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

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Abstract.   Environmental niche modeling is a valuable tool but it often fails to identify causal links between environmental gradients and individual- or population-level performance 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 measures of individual performance (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 metric, or differential environmental filtering by a direct environmental gradient operating at longer timescales.

Key words: congeners; Cyprinidae; environmental niche modeling; Great Plains; individual performance; mechanistic niche modeling; phylogenetic comparative approach.

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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 environ-

mental 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 environmen-

tal 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 (Jimenez-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 metrics (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 metrics 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, Buckley et al. 2010, Kearney et al. 2010, Thomas et al. 2012). Additionally, identifying interspecific variation in functional traits and the shape of performance curves (optimum and breadth) 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 et al. 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 metrics 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 metrics 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., first to fifth 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., first to ninth 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 coldwater assemblages at high elevations or in headwater

springs, to coolwater assemblages in mid-order streams, and finally to warmwater 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) promote 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 for 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 warmwater congeners occupying complementary stream-size niches. For example, the 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 warmwater stream fish communities is a consequence of direct environmental gradients (other than temperature and resources) 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 measures of individual performance (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 metrics 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 (Fig. 1A, B). 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 (no./m^2) 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 150 m and
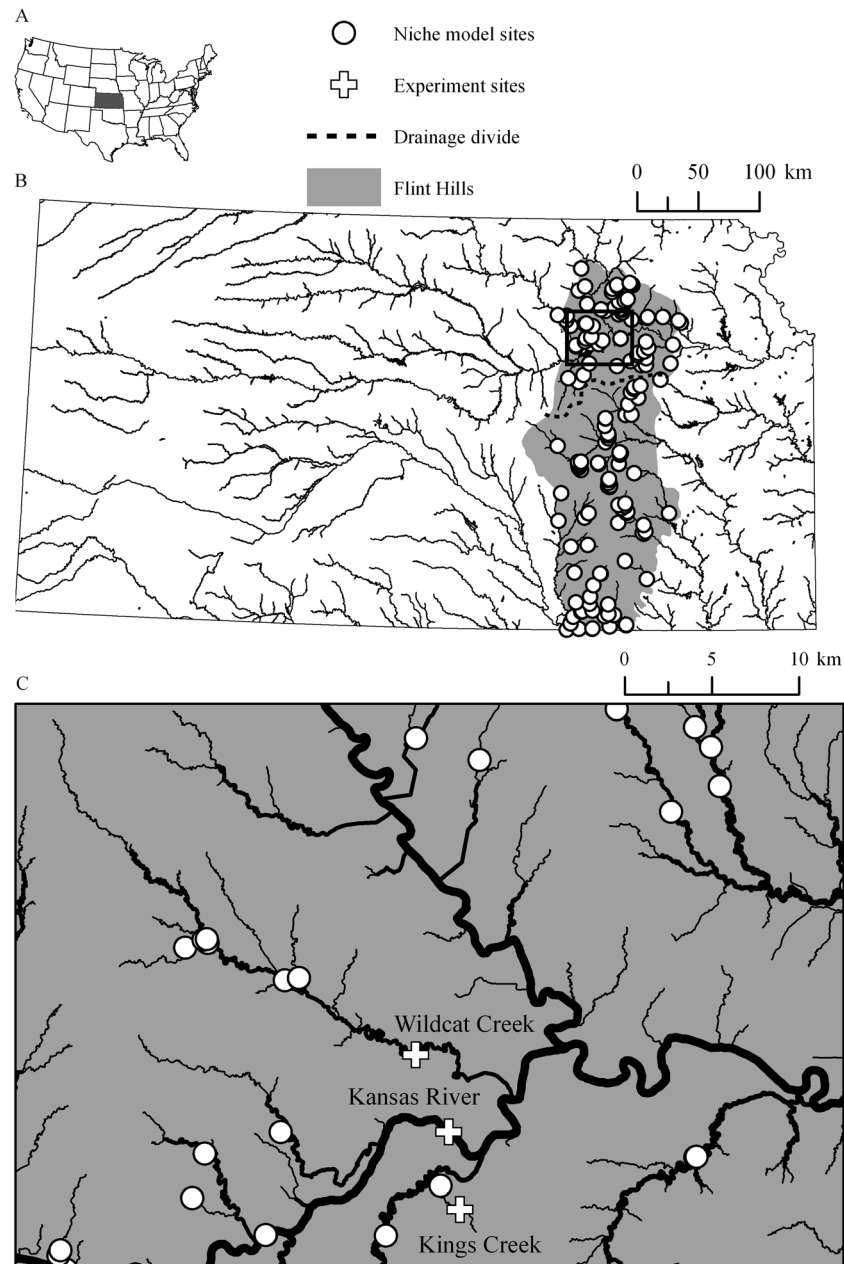
Fig. 1. (A) Study area in Kansas, USA, (B) locations of 221 KDWPT stream survey locations in the Flint Hills EPA Level III ecoregion used for niche models, and (C) locations of small, medium, and large streams in the northern Flint Hills where field experiments were conducted.

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 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: 10 site-scale variables measured at the time of fish sampling, two GIS-derived segment-scale variables, and 11 GIS-derived catchment-scale variables (Appendix). 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, orthogonal 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 2011) 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 (Fig. 2A, B). Treatments crossed species (*P. notatus* or *P. vigilax*) and stream size (second, fourth, or eighth order stream; hereafter referred to as small, medium, and large streams) in a two by three factorial design. Experiments were carried out in enclosures (91 cm length × 61 cm width × 76 cm height) constructed of a pine wood frame and hardware cloth (3 mm mesh) on the sides and bottom, and secured to the streambed with steel rebar (Fig. 2C). Enclosures were placed in Kings Creek, a second order tributary of the Kansas River, Wildcat Creek, a fourth order tributary of the Kansas River, and the Kansas River proper, an eighth order river mainstem in the Flint Hills, Riley County, Kansas, USA (Fig. 1C). This gradient spanned three and four orders of magnitude in mean annual discharge and catchment area, respectively (see Table 1 for site characteristics). Enclosures were placed in streams 5–10 d prior to the start of the experiments to facilitate algae accrual, organic matter accumulation, and macroinvertebrate colonization. Enclosures were placed in meso-habitats 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 (M. J. Troia and K. B. Gido, *unpublished data*).

Experiment 1: spawning success

Experiment 1 consisted of two runs starting on 5 June 2012 and 20 June 2012, each lasting 10 d. For each run five or six enclosures per treatment were stocked with one age-1 male and three age-
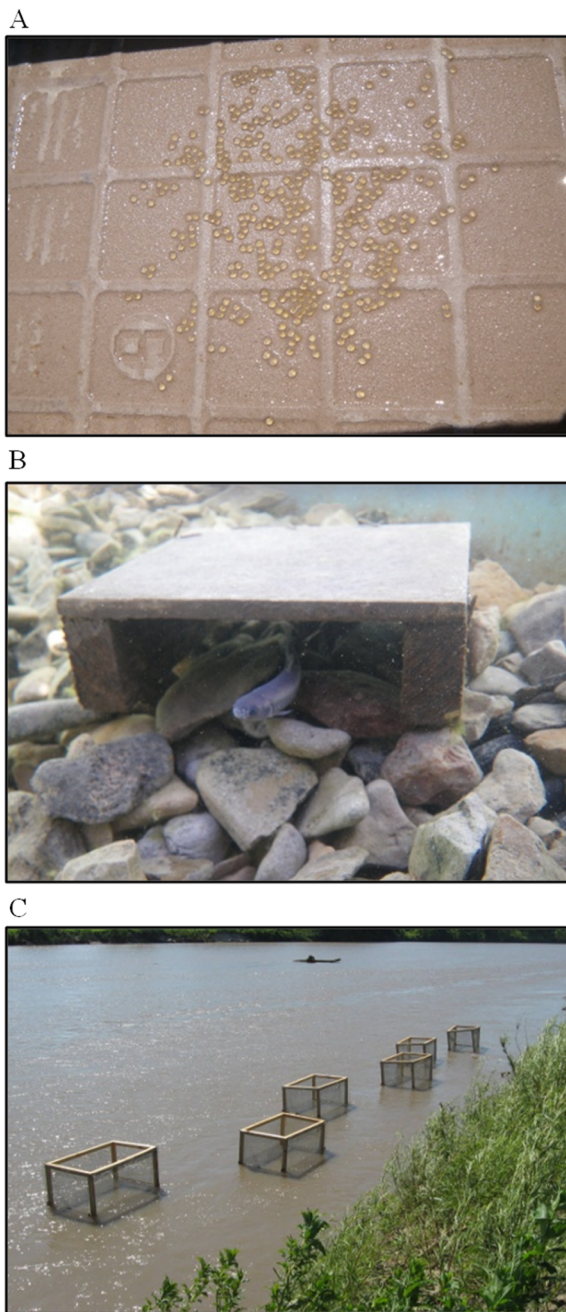
Fig. 2. (A) *Pimephales notatus* eggs on the underside of a spawning tile. (B) Male *P. notatus* guarding a spawning tile. (C) Experimental enclosures in the large stream (Kansas River).

1 females. Only reproductively active individuals, determined from the presence of breeding tubercles on males and an exterior ovipositor on females were used (Flickinger 1969). Mean eviscerated male wet mass was 3.5 g and 3.7 g for *P. notatus* and *P. vigilax*, respectively and did not differ significantly between species or among stream sizes (Table 2). Eviscerated female mass was significantly lower for *P. vigilax* (mean = 1.3 g) 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 fourth 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 (15 cm length $\times$ 15 cm width) suspended 4.5 cm above the enclosure bottom with pine board sides (1.5 cm width $\times$ 4.5 cm height $\times$ 15 cm length) (Fig. 2B).

Enclosures were observed daily and spawning crevices were checked for eggs, photographed if present, and returned to the enclosure (Fig. 2A). After 10 d, 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 per gram of wet eviscerated female mass per day. 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 d. 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

Table 1. Environmental characteristics of field experiment sites.

Characteristic	Small stream	Medium stream	Large stream
Site characteristics			
Strahler order	2	4	8
Catchment area (km^2)	11.2	224	117,746
Mean annual discharge (m^3/s)	0.05	0.25	51.50
Grassland (%)	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]	1.0[C]
Benthic organic matter (mg/100 cm^3)	36.2[A]	34.4[A]	574.8[B]
Chlorophyll a (mg/m^2)	8.4[A]	11.4[A]	31.0[A]
Filamentous algae (%)	0.3[A]	22.6[B]	0.0[A]
Benthic macroinvertebrate density (no./100 cm^3)	1.9[A]	1.2[A]	13.9[B]
Zooplankton density (no./L)	7.4[A]	4.8[A]	0.01[B]

Notes: Mean annual discharge from USGS gages #6879650, #06879810, and #06879100 for small, medium and large stream, respectively. Different letters denote statistically significant differences at $P < 0.05$ based on ANOVA and Tukey's Honestly Significant Differences.

growth (M. J. Troia and K. B. 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 standard length was significantly higher for *P. notatus* (mean = 38.7 mm) compared to *P. vigilax* (mean = 30.5 mm). *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 = 37.3 mm) compared to the small stream (mean = 40.2 mm) (Table 2). Three plastic baskets (10 cm length × 10 cm width × 10 cm height, 2 cm × 1.25 cm 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 macroinvertabrates. Substrates were harvested from the streambed within two meters 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

Table 2. Replication and body size of *Pimephales notatus* and *Pimephales vigilax* fish used in each experimental treatment.

	Small stream		Medium stream		Large stream	
Characteristic	*P. notatus*	*P. vigilax*	*P. notatus*	*P. vigilax*	*P. notatus*	*P. vigilax*
Experiment 1						
No. enclosure replicates	11	11	11	11	11	11
Mean male eviscerated wet mass	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						
No. enclosure 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]	31.0[C]

Note: Different letters denote statistically significant differences at $P < 0.05$ based on ANOVA and Tukey's Honestly Significant Differences.

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 d, 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 thirtieth 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 30 d. To quantify condition, we extracted storage lipids and measured content (% of eviscerated body mass). Each individual was eviscerated, dried in an oven at 40°C for 72 h, and weighed to the nearest 0.1 mg. To extract storage lipids, each individual was rinsed four times for 72 h in 20 mL of petroleum ether. Lipid-extracted individuals were dried again at 40°C for 72 h 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 54 10 × 10 cm 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 min, and incubated in complete darkness for 12 h 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 6 L of water and agitated to suspend and homogenize organic matter after which a 0.5-L water sample was collected and preserved in 10% formalin for measurement of BOM. The remaining material in the bucket was elutriated three to six times and passed through a 250-µm mesh sieve to capture macroinvertebrates, which were preserved in 10% formalin. To quantify zooplankton density, 12 L of water from each enclosure was passed through a 47-µm mesh sieve to capture zooplankton, which were preserved in 10% formalin. In the laboratory, BOM was quantified as ash-free dry mass of the 0.5-L 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 less than four mm in length were counted because gape limitation prevented consumption of larger prey items by 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 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. Pairwise 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). 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 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 (Fig. 3). The low predictive capability of basin indicated that any interbasin differences in stream size niche dimensions are negligible for the seven species that occur in both basins. Smoothing functions revealed strong complementary relationships between density and stream-size for congeneric pairs (Fig. 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 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, Fig. 5A).

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 1). Contrary to expectations and attributed to drought conditions, turbidity was highest in the small stream. Substrate diameter was lowest in the large stream, highest in the medium-sized stream, and intermediate in the small stream (Table 1).

Daily probability of juvenile survival was high, ranging from 0.97 to 1.00, and did not differ significantly between species or among stream sizes (Table 4, Fig. 5B). Daily growth rate ranged from 0% to 1.27% and was higher in the large stream than in the medium and small streams but was not different between species (Table 4, Fig. 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.*

Table 3. Results of environmental niche models (generalized additive models) for eight species.

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

Notes: Basin is a nominal predictor variable representing Kansas or Arkansas basin. Basin was not used in the *Cyprinella camura* model because this species occurs only in the Arkansas basin.

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, Fig. 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 (56.1–82.1%), 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 13 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
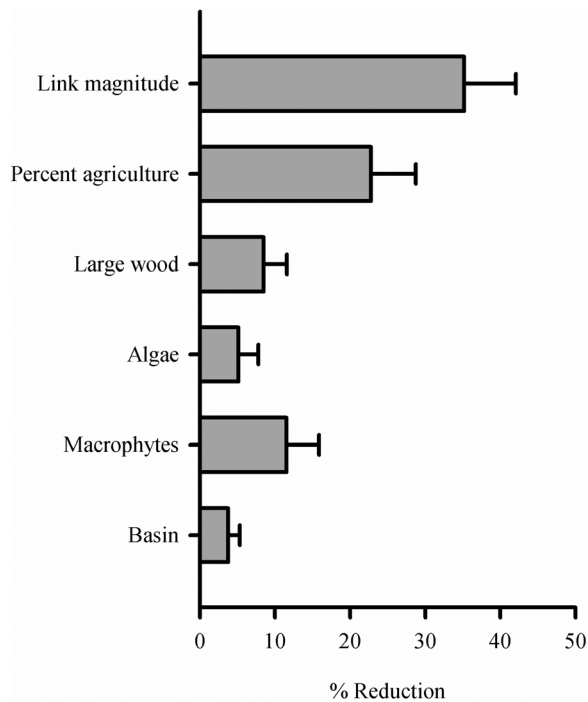
Fig. 3. Mean (± 95% confidence intervals) predictive capability of environmental variables included in niche models of eight species. Predictive capability was calculated as the reduction in deviance explained by a model without a predictor variable relative to a global model containing all predictor variables.

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 1997). 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 1987). This filter operates at seasonal and interannual timescales and did not affect individual performance measured over the 10 and 30 d 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). Nevertheless, these species might respond differently 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.
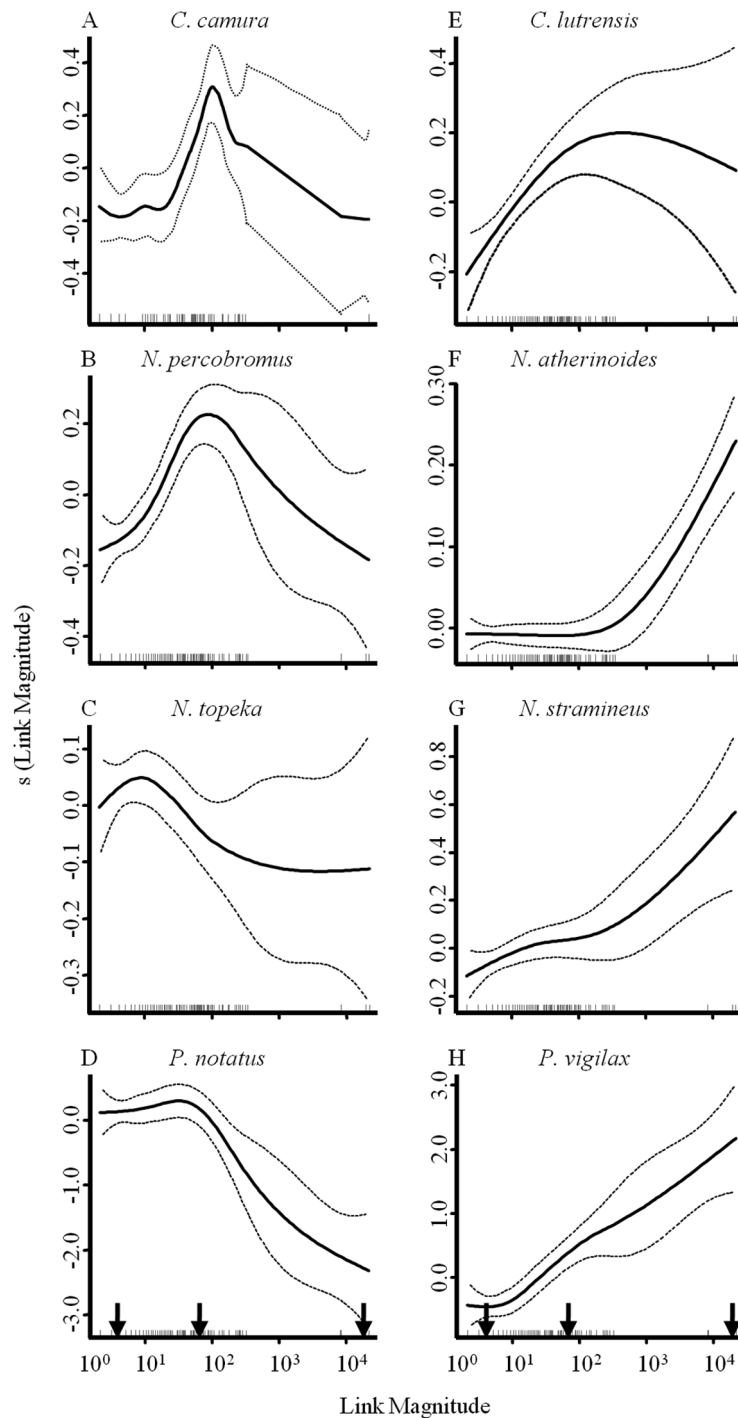
Fig. 4. Smoothing functions (solid lines) and 95% confidence bands (dotted lines) generated from GAMs showing the relationship between link magnitude (a measure of stream size) and density of (A–D) tributary and (E–H) river mainstem species. Vertical black arrows in (D) and (H) indicate link magnitudes of the small, medium, and large streams (from left to right) where field experiments were conducted for *Pimephales notatus* and *P. vigilax*. Vertical gray dashes indicate the distribution of the 221 KDWPT sites along the stream-size gradient.

Table 4. Results of two-way ANOVA showing effect of stream size, species, and interaction between stream size and species on four individual performance metrics for field mesocosm experiments.

Treatment	Survival			Growth			Storage lipids			Spawn success		
	df	F	P	df	F	P	df	F	P	df	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	0.52	1, 27	14.29	<0.001***	1, 58	16.54	0.0001***
Interaction	2, 27	4.10	0.03	2, 27	0.86	0.44	2, 27	0.49	0.62	2, 58	2.69	0.08

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 chars (*Salvelinus species*) in Japan where a temperature gradient shifts competitive superiority such that the high elevation species performs better at lower tem-
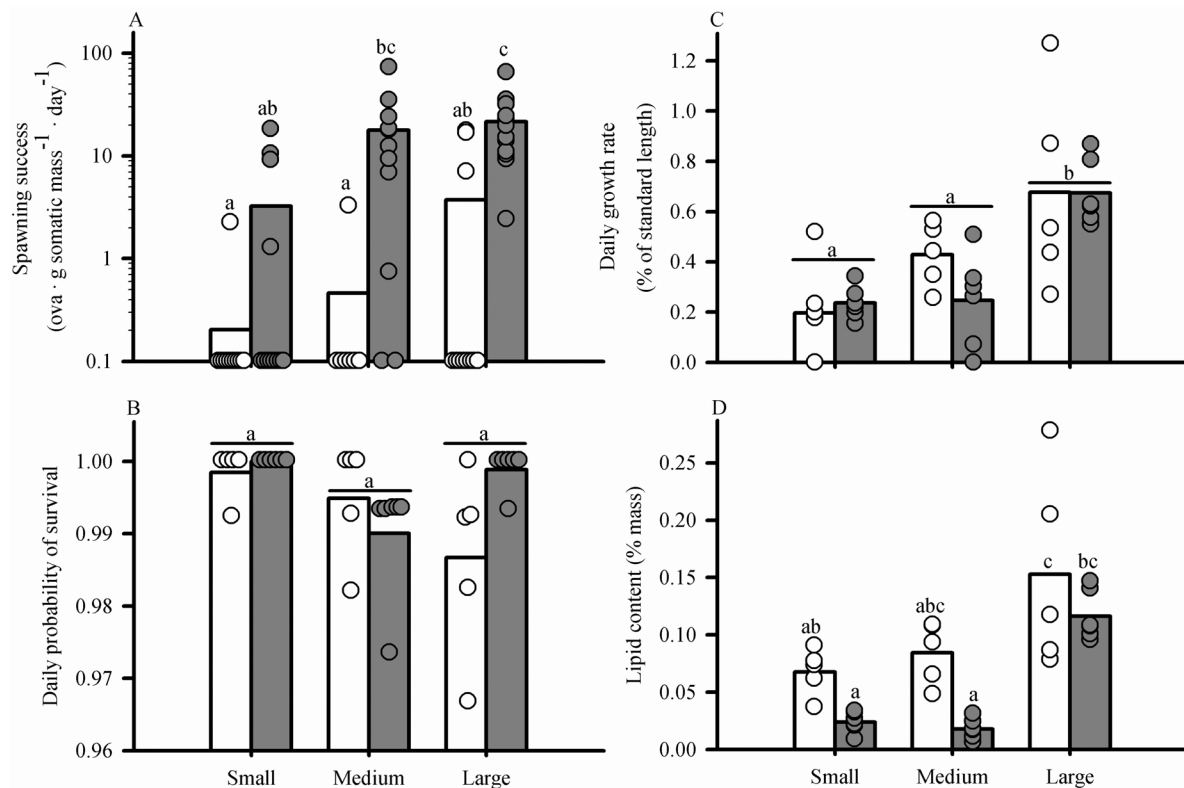

Fig. 5. Individual performance for *P. notatus* (white bars) and *P. vigilax* (gray bars) from experimental enclosures in small, medium, and large streams. (A) Adult spawning success. (B) juvenile survival rate, (C) juvenile growth rate, and (D) juvenile condition. Bars represent means for each treatment and circles represent values for each enclosure (replicate). 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.
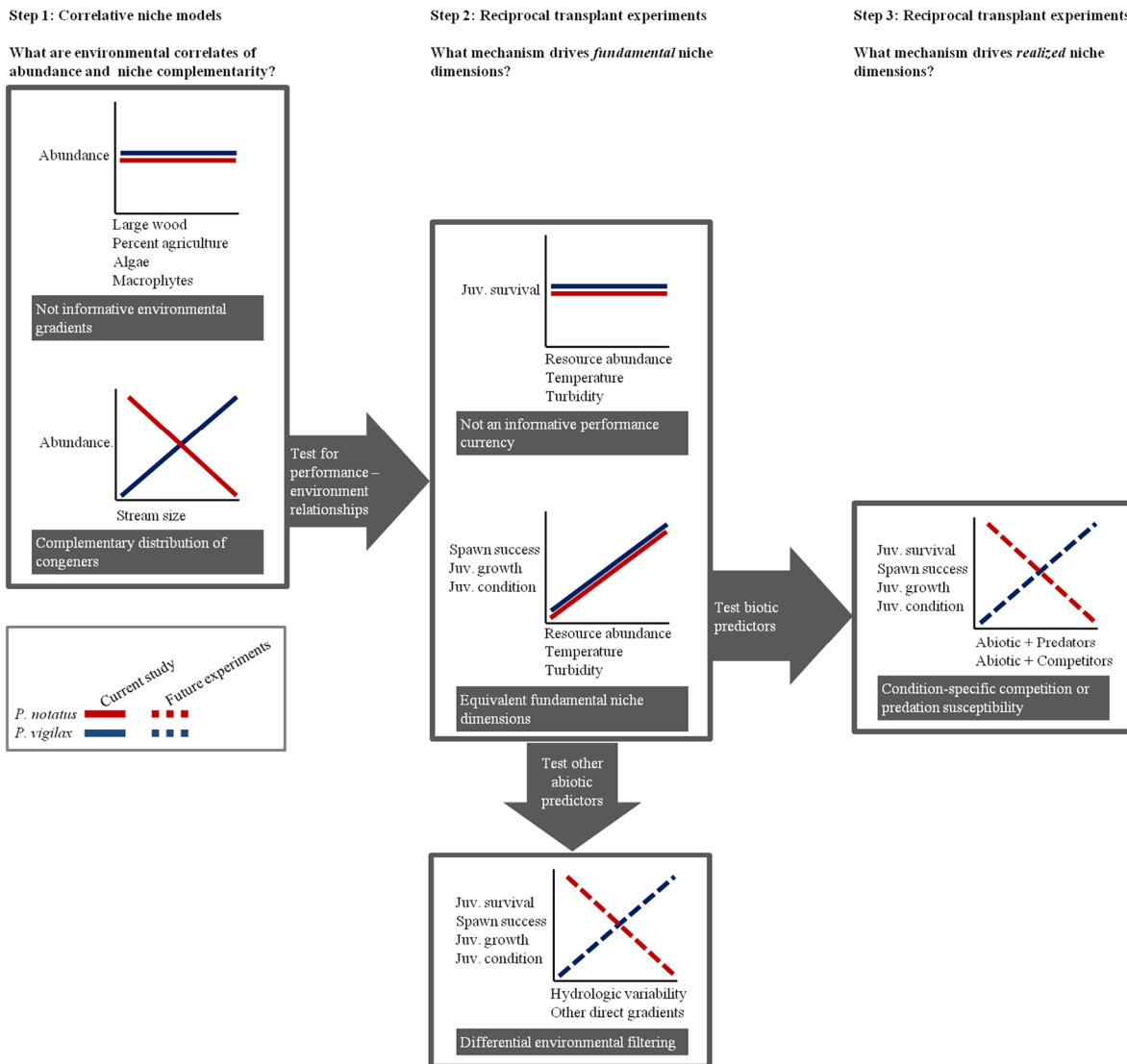
Fig. 6. A three step analytic framework for the development of mechanistically-based environmental niche models using the congeneric species pairs.

peratures 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 food resource type, 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 (Fig. 6). First, correlative environmental niche models

offer a quantitative and objective approach to identify congeners with complementary distributions as well as candidate environmental gradients which can be tested as direct environmental predictors (Fig. 6, Step 1). 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 individual performance along direct environmental gradients to identify which performance metrics are informative with regard to characterizing fundamental niche dimensions. Using reciprocal transplant field experiments, we demonstrate that several performance metrics differ in their response to environmental gradients (Fig. 6, Step 2). 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 metrics are informative whereas others are not, which demonstrates the necessity of evaluating multiple performance metrics 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). Third, our experiments suggested that two stream fish species have similar fundamental niches and point toward further experiments to test for other abiotic filters, predation susceptibility, or condition-specific competition (Fig. 6, Steps 2–3). 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.

ACKNOWLEDGMENTS

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Principal components analysis loadings of 23 environmental variables on interpretable axes. Superscripts indicate variables loading most strongly (positively or negatively) on each axis and 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

Note: Predator density is the $\log_{10}$-transformed density of adult individuals of the following piscivorous species: *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 vitrius.*