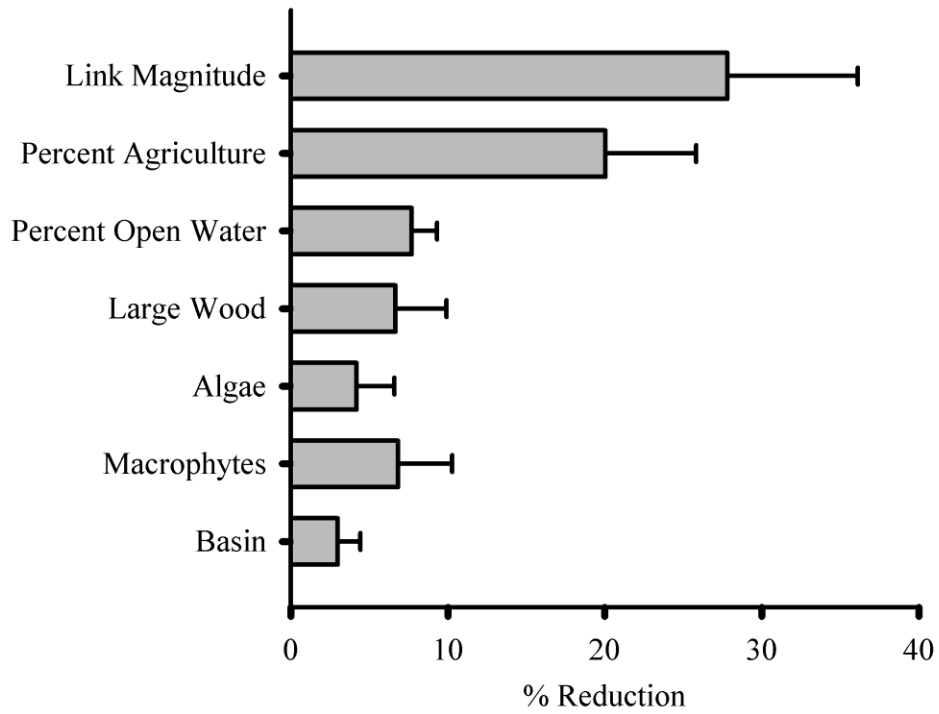


Figure 4.4 Smoothing functions (solid lines) and 95% confidence bands (dotted lines) generated from GAMs showing the relationship between stream size (link magnitude) and abundance of (A-D) tributary and (E-H) river mainstem species. Arrows in (D) and (H) indicate link magnitudes of Kings Creek, Wildcat Creek, and the Kansas River (from left to right) where field experiments were conducted for *P. notatus* and *P. vigilax*. Vertical gray dashes indicate the distribution of the 221 KDWPT sites along the stream-size gradient.

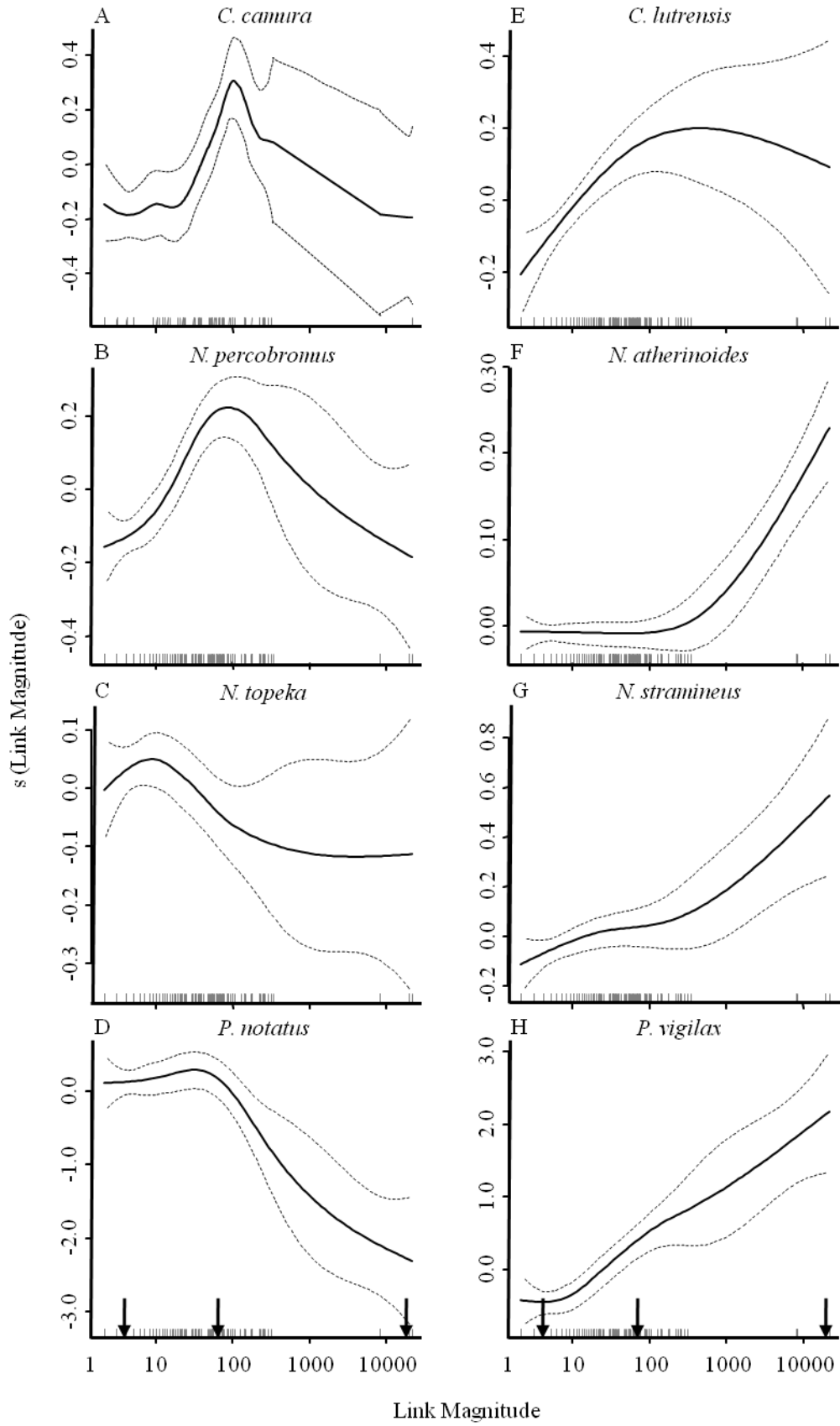


Figure 4.5 Individual performance for *P. notatus* (white bars) and *P. vigilax* (gray bars) from experimental enclosures in small, medium, and large streams. (A) Number of deposited ova per gram of wet somatic female mass per day for adults. (B) Probability of daily survival, (C) percent increase in total length per day, and (D) lipid content as percent of dry somatic mass for juveniles. Bars represent means for each treatment and circles represent values for each enclosure. Zero values are expressed as 0.1 in panel A to facilitate plotting on a log₁₀ scale. Overlapping circles are offset on the x-axis in panels A and B.

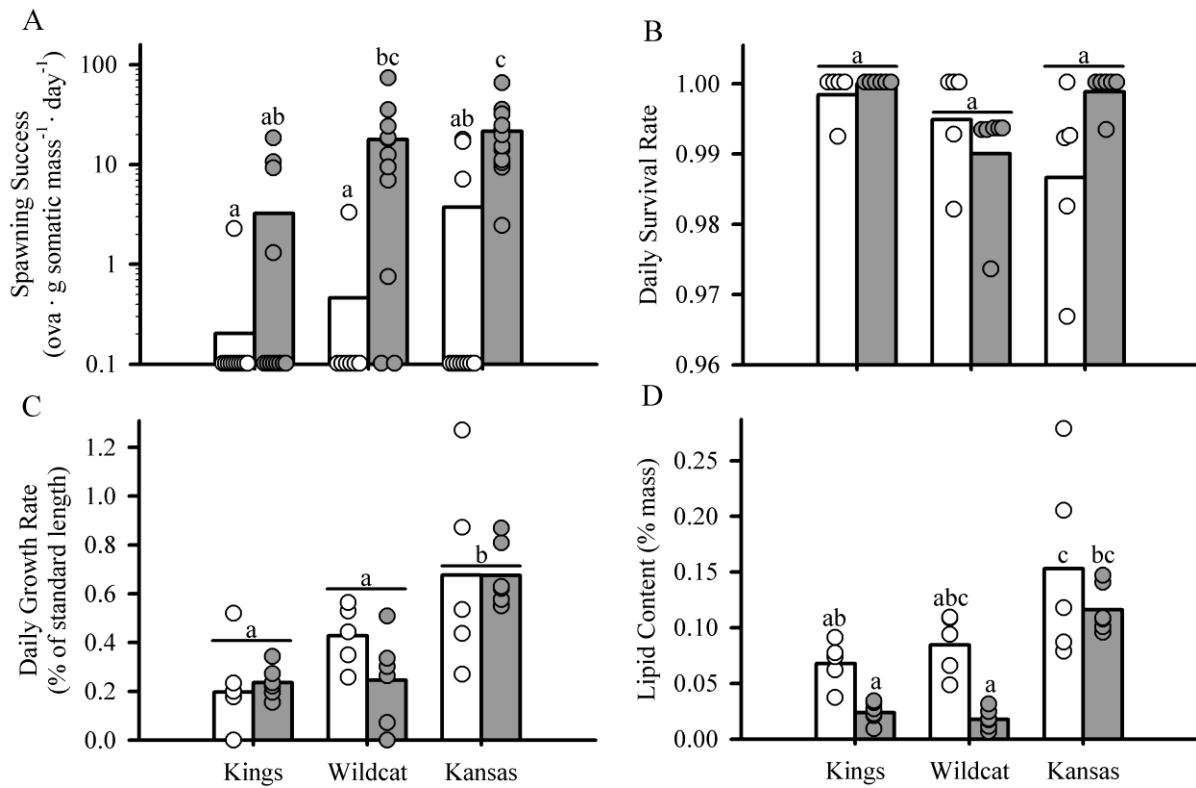


Figure 4.6 A three step analytic framework for the development of mechanistically-based environmental niche models using the congeners *P. notatus* and *P. vigilax* as a model study system. Red and blue lines represent *P. notatus* and *P. vigilax*, respectively. Solid lines represent known relationships from the current study and dashed lines represent additional relationships that should be quantified.

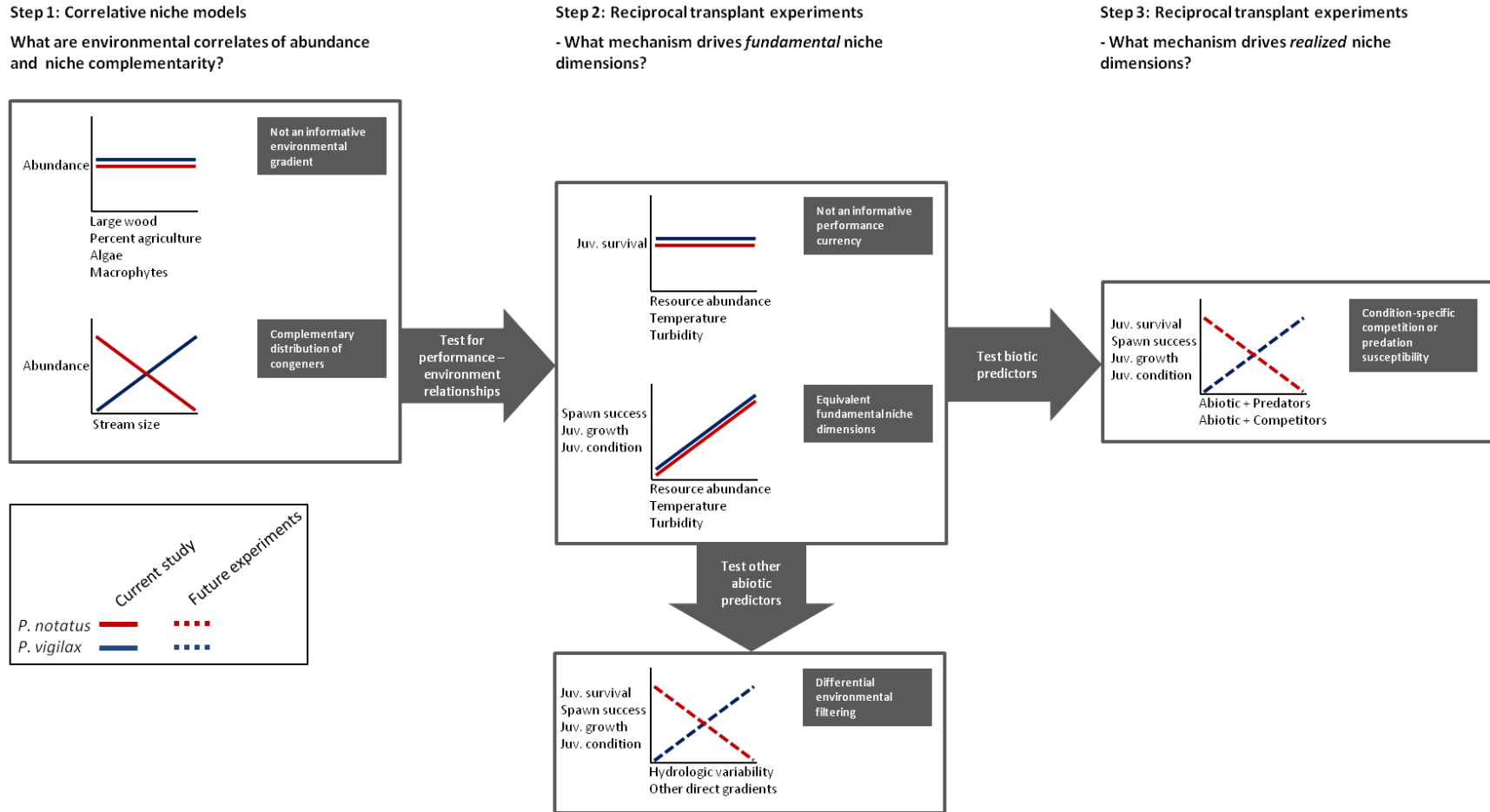


Table 4.1 Principal Components Analysis (correlation matrix) loadings of 23 environmental predictor variables on interpretable PC axes. Axis interpretability was determined from broken stick models. Percent of variance explained by each axis is shown in parentheses. Superscripts indicate variables loading most strongly (negatively or positively) on each PC axis, which were used as predictor variables in environmental niche models.

Variable	Category	PC1 (25.3)	PC2 (16.2)	PC3 (13.2)	PC4 (10.5)	PC5 (8.2)
Basin relief	Catchment	-0.03	-0.02	-0.05	-0.02	-0.01
Maximum elevation	Catchment	-0.02	0.00	0.02	0.00	0.00
Organic matter	Catchment	-0.04	-0.02	0.01	-0.01	0.03
Percent agriculture ^{PC3}	Catchment	0.20	0.27	0.55	0.19	-0.28
Percent forest	Catchment	0.17	0.10	0.10	0.03	0.08
Percent grassland	Catchment	-0.03	-0.05	-0.11	-0.05	0.07
Percent surface water	Catchment	0.03	-0.09	-0.11	0.00	0.06
Percent urban	Catchment	0.02	0.28	0.40	0.14	-0.16
Percent wetland	Catchment	0.05	-0.01	-0.05	0.01	0.02
Soil bulk density	Catchment	0.00	0.00	0.00	0.00	0.00
Soil erodibility factor	Catchment	0.00	0.01	0.01	0.00	0.00
Link magnitude ^{PC1}	Segment	0.61	0.15	-0.44	0.00	-0.21
Reach gradient	Segment	-0.28	-0.05	0.27	-0.05	-0.02
Algae ^{PC2}	Site	-0.17	0.84	-0.21	-0.36	0.04
Canopy	Site	-0.26	0.05	-0.03	0.13	0.12
Large wood ^{PC5}	Site	0.34	0.11	0.10	0.36	0.62
Macrophytes ^{PC4}	Site	-0.38	0.20	-0.35	0.76	-0.07
Small wood	Site	0.19	0.17	0.15	0.10	0.33
Substrate diameter	Site	-0.19	0.06	-0.01	-0.10	0.10
Substrate embeddedness	Site	0.03	0.00	0.01	0.06	-0.05
Undercut bank	Site	-0.11	0.02	0.00	-0.22	0.53
Width to depth ratio	Site	0.12	0.03	-0.14	0.02	-0.13
Predator density*	Site	-0.11	0.05	0.12	-0.06	-0.04

* Log₁₀-transformed density of adult individuals of the following piscivorous species captured during KDPWT sampling: *Ameiurus melas*, *Ameiurus natalis*, *Ictalurus punctatus*, *Lepomis cyanellus*, *Lepomis gulosus*, *Lepisosteus oculatus*, *Lepisosteus osseus*, *Lepisosteus platostomus*, *Micropterus dolomieu*, *Micropterus punctulatus*, *Micropterus salmoides*, *Morone americana*, *Morone chrysops*, *Pomoxis annularis*, *Pomoxis nigromaculatus*, *Pylodictis olivaris*, *Sander vitreus*.

Table 4.2 Environmental characteristics of the small, medium, and large streams (Kings Creek, Wildcat Creek, and the Kansas River, respectively) where field experiments were carried out.

Environmental Variables	Stream Size		
	Small	Medium	Large
Site Characteristics			
Strahler Order	2	4	8
Link Magnitude (# of upstream segments)	3	49	19,731
Catchment Area (km ²)	11.2	224	117,746
Mean Discharge (m ³ ·sec ⁻¹)	0.05 ¹	0.25 ²	51.50 ³
% Native Prairie	74.0	52.0	50.2
% Agriculture	18.8	39.0	46.8
% Forest	0.1	5.8	1.0
% Other Land Cover	7.1	3.2	2.0
Experiment 1			
Mean Water Temperature (°C)	22.4	25.7	27.3
Turbidity (NTU)	0.1	2.3	11.2
Experiment 2			
Mean Water Temperature (°C)	17.2	19.0	20.9
Turbidity (NTU)	9.3	2.0	6.1
Substrate Diameter (mm)	53.1 ^a	62.1 ^b	1 ^c
Benthic Organic Matter (mg·100 cm ⁻³)	36.2 ^a	34.4 ^a	574.8 ^b
Chlorophyll <i>a</i> (mg·m ⁻²)	8.4 ^a	11.4 ^a	31.0 ^a
Filamentous Algae (% coverage)	0.3 ^a	22.6 ^b	0.0 ^a
Benthic Macroinvertebrate Density (individuals·100 cm ⁻³) ¹	1.9 ^a	1.2 ^a	13.9 ^b
Zooplankton Density (individuals·L ⁻¹)	7.4 ^a	4.8 ^a	0.01 ^b

¹USGS Gage #6879650, 33 years; ²USGS Gage #06879810, 1 year; ³USGS Gage #06879100, 48 years. Different letters denote statistically significant differences ($\alpha=0.05$) between treatments based on ANOVA and Tukey's Honestly Significant Differences post-hoc tests.

Table 4.3 Experimental replication and body size of *P. notatus* and *P. vigilax* in enclosures from small, medium, and large streams (Kings Creek, Wildcat Creek, and the Kansas River, respectively) containing *P. notatus* or *P. vigilax*.

	Small		Medium		Large	
	<i>P. notatus</i>	<i>P. vigilax</i>	<i>P. notatus</i>	<i>P. vigilax</i>	<i>P. notatus</i>	<i>P. vigilax</i>
Experiment 1						
Number of enclosures (replicates)	11	11	11	11	11	11
Mean male eviscerated wet mass (g)	3.6 ^a	3.8 ^a	3.4 ^a	3.3 ^a	3.6 ^a	3.9 ^a
Mean female eviscerated wet mass (g)	1.4 ^a	1.2 ^b	1.4 ^{ab}	1.2 ^{ab}	1.5 ^a	1.4 ^{ab}
Experiment 2						
Number of enclosures (replicates)	5	6	5	6	5	6
Mean starting standard length (mm)	40.2 ^a	30.2 ^c	38.5 ^{ab}	30.4 ^c	37.3 ^b	31 ^c

Different letters denote statistically significant differences ($\alpha=0.05$) between treatments based on ANOVA and Tukey's Honestly Significant Differences post-hoc tests.

Table 4.4 Degrees of freedom for smoothing function and F- and P-values for six environmental variables used in niche models for eight study species. Bolded parameters indicate statistically significant ($\alpha < 0.05$) smoothing functions.

<i>Species</i>		Environmental Predictors						Deviance Explained (%)
		Link Magnitude	Percent Agriculture	Large Wood	Algae	Macrophytes	Basin ^a	
<i>Cyprinella camura</i>	e.d.f.	3.75	4.64	2.21	2.37	3.14	n/a	35.9
	F	3.80	1.69	1.39	0.16	1.48	n/a	
	P	0.005	0.14	0.25	0.99	0.22	n/a	
<i>Cyprinella lutrensis</i>	e.d.f.	4.17	5.62	4.52	1.18	2.73	-0.02 ^b	36.5
	F	6.99	4.53	0.92	0.22	1.25	-0.15 ^c	
	P	<0.001	<0.001	0.47	0.99	0.29	0.88	
<i>Notropis percobromus</i>	e.d.f.	6.57	5.93	5.21	6.57	4.52	0.11 ^b	37.0
	F	5.76	4.50	0.23	1.55	1.70	1.48 ^c	
	P	<0.001	<0.001	0.99	0.23	0.13	0.14	
<i>Notropis atherinoides</i>	e.d.f.	3.32	1.05	1.42	6.70	3.47	-0.04 ^b	25.3
	F	15.24	2.20	0.00	0.03	0.09	-2.66 ^c	
	P	<0.001	0.12	0.99	0.99	0.99	0.01	
<i>Notropis topeka</i>	e.d.f.	3.23	7.90	4.07	3.50	4.95	0.06 ^b	17.9
	F	2.55	1.74	1.10	0.00	1.01	1.31 ^c	
	P	0.04	0.09	0.38	0.99	0.41	0.19	
<i>Notropis stramineus</i>	e.d.f.	4.44	8.29	3.39	5.54	3.01	-0.11 ^b	39.4
	F	2.36	5.64	3.52	3.51	0.85	-1.88 ^c	
	P	0.04	<0.001	0.01	0.00	0.48	0.06	
<i>Pimephales notatus</i>	e.d.f.	3.60	1.07	1.03	7.44	4.73	0.10 ^b	26.9
	F	4.91	1.52	2.16	1.40	2.19	1.23 ^c	
	P	<0.001	0.21	0.13	0.20	0.05	0.22	
<i>Pimephales vigilax</i>	e.d.f.	4.54	2.73	8.50	4.71	5.56	0.05 ^b	43.9
	F	12.40	1.30	5.47	0.11	0.33	3.21 ^c	
	P	<0.001	0.27	<0.001	0.99	0.85	0.32	

^a Nominal variable representing Kansas River basin or Arkansas River basin; ^b parameter estimate; ^c t-value.

Table 4.5 Two-way analysis of variance showing effect of stream size, species, and stream size * species interaction on four individual performance currencies measured during experiments. Bolded parameters are indicate statistically significant effects ($\alpha = 0.0125$ following Bonferroni adjustment). See Figure 4.5 for pair-wise comparisons between treatment levels.

Effect	Survival			Growth			Storage lipids			Spawn success		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Stream size	2, 27	3.21	0.06	2, 27	14.08	<0.0001	2, 27	20.06	<0.0001	2, 58	5.63	<0.0001
Species	1, 27	1.46	0.24	1, 27	0.42	0.5244	1, 27	14.29	0.0008	1, 58	16.54	0.0001
Stream size * Species	2, 27	4.10	0.03	2, 27	0.86	0.44	2, 27	0.49	0.62	2, 58	2.69	0.08

Chapter 5 - Conclusions

A fundamental goal of ecology is to understand environmental associations of species and predict their distribution across landscapes. This is particularly important for freshwater fishes because anthropogenic environmental change—including habitat degradation, water pollution, hydrologic alteration, and introduction of non-native species—threatens the persistence of many species (Dudgeon et al. 2006). Understanding the natural and anthropogenic environmental factors that constrain species' distributions is essential for preserving existing populations of native species and restoring degraded stream habitat to rehabilitate declining populations of native species (Ebersole et al. 1997, Bond and Lake 2003). Accurate prediction of species' distributions has been limited by four issues, listed below, that I addressed in Chapters 2, 3, and 4 of this dissertation using a variety of experimental and observational approaches.

Functional traits of species impose constraints with regard to abiotic and biotic gradients during the process of community assembly (McGill et al. 2006, Violle et al. 2007, Frimpong and Angermeier 2010), but few studies have evaluated functional trait dispersion in stream fish communities. In Chapter 2, I used null models to show that functional traits of stream fishes are mostly underdispersed, indicating that Great Plains stream fish communities are assembled by abiotic environmental filters. Perhaps more importantly, I showed that this dispersion varies among different types of functional traits that are associated with different aspects of species' autecologies. Second, evaluating how the manipulation of spatial scales affects the interpretation of species-environment relationships is an ongoing problem in ecology (Levin 1992, Fausch et al. 2002). In Chapter 2, I showed that tests of community assembly exhibit some scale dependence. I concluded that abiotic environmental filtering operates at mesohabitat and reach resolutions as well as reach and basin extents. The relationship between stream network position and the filtering of reproductive life history traits was dependent on the spatial scale of analysis. In Chapter 3, I showed that the extent at which correlative community-environment models are developed strongly affects the predictive capability of different environmental variables, but does not affect overall model performance. Third, an incomplete understanding of the generality of species-environment relationships has limited the ability of conservationists and natural resource managers to accurately predict changes in species' distributions under novel environmental conditions (Saupe et al. 2002, Wenger and Olden 2012). In Chapter 3, I showed that stream

network position is a consistent (i.e., general) predictor of community composition across thirteen sub-basins in Kansas. By contrast, local- and catchment-scale environmental variables were less generalizable and differed substantially in predictive capability among sub-basins which was attributable to the presence of ecoregional transitions in some sub-basins but not other sub-basins. Fourth, accurate prediction of species' distributions and abundances under novel environmental conditions also depends on knowledge of the causative mechanisms that underlie species-environment correlations (Kearney and Porter 2010, Saupe et al. 2012). In Chapter 4, I used field enclosure experiments to show that, in contrast to predictions based on distributional patterns, individual performance of two congeneric minnows increases with stream size and probably stems from increased resource availability, temperature, or both.

Taken together, these studies demonstrate the context dependencies of characterizing habitat associations of stream fishes. For example, the strength of community-environment relationships varies among regions and depends on ecoregional transitions occurring within each region. The spatial extent at which community-environment relationships are evaluated also influences which environmental factors (stream network position versus catchment land cover) drive species distributions. These studies also reveal several generalities among one another and also among previous, well-accepted paradigms of species-environment associations in temperate streams (Vannote et al. 1980, Schlosser et al. 1987). For example, stream size and associated environmental gradients were important factors driving multiple aspects of stream fish ecology including: the dispersion of reproductive life history strategies (Chapter 2); the relative abundance of species within a local community (i.e., a stream reach; Chapters 3 and 4); habitat partitioning among closely-related species (Chapter 4); and somatic growth, condition, and spawning success (Chapter 4). By identifying which aspects of species-environment associations are general and which are idiosyncratic, these studies will be useful for management of stream fish biodiversity in the Great Plains.

References

- Bond, N.R., Lake, P.S. 2003. Characterizing fish-habitat associations in streams as the first step in ecological restoration. *Austral Ecology* 28: 611–621.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Staissny, M.L.J., Sullivan, C.A., 2006.

- Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* 81:163–182.
- Ebersole, J.L., Liss W.J., Frissell C.A. 1997. Restoration of stream habitats in the western United States: Restoration as reexpression of habitat capacity. *Environmental Management* 21: 1–14.
- Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. *Bioscience* 52:483–498.
- Frimpong, E. and Angermeier, P. 2010. Trait-based approaches in the analysis of stream fish communities. – In: Gido, K.B. and Jackson, D.A. (eds), *Community ecology of stream fishes: concepts, approaches, and techniques*. Am. Fish. Soc. Symp. 73: pp. 109–136.
- Jiménez-Valverde, A., Nakazawa, Y., Lira-Noriega, A., Peterson, A.T. 2009. Environmental correlation structure and ecological niche model projections. *Biodiversity Informatics* 6:28–35.
- Kearney, M. and W.P. Porter. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Saupe, E.E., Barve, V., Myers, C.E., Soberon, J., Barve, N., Hensz, C.M., Peterson, A.T., Owens, H.L., Lira-Noriega, A. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. *Ecological Modelling* 237:11–22.
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Wenger, S. J., Olden, J.D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3:260–267.