Received: 8 April 2020 | Accepted: 18 November 2020
DOI: 10.1111/fwb.13668

ORIGINAL ARTICLE

Freshwater Biology WILEY

Disentangling effects of predators and landscape factors as drivers of stream fish community structure

Lindsey A. Bruckerhoff[1,2] | **Keith B. Gido**[2] | **Michael Estey**[3] | **Pamela J. Moore**[4]

[1]Department of Watershed Sciences, Utah State University, Logan, UT, USA
[2]Division of Biology, Kansas State University, Manhattan, KS, USA
[3]Habitat and Population Evaluation Team Office of Conservation Science, U.S. Fish and Wildlife Service, Fergus Falls, MN, USA
[4]Marais des Cygnes National Wildlife Refuge, U.S. Fish and Wildlife Service, Pleasanton, KS, USA

Correspondence
Lindsey A. Bruckerhoff, Department of Watershed Sciences, Utah State University, 5210 Old Main Hill, NR 210, Logan, UT 84322, USA.
Email: lindsey.bruckerhoff@usu.edu

Funding information
Kansas State University; U.S. Fish and Wildlife Service

Abstract

1. Experimental and fine-scale studies indicate predators can have strong effects on stream fishes. It is unclear, however, how predators interact with landscape factors to influence stream fish communities at scales relevant to management and conservation. Because predators and prey respond to environmental variability, measuring community responses to predators requires resolving the effects of abiotic factors on both predators and prey.
2. We collected stream fish community data in the summers of 2017 and 2018 and paired structural equation modelling with multivariate methods to identify abiotic factors that influenced the distribution of a predatory fish, largemouth bass (*Micropterus salmoides*) and community structure of stream fish. We then compared how fish species richness and community composition responded to the presence of bass mediated by environmental factors.
3. Probability of occurrence of bass increased with catchment area, while richness responded to both natural and anthropogenic characteristics of streams and their catchments. Contrary to our prediction, richness was higher at sites with bass and several species exhibited positive co-occurrence and abundance patterns with bass, while only one species had a negative relationship.
4. Higher diversity of stream fishes in the presence of bass highlights the difficulties in understanding the combined effects of predators and environmental variation, both natural and human induced, as drivers of community structure. We discuss several challenges to understanding the effects of predators in natural systems, including unmeasured environmental variability, mismatch of spatial and temporal scales, and context dependency of ecological responses.

KEYWORDS
freshwater fish, indirect effect, introduced species, largemouth bass, predators

1 | INTRODUCTION

Do predators influence stream fish communities? This question is not only a fundamental aspect of basic community ecology, but also has implications regarding the conservation of freshwater fishes. Although stream fishes participate in all types of biotic interactions, understanding predator–prey interactions is of particular interest because predators can produce strong effects across all levels of biological organisation (Cucherousset & Olden, 2011). Further, predatory fishes have been both introduced to (Welcomme, 1988) and lost from (Estes et al., 2011; Winemiller et al., 2016) freshwater systems globally. Negative effects of introduced predators in lake systems are well known, including reduced abundance of small-bodied fishes (Jackson, 2002; MacRae & Jackson, 2001), homogenisation of freshwater fauna (Rahel, 2002), species extinctions (Kaufman, 1992; Ligtvoet et al., 1991), and changes in food web structure (Vander Zanden et al., 2004). Most of what we know about predator effects in streams has been observed at relatively fine spatial scales (mesocosm experiments or within a stream reach). Direct consumption by piscivores increases mortality rates and decreases densities of prey, mediated by predator and prey identity (Marsh-Matthews et al., 2013; Schlosser, 1987), body size (Layman & Winemiller, 2004; Magoulick, 2004; Schlosser, 1988), habitat characteristics (Angermeier, 1992; Harvey & Stewart, 1991; White & Harvey, 2001), and predator density (Gilliam & Fraser, 1987; Harvey, 1991). Non-consumptive effects are wide ranging, including well-documented shifts in habitat use (Fraser & Gilliam, 1992; Greenberg, 1994; Harvey, 1991; Magoulick, 2004; Power et al., 1985; Schlosser, 1987, 1988) and changes in prey activity levels, foraging behaviour, growth, life history, reproduction, and movement/dispersal patterns (reviewed in Hoeinghaus & Pelicice, 2010). Predators can increase emigration rates (Fraser & Gilliam, 1992; Power et al., 1985; Schaefer, 2001) or act as both barriers and promoters of dispersal (Fraser et al., 1995). While experimental studies provide evidence for several mechanisms that may elicit a variety of prey responses to predators, we do not yet understand the role of these mechanisms in structuring stream fish communities in natural stream systems or how predators interact with landscape factors to produce patterns of fish assemblage structure.

Several studies have documented effects of predators on prey fishes in natural streams. Much of this literature documents relationships between a non-native predator with one or several prey species. Nonindigenous predators can lower prey abundance at local sites (Gilliam et al., 1993; Labbe & Fausch, 2000), create source–sink dynamics (Woodford & McIntosh, 2010), and influence genetic diversity (Vanhaecke et al., 2015). Negative associations between predator–prey pairs have been observed across drainage basins, revealed through both taxonomic and functional group analysis (Giam & Olden, 2016; Hoeinghaus et al., 2007). Non-native predation pressure may be uneven throughout stream networks (Hedden et al., 2016), and non-native predators may feed disproportionately on native prey fishes relative to non-native prey (Pilger et al., 2008), altering food web dynamics and lowering abundance of native fishes (Walsworth et al., 2013). These studies highlight the potential for non-native and invasive predators to influence fish community structure, and we predict that predators interact with abiotic factors to produce patterns of stream fish community structure across stream networks.

Understanding how community structure responds to predators in stream requires isolating predation effects from abiotic drivers of community structure. Natural landscape features, including both terrestrial and stream network attributes, influence fish communities, and anthropogenic landscape modifications can significantly alter population and community dynamics of stream fishes (Allan, 2004; Schlosser, 1991). Attributes throughout a catchment interact at hierarchical spatial scales to influence the ecological integrity of streams by driving habitat characteristics, water quality, connectivity, flow regime, and biotic processes (Labbe & Fausch, 2000; Poff, 1997). Landscape context may therefore not only influence the distributions of predators and prey, and therefore where they overlap in space and time, but also influence the magnitude of predation impacts. For example, densities of native small-bodied cyprinids in the Gila River catchment of New Mexico declined during low-flow years but were lowest at sites that also had non-native *Micropterus dolomieu* (Stefferud et al., 2011). Ecologists recognise the complex interactions of landscape factors at multiple spatial scales and strive to conserve stream fish communities using a *riverscape* perspective (Fausch et al., 2002). To conserve fishes across riverscapes, we need to understand how biotic processes, such as predation, interact with abiotic factors across spatial scales to produce patterns of community assembly.

1.1 | Objectives

We assessed the effect of a predator on stream fish community structure (richness and composition) mediated by abiotic factors. Our goal was to identify abiotic drivers of fish community structure and the presence of predators, then control for abiotic drivers to assess how fish community structure in prairie streams responded to the presence of a widely introduced predator, largemouth bass (*Micropterus salmoides*, Centrarchidae). Largemouth bass, while probably native to the eastern edge of our study area (Flint Hills ecoregion, U.S.A.), have been intensively stocked in the region and represent a potential increase in predation pressure relative to historic levels. We predicted natural attributes of stream networks, especially stream size, would drive patterns of community structure and predicted presence of largemouth bass would be positively associated with a predominant landscape modification in our study area: small impoundments. We also predicted largemouth bass would be negatively associated with cyprinid fishes (Schrank et al., 2001), driving lower species richness at sites with bass. Predation pressure in streams has probably changed and will continue to change over time in response to stocking programmes, accidental introductions, impounding waterways, overfishing, habitat fragmentation and alteration, and changing temperature and flow regimes. Stream fish communities already face challenges responding directly to these same alterations, so we need to understand how alterations in predation pressure influence fish communities to manage and conserve this threatened fauna.

2 | METHODS

2.1 | Study area

This study was conducted in Great Plains prairie streams in the Neosho and Kansas River basins in the Flint Hills ecoregion of eastern Kansas (Figure 1). Great Plains prairie streams are characterised by a large proportion of intermittent streams with highly variable

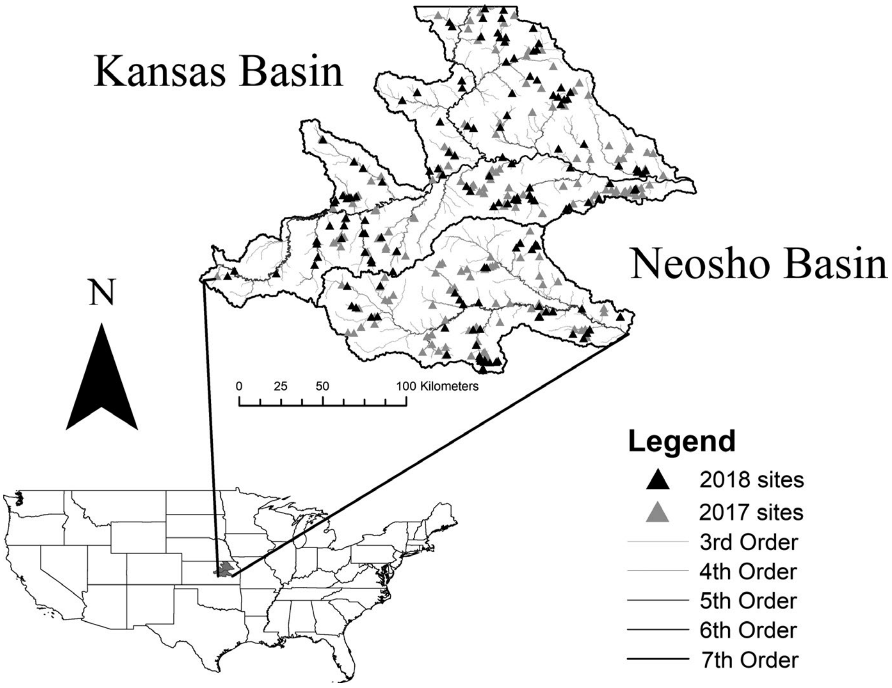

FIGURE 1 Fish communities were sampled in wadeable stream reaches throughout the Kansas and Neosho river basins in eastern Kansas, U.S.A. in 2017 and 2018.

hydrographs and catchments historically dominated by grasslands (Dodds et al., 2004). Small impoundments are a major landscape modification in and around the Flint Hills (Perkin et al., 2015). Impoundments are often stocked with sportfishes (especially largemouth bass) that may increase predation in nearby streams by escaping from ponds and expanding their distribution across the landscape and likewise, occurrence of bass has increased in catchments within the study area after the construction of small impoundments (Hedden et al. unpublished data). Our study area is on the western edge of what is considered the native range of largemouth bass, but because largemouth bass have been moved around and stocked since the late 1800s (Long et al., 2015), it is likely that many largemouth bass in the study area are from stocking efforts. The non-native status of largemouth bass in our study area may be unclear, but this system provided the opportunity to investigate the relationships between altered predation pressure, abiotic factors, and stream fish assemblage structure. Although there are other native predators in the system, including other large centrarchid species such as spotted bass (*Micropterus puntulatus*) and green sunfish (*Lepomis cyanellus*), we were primarily interested in the effects of largemouth bass due to their widespread introductions, both regionally and globally, and known strong effects on stream ecosystems (Power et al., 1985)

2.2 | Site selection

Sites were selected using a random-stratified design (Bruckerhoff & Gido, 2019) with the goal of capturing both the hierarchy of stream networks (drainage basin and stream order) and land use. Major anthropogenic land use gradients in the region used for stratification included percentage of cultivated land, number of impoundments, and number of road crossings in each 10-digit Hydrologic Catalog Unit (HUC; Seaber et al., 1987) catchment within the study area. We calculated the proportion of agricultural land using Landsat raster data from the Kansas Satellite Imagery Database (KARS, 2006), the number of impoundments using both the National Wetlands Inventory (USFWS, 2018) and National Hydrography Dataset (USGS, 2016), and the number of road crossings by calculating intersections between the 2001 Topologically Integrated Geographic Encoding and Referencing (TIGER) database (US Census Bureau, 2001) and a modified stream layer based on NHD stream lines. We then classified each HUC into three classes based on 15% and 85% quantiles for the three land use variables. We randomly drew two stream segments across all combinations of stream order (first to fourth order) and the three classifications (low, medium, high) of the three land use variables (road crossing density, percent agriculture, impoundment density). We limited our sites to first to fourth order streams to target wadeable streams.

Our random stratification process provided us with around 200 stream segments with each iteration. We then tried to sample the randomly selected stream segments but were often limited by landowner permission. After a round of selected streams had been successfully or unsuccessfully sampled, a new round of sites was drawn (without replacement) and targeted for sampling.

2.3 | Stream fish and habitat sampling

We collected stream fish community data in the summers of 2017 and 2018 from several pools and riffles (mesohabitats) at each site. We aimed to sample at least two pools and two riffles at each site but were sometimes limited by habitat availability or landowner permission. Typically, we sampled enough mesohabitats to cover 8 times the median width at each site. Fishes were sampled using single pass backpack electroshocking (Smith-Root LR-20) followed by multiple seine hauls (straight seine, 4.6 × 1.8 m, 3.2-mm mesh) in all habitat types (debris, vegetation, root wads, etc.) within each mesohabitat. Only electrofishing was used in riffle mesohabitats. Most fish were identified, measured, counted, and released in the field, except small specimens difficult to identify in the field were preserved in a 10% formalin solution and identified in the laboratory.

We measured habitat characteristics in all sampled mesohabitats. Width was measured at a minimum of three transects in each mesohabitat (more transects were added in pools or riffles longer than 30 m). Along each transect, we documented the depth and substrate type (modified Wentworth scale; Wentworth, 1922) for five points and measured canopy cover using a densiometer at the centre of each transect. We also measured the length of each mesohabitat and the dimensions of any cover habitat (root wads, overhanging vegetation, boulders, log complexes, etc.).

2.4 | Geospatial data

We delineated catchment boundaries of all sampled sites using Arc Hydro Tools in ArcMap 10.4 (ESRI, 2011) using digital elevation models from the National Elevation Dataset (USGS, 2002) and stream lines from the National Hydrography Dataset (USGS, 2016). Use of the term *catchment* in this paper refers to true upstream catchments delineated from the downstream point of all sites (Omernik et al., 2017). Within each catchment, we calculated the area, density of roads, the proportion of catchment surface area impounded, and proportion of cultivated land (cropland planted with corn, soybeans, sorghum, winter wheat, or alfalfa, or land used as fallow or planted with multiple crops) using the same datasets used in stratification procedures. We also calculated the linear distance to the nearest impoundment from each site.

2.5 | Analysis

We first identified abiotic drivers of largemouth bass presence, stream fish richness, and community composition. By identifying abiotic drivers, we could then control for these factors while assessing the effects of largemouth bass on stream fish community richness and composition. All abiotic factors included in analyses and transformations used to improve linearity and minimise variability are included in Table 1. The decision to transform variables was made before running models based on histograms of each predictor variable. Because our goal was to control for abiotic variables when assessing the influence of largemouth bass on stream fish communities, we first needed to identify which abiotic variables were associated with largemouth bass presence, richness, and community composition. Our overall framework included developing a single model that included all potential predictors for each response variable, identifying significant abiotic predictors, and then running final models that included identified abiotic predictors and the effect of largemouth bass presence. Because we completed two tests (narrowing abiotic predictors and testing effects of predators) on each response variable (richness, abundance-based composition, presence/absence-based composition), we used Bonferroni-adjusted α levels (97.5% confidence intervals and an adjusted α level of 0.025) to control for potentially inflated Type I errors. Correlations between predictor variables were assessed before building models. The proportion of upstream area

TABLE 1 Abiotic variables included in richness and composition models were collected at catchment and reach scales

Scale	Variable	Description	Transformation
Catchment	Catchment area (km^2)	Total upstream catchment area from the downstream point of each sample site	Logarithmic
	Proportion of catchment agriculture	Proportion of agricultural land in each catchment	Square root
	Proportion of catchment impounded	Proportion of impounded area in each catchment	Logarithmic
	Catchment road crossing density (no. per km^2)	Density of road crossings (all road types) in each catchment	Logarithmic
Reach	Distance to nearest impoundment (km)	Euclidean distance to nearest impoundment	Logarithmic
	Proportion of large substrates	Proportion of samples containing pebble, cobble, or boulder substrates using a modified Wentworth scale (Wentworth, 1922)	None
	Mean Depth	Mean pool depth at each site	Logarithmic

impounded had a high variance inflation factor in the preliminary richness model, so it was dropped from that analysis. All other predictor variables had variance inflation factors <2 in all models, so multicollinearity was not considered an issue. All analyses were completed in Microsoft R Open 3.5.3 (Microsoft Corporation & R Core Team, 2019).

2.5.1 | Largemouth bass presence and richness

We used binomial generalised linear mixed effect models with logit link function with presence of largemouth bass as a response and Gaussian mixed effect models with rarefied richness as a response to identify abiotic variables driving richness and largemouth bass presence. We used rarefied richness to control for different probabilities of detecting more species with different numbers of individuals sampled using Hurlbert's (1971) equation based on a sample size equal to the mean number of individuals caught across all sites (320 individuals). We used the mean number of individuals caught across all sites instead of the minimum number caught because the minimum number of individuals caught at a site was only two. By using the mean, richness values were not corrected at sites in which fewer fish were captured, and richness was corrected (lowered) at sites in which more than 320 individuals were captured. We also ran models using raw richness values and observed the same patterns, so only rarefied richness is presented here. Because we were interested in using generalised linear mixed effect models as a variable reduction tool and were not interested in interactive effects, we only developed global, additive effect models for each response variable. To account for spatial autocorrelation in fish community structure responses to abiotic factors (Bruckerhoff et al., 2019), we included HUC level 10 catchment nested within major drainage basin as a random effect to control for spatial clumping of sites within catchments. Year was also included as a main effect in all models. We developed a single model for each response variable and used these models to identify variables to be included in further analysis directly testing the effect of largemouth bass on species richness mediated by abiotic factors. We only retained variables for further analysis in which 97.5% confidence intervals, calculated using both the Wald method and likelihood ratio tests, did not include 0. All mixed effect models were developed using the package *lme4* (Bates et al., 2015).

A structural equation model (SEM) was developed to test the relationship between presence of largemouth bass and stream fish species richness using the package *piecewiseSEM* (Lefcheck, 2016). Structural equation models allow for the simultaneous analysis of multiple predictors and response variables (Shipley, 2000). The package *piecewiseSEM* allows SEM to be applied to generalised, mixed effect models and uses directed acyclic SEM, in which goodness of fit is determined using Shipley's test of directed separation (Shipley, 2000, 2009). We constructed a single SEM model that included abiotic variables identified in exploratory generalised linear mixed effect models as predictors of largemouth bass presence and rarefied richness. The mediated effect of largemouth bass presence on richness, the predictor of primary interest, was also included. We also included the random effect of HUC level 10 catchment nested within major basin across all paths to control for spatial clumping of sites within drainages. No latent variables were included in our model. In addition to SEM, we also compared conditional r^2 values obtained from a linear mixed effect model including only the effect of abiotic variables to a model including abiotic variables and the presence of largemouth bass as predictors. We included this comparison as an estimate of the explanatory power of including largemouth bass as a predictor of richness.

2.5.2 | Community composition

We used the function *manyglm* from the package *mvabund* (Wang et al., 2012) to identify abiotic variables influencing fish community composition and the effect of largemouth bass on community composition. This function allows individual generalised linear models to be developed for each species, provides a global estimate of significance that controls for multiple testing and can be more powerful than distance-based multivariate methods (Wang et al., 2012). We used this analysis to test the effect of largemouth bass on both the relative abundance of species and the occurrence (presence/absence) of species. Our fish community matrices for both analyses included pooled fish collected at each stream reach (mesohabitats were pooled together). We only included fish with total lengths above 30 mm to avoid bias associated with different spawning times and sampling efficiency of small fishes. We also removed largemouth bass from the community matrices because their presence was used as a predictor variable. Models were developed separately for the two drainage basins, as some species do not occur in both basins. As with largemouth bass occurrence and richness models, we included the effect of year in all models. Because random effects cannot be included in *manyglm* models, we included HUC level 10 catchment as a fixed effect. We ran two models for each community matrix: one that included all abiotic predictors and a second that only included significant abiotic predictors and the effect of largemouth bass presence. Significance of predictors at the community level were assessed using Bonferroni adjusted p values.

For our abundance-based analysis, we used negative binomial distributions appropriate for overdispersed count data. To eliminate the influence of rare species, only species present in at least 5% of samples were used. Since these models included raw counts, we included the total number of individuals captured at each site as a predictor variable. This allows the interpretation of results to be similar to interpreting relative abundance of species to control for varying effort in sampling across sites but avoids the quantitative difficulties of using relative abundances (proportions) as response variables (Warton & Hui, 2011). For the presence/absence analysis, we did not remove rare species as was done for the abundance analyses and models were built using a binomial distribution appropriate for binary data.

3 | RESULTS

Our final dataset included abiotic and fish community data for 336 stream sites (188 sites in 2017, 148 in 2018; Figure 1), with catchment area of sites ranging 0.06–725.74 km^2. Fifty-five species (Table S1) were captured across all sites, and mean species richness was 10 species. We collected largemouth bass at 26% of sites.

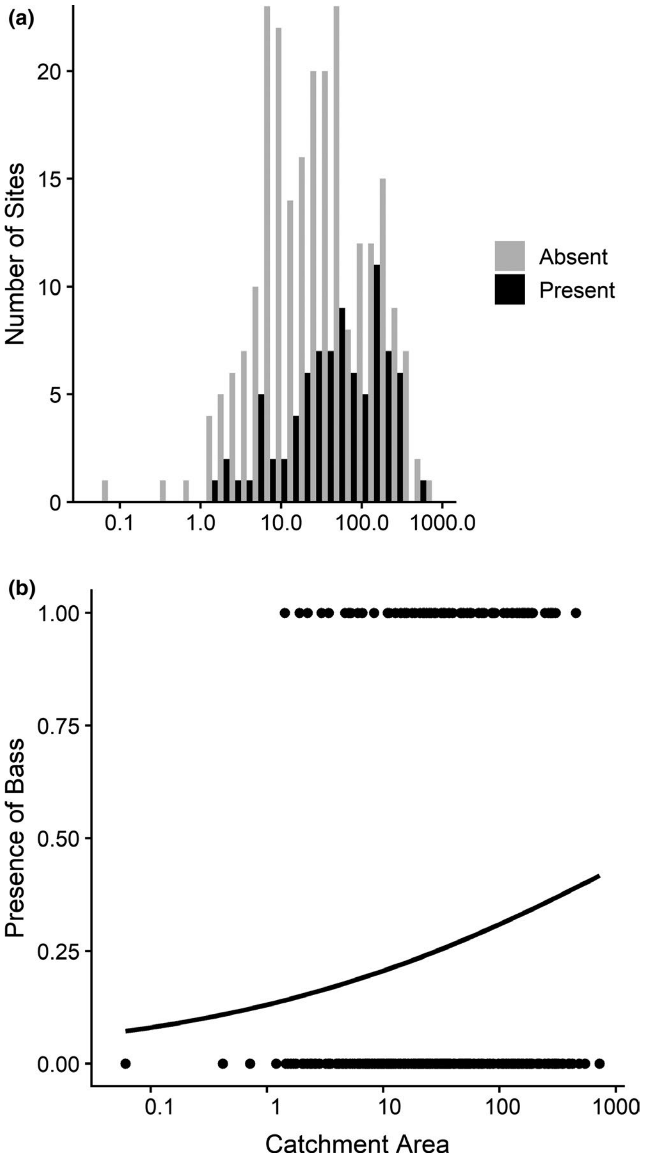

FIGURE 2 Bass were present at more sites with larger catchment areas (a), and the probability of occurrence of bass increased positively with catchment area across all sites (b). Catchment area (km^2) is displayed on a log-transformed axis in both panels and the line displays the predicted probability of occurrence while points display raw data of bass presences and absences in panel b

Preliminary mixed effect models suggested probability of largemouth bass occurrence increased with catchment area (Figure 2), so this was the only predictor of largemouth bass presence included in the SEM (Table 2). We included substrate size, mean depth, catchment agriculture, road crossing density, and catchment area as predictors of richness (Table 2) based on preliminary mixed effect models. We therefore only included catchment area as a predictor of largemouth bass presence, but included links of all other abiotic factors and largemouth bass as drivers of richness in the SEM. Shipley's test of directed separation produced a Fisher's *C* of 8.122 and *p* value of 0.42, indicating good model fit and no missing paths in the model. The estimated conditional r^2 was 0.49 for richness and 0.06 for the presence of largemouth bass. All paths were significant (Table 2). Richness increased in response to catchment area, the proportion of large substrates and mean pool depth, but decreased with increasing catchment agriculture and density of road crossings (Figure 3). Largemouth bass presence had the strongest effect on richness, with an increase of around four species at sites with largemouth bass mediated by environmental factors included in SEM (no largemouth bass: predicted richness = 8.9, *SE* = 0.18; largemouth bass present: predicted richness = 13.2, *SE* = 0.26). Conditional r^2 values from linear mixed effect model indicated the model including the effect of largemouth bass described about 7% more variance (r^2 = 0.49) compared to a model only including abiotic factors (r^2 = 0.42).

The presence of largemouth bass was a significant predictor of species abundances in the Kansas basin, but not in the Neosho (Table 3). Despite significance at the community level, no individual species abundance in the Kansas basin exhibited a significant response to largemouth bass presence. Three species contributed more than 10% of deviance described by the presence of largemouth bass in the Kansas basin (yellow bullhead *Ameiurus natalis*, Ictaluridae: 16%, southern redbelly dace *Chrosomus erythrogaster*, Leuciscinae: 16%, and bluegill *Lepomis machrochirus*, Centrarchidae: 12%). Yellow bullhead and bluegill exhibited higher abundances at sites with largemouth bass, while southern redbelly dace had lower abundance at sites with largemouth bass (Figure 4) Significant abiotic predictors of species abundance included year, HUC 10 level catchment, number of individuals, catchment area, and catchment agriculture for both the Kansas and Neosho river basins (Table 3). Four species had significant negative relationships with catchment area, while one had a significant positive relationship (Supporting information). Abundance of only one species, southern redbelly dace, responded significantly (and negatively) to catchment agriculture (deviance = 21.6, *p* = 0.03).

Like patterns of abundance, largemouth bass presence was a significant predictor of species occurrences (presence/absence) in the Kansas basin, but not in the Neosho (Table 3). One species, yellow bullhead, exhibited significant, positive co-occurrence patterns with largemouth bass (deviance = 27.0, *p* = 0.01). We observed yellow bullhead at 58% of sites with bass and 21% of sites without largemouth bass. Three additional species contributed to 10% or more of the deviance, including southern redbelly

TABLE 2 The structural equation model (SEM) included predictor variables identified in preliminary mixed effect models and included the random effect of Hydrologic Catalog Unit 10 catchment level nested within major drainage basin

Response	Predictor	Estimate	*SE*	*df*	*p* value	Standardised estimate
Bass presence	Catchment area	023	0.09	322	0.01	–
Richness	Large substrate	3.30	0.87	282	<0.01	0.16
Richness	Mean depth	5.20	1.79	282	<0.01	0.13
Richness	Catchment agriculture	−2.15	0.92	282	0.02	−0.13
Richness	Road crossing density	−2.78	1.01	282	0.01	−0.13
Richness	Catchment area	1.21	0.14	282	<0.01	0.39
Richness	Bass presence	3.17	0.44	282	<0.01	0.30

Shipley's test of directed separation indicated good model fit and no missing paths (Fisher's $C = 9.10$, $p = 0.52$).

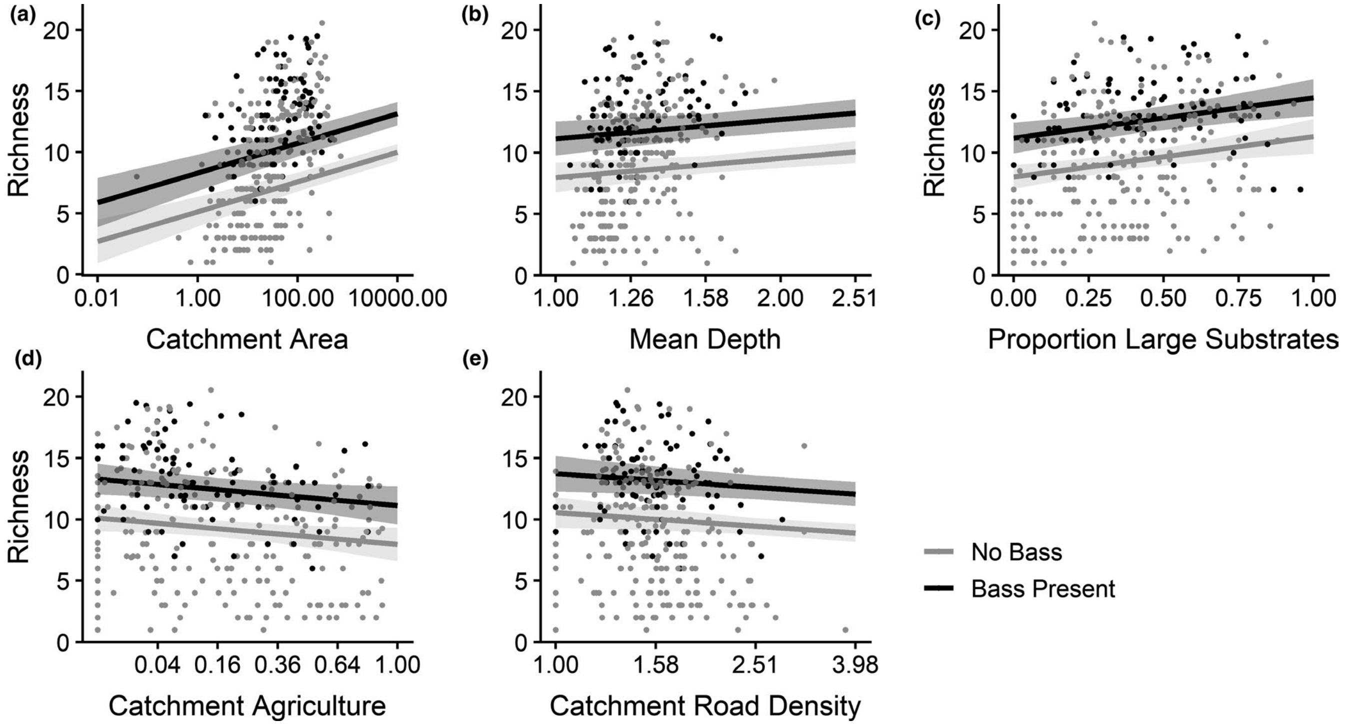

FIGURE 3 Richness increased significantly with catchment area (axis log scaled) (a), mean pool depth (axis log scaled) (b), and proportion of large substrates (c), but decreased with catchment agriculture (axis square root scaled) (d) and catchment road crossing density (axis log scaled) (e) and sites with bass had higher richness than sites without bass. Significance of these predictors was identified both based on preliminary hierarchical models and through a structural equation model; shading represents 97.5% confidence intervals around regression lines exhibited marginal means of bass and abiotic variable effects. Points are raw rarefied richness values

dace (15%), bluegill (10%), and redfin shiner (*Lythurus umbratilis*, Cyprinidae: 13%). Bluegill and redfin shiner exhibited positive, although not significant, co-occurrence patterns with largemouth bass, occurring at 63 and 42% of sites with largemouth bass but only 29 and 19% of sties without largemouth bass. Southern redbelly dace exhibited a negative co-occurrence pattern, occurring at only 10% of sites with largemouth bass and at 23% of sites without largemouth bass. In the Kansas basin, catchment area, catchment agriculture, the proportion of catchment impounded, and mean depth significantly influenced occurrence patterns (Table 3). Logperch (*Percina caprodes*, Percidae) had a significant positive relationship with mean depth (deviance = 22.9, $p = 0.01$) and common carp (*Cyprinus carpio*, Cyprinidae) had a significant, positive relationship with the proportion of the catchment impounded (deviance = 25.6, $p < 0.01$). Species specific responses to the presence of largemouth bass and abiotic factors are in Table S2.

TABLE 3 Final *manyglm* models (Wang et al., 2012) included predictors identified in preliminary models for each drainage basin; all included counts of species as predictors and year, Hydrologic Catalog Unit (HUC) level 10 catchments, and the total number of individuals captured at each site as predictors

	Kansas Basin						**Neosho Basin**					
	Abundance			**Presence/Absence**			**Abundance**			**Presence/Absence**		
Variable	***df***	**Deviance**	***p***	***df***	**Deviance**	***p***	***df***	**Deviance**	***p***	***df***	**Deviance**	***p***
HUC 10	**178**	**1,904.3**	**0.001**	**178**	**1,566.3**	**0.001**	**106**	**852.5**	**0.001**	**106**	**687.7**	**0.001**
Number of Individuals	**177**	**900.1**	**0.001**	**177**	**602.1**	**0.001**	**105**	**429.1**	**0.001**	**105**	**273.2**	**0.001**
Year	**176**	**79.2**	**0.001**	**176**	**105.9**	**0.001**	–	–	–	**104**	**78.8**	**0.003**
Landscape												
Catchment area (km^2)	**175**	**281.4**	**0.016**	**175**	**374.2**	**0.001**	104	203.6	0.065	**103**	**110.7**	**0.001**
Proportion of catchment agriculture	**174**	**106.1**	**0.002**	**174**	**136.2**	**0.001**	–	–	–	–	–	–
Proportion of catchment impounded	–	–	–	**173**	**116.3**	**0.001**	–	–	–	**102**	**64**	**0.01**
Catchment road crossing density (no. per km^2)	–	–	–	–	–	–	–	–	–	–	–	–
Local												
Distance to nearest impoundment (km)	–	–	–	–	–	–	–	–	–	–	–	–
Proportion of large substrates	–	–	–	–	–	–	–	–	–	–	–	–
Mean depth	–	–	–	**172**	**165**	**0.001**	–	–	–	–	–	–
Predators												
Bass presence	**174**	**98.5**	**0.018**	**172**	**98.4**	**0.005**	105	49	0.483	103	39.8	0.29

Note: This table indicates significance of variables in final models including the effect of bass presence on stream fish community composition for both species abundances and occurrences. Models were developed separately for each major drainage basin. Significant variables are in bold.

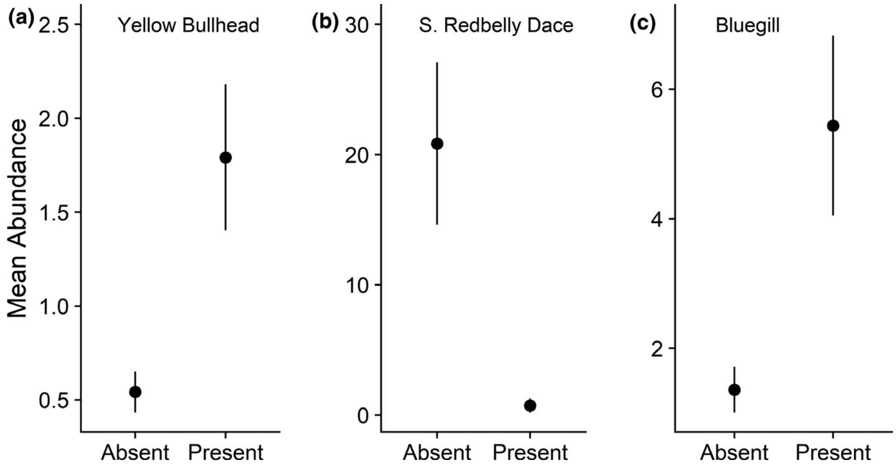

FIGURE 4 Three species, including yellow bullhead (a), southern redbelly dace (b), and bluegill (c), contributed more than 10% of deviance to the significant effect of largemouth bass on abundance-based community composition. Points represent mean abundance at sites where bass are present or absent and lines represent standard error

4 | DISCUSSION

We observed a positive association between stream fish species richness and the presence of largemouth bass. This relationship could be driven by unmeasured environmental variability or be a true outcome of biological interactions. Habitats associated with high species richness may also be good habitats for largemouth bass, but we may not have captured these important habitat conditions despite our best efforts to design a study to capture major environmental gradients. The only significant predictor of largemouth bass presence, catchment area, explained 6% in the variation in largemouth bass occurrence. The small amount of variation captured by this model probably indicates either high sampling error (variability in detecting bass) or relevant abiotic variables were not included in our analysis. Hydrology, for example, can drive stream fish community structure (Mims & Olden, 2012; Poff & Allan, 1995) and the presence of bass (Almeida & Grossman, 2014; Bae et al., 2018). Stable hydrology is typically associated with equilibrium life history strategies (Mims & Olden, 2012), and may explain co-occurrence patterns between largemouth bass and other species with similar life histories like black bullhead and bluegill. Temperature is also a strong driver of largemouth bass distributions (Bae et al., 2018; Sowa & Rabeni, 1995), but was not considered in this analysis. Temperature may have explained the negative co-occurrence and abundance patterns between southern redbelly dace and largemouth bass, as dace are known to inhabit relatively small, cool streams (Frenette et al., 2019). Sampling variability, such as local conditions at sites probably also introduced variation in our ability to detect largemouth bass presence. Further, some environmental variables could have been measured at the wrong spatial scale (Fausch et al., 2002). We predicted metrics capturing small impoundment distributions (upstream impounded area, distance to nearest impoundment) would be significant predictors of largemouth bass presence. The lack of relationship was surprising because other studies suggest largemouth bass are associated with altered flow regimes downstream of impounded waters (Almeida & Grossman, 2014; Bae et al., 2018), and another study within the Flint Hills indicated small impoundments are associated with declines in native and endangered fishes, presumably by supplementing largemouth bass populations in streams through emigration (Mammolitti, 2002; Schrank et al., 2001). It is possible that our summary metrics of small impoundment distributions were measured at spatial scales weakly related to the responses measured, potentially biasing observed relationships between predators and fish community structure. Developing innovative techniques for identifying and capturing potentially confounding factors is critical in field-based studies of biotic interactions and may have particularly important implications for studying impacts of non-native species (see Challenges and Future Directions and Conclusions).

In addition to unmeasured habitat conditions, theory would suggest positive associations between stream fish species richness and largemouth bass may be due to facilitation. Predators can contribute to increased richness by disproportionately feeding on competitive species, acting as a *keystone predator* (Paine, 1969). Thus, predation might allow coexistence by preventing competitive exclusion (Caswell, 1978; Paine, 1966). It is possible largemouth bass promote coexistence, and therefore higher richness, by reducing the intensity of competitive interactions among competitors. Predators also might maintain increased diversity and coexistence by preventing *mesopredator release* (Ritchie & Johnson, 2009), in which loss of apex predators allows lower trophic level predators to increase in abundance, causing declines or local extinction of prey species (Courchamp et al., 1999). We did not, however, observe higher densities of any species (except southern redbelly dace) expected to be a strong predator or competitor at sites in which largemouth bass were absent, which is inconsistent with these mechanisms of coexistence. Conversely, we actually observed increased abundance and occurrence of another predator, yellow bullhead, at sites with largemouth bass. Although field studies across organisms and systems, including streams (Rodríguez-Lozano et al., 2015), suggest predation can facilitate coexistence (Gurevitch et al., 2000; Ritchie & Johnson, 2009), we express caution in this interpretation of our results without corresponding empirical evidence.

In addition to predator associations with richness, predators can also influence community composition. Largemouth bass co-occurred with yellow bullhead, and although not statistically significant, possibly due to low statistical power, we were able to identify several other species likely to be contributing to the significant effect of largemouth bass at the community level, including bluegill. Larger prey species, such as bullheads and bluegill, might not respond negatively to largemouth bass due to gape limitation. Hambright (1994) found gape-limited predation can lead to dominance by deep-bodied species when fish communities are made up of a mix of body sizes. Thus, positive associations with bluegill and bullhead species could be driven by largemouth bass consuming shallow-bodied species (Hambright, 1991), such as minnows. Although juvenile bullhead (Phelps et al., 2005; Rickett, 1976) and bluegill (Olsen, 1996; Turner & Mittelbach, 1990) are known prey of largemouth bass, these species are probably too large or difficult to handle (due to spines) to be consumed by largemouth bass after they reach some threshold size. Escaping predation by growing to large sizes is an evolutionary response of prey fish to predators (Reznick et al., 1990) and potentially a mechanism contributing ecosystem dynamics in reservoir systems (e.g. *Dorosoma cepedianum*, Michaletz, 1998; Noble, 1981; Vanni et al., 2005), so it is possible that similar size-based interactions influence stream fish community structure.

The shared evolutionary history between largemouth bass and the fish communities in this study may have also influenced observed relationships. Many fish species in the study area are piscivorous at least at some point in their life or share a similar trophic role as largemouth bass (e.g. spotted bass *Micropterus punctulatus*). The prairie stream fishes face predation from many sources, so community responses to predation are likely to involve multiple predators and complex linkages across species. Further, we consider largemouth bass supplemented predators in the system, as largemouth bass are frequently stocked in impoundments, increasing their occurrence (Hedden et al. unpublished data) and potentially density in streams. These stream fish communities are probably not naïve to largemouth bass and may have antipredator behaviours that would minimise top-down, consumptive effects of supplemented largemouth bass in the system (Sih et al., 2010). Our results may support the idea that stocking native fish predators for recreational fishing may therefore be less detrimental to native fish communities than stocking non-native predators. However, native predators may still exert strong non-consumptive effects on native fish (Power et al., 1985; Sih et al., 2010), albeit our study was probably at too broad a spatial scale to pick up non-consumptive effects.

Fish community structure, including richness and composition, responded to both natural variation in stream habitats and landscape alterations. As expected, species richness increased positively with stream size, pool depth, and the proportion of large substrates (Schlosser, 1987) but decreased with increasing road crossing density and catchment agriculture (Allan, 2004; Perkin & Gido, 2012; Wang et al., 1997). Road crossings can fragment stream systems, especially on smaller-order streams, leading to less accessibility and lower species richness (Perkin & Gido, 2012). Upstream agriculture can lead to lower species richness and shifts in community structure due to changes in water chemistry, altered flow regimes, and increased sediment inputs (Allan, 2004). We also detected significant responses of fish communities to catchment agriculture and upstream impoundments. Southern redbelly dace had a negative relationship with agriculture, which has been observed in other studies (Stasiak, 2007), and common carp exhibited a positive relationship with the proportion of the catchment impounded, which is likely to be a result of the prevalence of carp in larger reservoirs. Overall, our targeted sampling to capture these complex environmental gradients allowed us to quantify responses of fishes to landscape alterations and natural heterogeneity, which is often difficult to detect (Bruckerhoff & Gido, 2019). Even accounting for these known gradients revealed complex relationships between stream fish community structure and the presence of predators.

5 | CHALLENGES AND FUTURE DIRECTIONS

Quantifying predator effects requires disentangling complex interactions between predators, prey, and the abiotic environment, which presents several challenges. As already discussed, it is difficult to capture all sources of variability driving both predator distributions and abundance and stream fish community structure. Despite our best efforts, including a sampling protocol designed specifically to capture landscape gradients, we predict some of the associations between predator presence and community structure observed here were probably driven by unmeasured environmental variability or other factors influencing stream fish. Further, predator effects are likely to be context dependent, interactive, and plastic, so that the effects of a predator on community structure is likely to be dependent on the abiotic and biotic context in which interactions take place. Predator behaviors, diets, and interactions with other species may be plastic (Chamberlain et al., 2014), so that the same species effects on communities in one context may not predict effects in another (Preston et al., 2018). Last, measuring prey responses to predators is confounded by bias associated with the scale in which measurements are made. For example, consumption rates are known to vary across different scales of measurement (Englund & Leonardsson, 2008) and are typically underestimated at fine scales (Bruckerhoff et al., unpublished data). In the current study, estimates of species richness, occurrences, and relative abundance may also be influenced by the scale at which we measured these responses (reach scale), potentially biasing estimates of predator effects.

6 | CONCLUSIONS

Predator–prey interactions are complex, but critical to understand as we try to manage diverse assemblages of native and non-native fishes. Our study design revealed a positive relationship between largemouth bass and fish species richness, but did not provide insight into the mechanisms driving this relationship or any long-term changes in community composition in response to largemouth bass expansion in the study area. To better quantify how predators shape communities in stream systems, we need more mechanistic studies of predator effects on community structure and ecosystem processes. Long-term, manipulated studies at coarse scales, such as replicated catchments, are probably the best way to understand both the context dependency and long-term outcomes of predators being both lost from and introduced into systems. Unfortunately, decisions to remove or control predators need to be made now, so allocating time and resources to more mechanistic studies is not always feasible. Our data help establish a baseline of expectations when quantifying predator effects in natural systems, and we hope our efforts set the path for other researchers to think creatively about how to understand the role of predators in structuring stream fish communities in the context of continued landscape modification, species introductions, and species declines to better conserve freshwater fishes.

ACKNOWLEDGMENTS

We thank the U.S. Fish and Wildlife Service Directorate Fellowship Program for introducing the coauthors and for funding the initial stages of this work. Funding was provided by Kansas State University and U.S. Fish and Wildlife Service Habitat and Population Evaluation Team. We also thank Chase Beyer, Matt Couchman, Austin Earl, Tanna Fanshier, Sam Forbes, Andrew Frazier, Jennie Girll, Andrew Hagemann, Sky Hedden, Garrett Hopper, Kristin Kersten, Donovan Michael, Casey Pennock, Kelsey Porter, Elizabeth Renner, Emily Samuel, and John Smith for field assistance. All applicable institutional and/or national guidelines for the care and use of animals were followed under Kansas Department of Wildlife, Parks, and Tourism permit No. 842778789, U.S. Fish and Wildlife Service permit No. TE067729-4 and Kansas State University Institutional Animal Care and Use Committee permit No. 3746.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

ORCID

Lindsey A. Bruckerhoff https://orcid.org/0000-0002-9523-4808
Keith B. Gido https://orcid.org/0000-0002-4342-161X

REFERENCES

Allan, J. D. (2004). Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122

Almeida, D., & Grossman, G. (2014). Regulated small rivers as 'nursery' areas for invasive largemouth bass *Micropterus salmoides* in Iberian waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(6), 805–817. https://doi.org/10.1002/aqc.2425

Angermeier, P. L. (1992). Predation by rock bass on other stream fishes: Experimental effects of depth and cover. *Environmental Biology of Fishes*, *34*(2), 171–180. https://doi.org/10.1007/BF00002392

Bae, M. J., Murphy, C. A., & Garcí-Berthou, E. (2018). Temperature and hydrologic alteration predict the spread of invasive largemouth bass (*Micropterus salmoides*). *Science of the Total Environment*, *639*(15), 58–66. https://doi.org/10.1016/j.scitotenv.2018.05.001

Bates, D., Maechler, M., Bolker, B. J., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bruckerhoff, L. A., & Gido, K. B. (2019). Assessing site-selection strategies for modeling the influence of landscape factors on stream fish assemblages. In R. M. Hughes, D. M. Infante, L. Wang, K. Chen, & B. de Freitas Terra (Eds.), *Advances in understanding landscape influences on freshwater habitats and biological assemblages* (pp. 159–178). American Fisheries Society Symposium 90.

Bruckerhoff, L. A., Leasure, D. R., & Magoulick, D. D. (2019). Flow–ecology relationships are spatially structured and differ among flow regimes. *Journal of Applied Ecology*, *56*, 398–412. https://doi.org/10.1111/1365-2664.13297

Caswell, H. (1978). Predator-mediated coexistence: A nonequilibrium model. *The American Naturalist*, *112*(983), 127–154. https://doi.org/10.1086/283257

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *14*, 881–980. https://doi.org/10.1111/ele.12279

Courchamp, F. J., Langlais, M., & Sugihara, G. (1999). Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology*, *68*(2), 282–292. https://doi.org/10.1046/j.1365-2656.1999.00285.x

Cucherousset, J., & Olden, J. D. (2011). Ecological impacts of nonnative freshwater fishes. *Fisheries*, *36*, 215–230. https://doi.org/10.1080/03632415.2011.574578

Dodds, W. K., Gido, K. B., Whiles, M. R., Fritz, M., & Matthews, W. J. (2004). Life on the edge: The ecology of Great Plains prairie streams. *BioScience*, *54*(3), 205–216.

Englund, G., & Leonardsson, K. (2008). Scaling up the functional response for spatially heterogeneous systems. *Ecology Letters*, *11*, 440–449. https://doi.org/10.1111/j.1461-0248.2008.01159.x

ESRI (2011). *ArcGIS desktop: Release 10*. Environmental Systems Research Institute.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, *333*, 301–306. https://doi.org/10.1126/science.1205106

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes: A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience*, *52*(6), 483–498.

Fraser, D. F., & Gilliam, J. F. (1992). Nonlethal impacts of predator invasion: Facultative suppression of growth and reproduction. *Ecology*, *73*(3), 959–970. https://doi.org/10.2307/1940172

Fraser, D. F., Gilliam, J. F., & Yip-Hoi, T. (1995). Predation as an agent of population fragmentation in a tropical watershed. *Ecology*, *76*(5), 1461–1472. https://doi.org/10.2307/1938148

Frenette, B. D., Bruckerhoff, L. A., Tobler, M., & Gido, K. B. (2019). Temperature effects on performance and physiology of two prairie stream minnows. *Conservation Physiology*, *7*(1). https://doi.org/10.1093/conphys/coz063

Giam, X., & Olden, J. D. (2016). Environment and predation govern fish community assembly in temperate streams. *Global Ecology and Biogeography*, *25*(10), 1194–1205. https://doi.org/10.1111/geb.12475

Gilliam, J. F., & Fraser, D. F. (1987). Habitat selection under predation hazard: Test of a model with foraging minnows. *Ecology*, *68*(6), 1856–1862. https://doi.org/10.2307/1939877

Gilliam, J. F., Fraser, D. F., & Alkins-Koo, M. (1993). Structure of a tropical stream fish community: A role for biotic interactions. *Ecology*, *74*(6), 1856–1870. https://doi.org/10.2307/1939943

Greenberg, L. A. (1994). Effects of predation, trout density and discharge on habitat use by brown trout, *Salmo trutta*, in artificial streams. *Freshwater Biology*, *32*(1), 1–11. https://doi.org/10.1111/j.1365-2427.1994.tb00860.x

Gurevitch, J. J., Morrison, A., & Hedges, L. V. (2000). The interaction between competition and predation: A meta-analysis of field experiments. *The American Naturalist*, *155*(4), 435–453. https://doi.org/10.1086/303337

Hambright, K. D. (1991). Experimental analysis of prey selection by Largemouth Bass: Role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society*, *120*(4), 500–508. https://doi.org/10.1577/1548-8659(1991)120%3C0500:EAOPSB%3E2.3.CO;2

Hambright, K. D. (1994). Morphological constraints in the piscivore-planktivore interaction: Implications for the trophic cascade hypothesis. *Limnology and Oceanography*, *39*(4), 897–912. https://doi.org/10.4319/lo.1994.39.4.0897

Harvey, B. C. (1991). Interactions among stream fishes: Predator-induced habitat shifts and larval survival. *Oecologia*, *87*, 29–36. https://doi.org/10.1007/BF00323776

Harvey, B., & Stewart, A. (1991). Fish size and habitat depth relationships in headwater streams. *Oecologia*, *87*, 336–342. https://doi.org/10.1007/BF00634588

Hedden, S. C., Gido, K. B., & Whiteny, J. E. (2016). Introduced flathead catfish consumptive demand on native fishes of the upper Gila River, New Mexico. *North American Journal of Fisheries Management*, *36*(1), 55–61. https://doi.org/10.1080/02755947.2015.1111280

Hoeinghaus, D. J., & Pelicice, F. M. (2010). Lethal and nonlethal effects of predators on stream fish species and assemblages: A synthesis of predation experiments. In K. B. Gido, & D. A. Jackson (Eds.), *Community ecology of stream fishes: Concepts, approaches, and techniques* (pp. 619–648). American Fisheries Society Symposium.

Hoeinghaus, D. J., Winemiller, K. O., & Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, *34*(2), 324–338. https://doi.org/10.1111/j.1365-2699.2006.01587.x

Hurlbert, S. H. (1971). The non-concept of species diversity: A critique and alternative parameters. *Ecology*, *52*(4), 577–586. https://doi.org/10.2307/1934145

Jackson, D. A. (2002). Ecological effects of *Micropterus* Introductions: The dark side of black bass. In D. P. Phillip, & M. S. Ridgway (Eds.), *Black Bass: Ecology, conservation, and management* (pp. 221–232). American Fisheries Society Symposium 31.

Kansas Applied Remote Sensing (KARS) Program (2006). *Kansas Satellite Image Database (KSID) 2004–2005*. Retrieved from http://www.kansasgis.org/

Kaufman, L. (1992). Catastrophic change in species-rich freshwater ecosystems. *BioScience*, *42*, 846–858. https://doi.org/10.2307/1312084

Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774–1791. https://doi.org/10.1890/1051-0761(2000)010[1774:DOISHR]2.0.CO;2

Layman, C. A., & Winemiller, K. O. (2004). Sized-based responses of prey to piscivore exclusion in a species-rich Neotropical river. *Ecology*, *85*(5), 1311–1320. https://doi.org/10.1890/02-0758

Lefcheck, J. S. (2016). PiecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Ligtvoet, W., Witte, F., Goldschmidt, T., Van Oijen, M., Wanink, J. H., & Goudswaard, P. C. (1991). Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology*, *42*, 214–232. https://doi.org/10.1163/156854291X00298

Long, J. M., Allen, M. S., Porak, W. F., & Suski, C. D. (2015). A historical perspective of black bass management in the United States. In M. D. Tringali, J. M. Long, M. S. Allen, & T. Birdsong (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (pp. 99–122). American Fisheries Society Symposium 82.

MacRae, P. A., & Jackson, D. A. (2001). The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 342–351. https://doi.org/10.1139/f00-247

Magoulick, D. D. (2004). Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia*, *527*(1), 209–221. https://doi.org/10.1023/B:HYDR.0000043302.32382.59

Mammolitti, C. S. (2002). The effects of small watershed impoundments on native stream fishes: A focus on the Topeka shiner and hornyhead chub. *Transactions of the Kansas Academy of Science*, *105*, 219–231. https://doi.org/10.1660/0022-8443(2002)105[0219:TEOSWI]2.0.CO;2

Marsh-Matthews, E., Thompson, J., Matthews, W. J., Gehever, A., Franssen, N. R., & Barkstedt, J. (2013). Differential survival of two minnow species under experimental sunfish predation: Implications for re-invasion of a species into its native range. *Freshwater Biology*, *58*(8), 1745–1754. https://doi.org/10.1111/fwb.12165

Michaletz, P. H. (1998). Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. *North American Journal of Fisheries Management*, *18*(1), 114–123. https://doi.org/10.1577/1548-8675(1998)018%3C0114:PCOGSI%3E2.0.CO;2

Microsoft Corporation and R Core Team (2019). *Microsoft R Open 3.5.3*.

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*(1), 35–45. https://doi.org/10.1890/11-0370.1

Noble, R. L. (1981). Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society*, *110*(6), 738–750. https://doi.org/10.1577/1548-8659(1981)110%3C738:MOFFII%3E2.0.CO;2

Olsen, M. H. (1996). Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. *Ecology*, *77*(1), 179–190. https://doi.org/10.2307/2265667

Omernik, J. M., Griffith, G. E., Hughes, R. M., Glover, J. B., & Weber, M. H. (2017). How misapplication of the hydrologic unit framework diminishes the meaning of watersheds. *Environmental Management*, *60*, 1–11. https://doi.org/10.1007/s00267-017-0854-z

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65–75. https://doi.org/10.1086/282400

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, *103*, 91–93. https://doi.org/10.1086/282586

Perkin, J. S., & Gido, K. B. (2012). Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications*, *22*(8), 2176–2187. https://doi.org/10.1890/12-0318.1

Perkin, J. S., Gido, K. B., Cooper, A. R., Turner, T. F., Osborne, M. J., Johnson, E. R., & Mayes, K. B. (2015). Fragmentation and dewatering transform Great Plains stream fish communities. *Ecological Monographs*, *85*(1), 73–92. https://doi.org/10.1890/14-0121.1

Phelps, Q. E., Ward, M. J., Paukert, C. P., Chipps, S. R., & Willis, D. W. (2005). Biotic and abiotic correlates with black bullhead population characteristics in Nebraska Sandhill lakes. *Journal of Freshwater Ecology*, *20*(2), 295–302. https://doi.org/10.1080/02705060.2005.9664969

Pilger, T. J., Franssen, N. R., & Gido, K. B. (2008). Consumption of native and nonnative fishes by introduced largemouth bass (*Micropterus salmoides*) in the San Juan River, New Mexico. *The Southwestern Naturalist*, *53*, 105–108. https://doi.org/10.1894/0038-4909(2008)53[105:CONANF]2.0.CO;2

Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, *16*(2), 391–409. https://doi.org/10.2307/1468026

Poff, N. L., & Allan, J. D. (1995). Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology*, *76*(2), 606–627. https://doi.org/10.2307/1941217

Power, M. E., Matthews, W. J., & Stewart, A. J. (1985). Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology*, *66*(5), 1448–1456. https://doi.org/10.2307/1938007

Preston, D. L., Henderson, J. S., Falke, L. P., Segui, L. M., Layden, T. J., & Novak, M. (2018). What drives interaction strengths in complex food webs? A test with feeding rates of a generalist stream predator. *Ecology*, *99*(7), 1591–1601. https://doi.org/10.1002/ecy.2387

Rahel, F. J. (2002). Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*, *33*, 291–315. https://doi.org/10.1146/annurev.ecolsys.33.010802.150429

Reznick, D. A., Bryga, H., & Endler, J. A. (1990). Experimentally induced life-history evolution in a natural population. *Nature*, *346*, 357–359. https://doi.org/10.1038/346357a0

Rickett, J. D. (1976). Growth and reproduction of largemouth bass and black bullheads cultured together. *The Progressive Fish-Culturist*, *38*(2), 82–85. https://doi.org/10.1577/1548-8659(1976)38[82:GAROLB]2.0.CO;2

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*, 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Rodríguez-Lozano, P., Verkaik, I., Rieradevall, M., & Prat, N. (2015). Small but powerful: Top predator local extinction affects ecosystem structure and function in an intermittent stream. *PLoS One*, *10*(2), e0117630. https://doi.org/10.1371/journal.pone.0117630

Schaefer, J. (2001). Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum* and *Cyprinella venusta*). *Freshwater Biology*, *46*(3), 379–388. https://doi.org/10.1046/j.1365-2427.2001.00685.x

Schlosser, I. J. (1987). The role of predation in age-and size-related habitat use by stream fishes. *Ecology*, *68*(3), 651–659. https://doi.org/10.2307/1938470

Schlosser, I. J. (1988). Predation risk and habitat selection by two size classes of a stream cyprinid: Experimental test of a hypothesis. *Oikos*, *52*(1), 36–40. https://doi.org/10.2307/3565979

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *BioScience*, *41*(10), 704–712. https://doi.org/10.2307/1311765

Schrank, S. J., Guy, C. S., Whiles, M. R., & Brock, B. L. (2001). Influence of instream and landscape-level factors on the distribution of Topeka shiners *Notropis topeka* in Kansas streams. *Copeia*, *2001*(2), 413–421.

https://doi.org/10.1643/0045-8511(2001)001[0413:IOIALL]2.0.CO;2

Seaber, P. R., Kapinos, F. P., & Knapp, G. L. (1987). *Hydrologic unit maps. U.S. geological survey water-supply paper 2294*. 63. Retrieved from https://water.usgs.gov/GIS/huc.html

Shipley, B. (2000). *Cause and correlation in biology: A user's guide to path analysis, structural equations, and causal inference*. Cambridge University Press.

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*(2), 363–368. https://doi.org/10.1890/08-1034.1

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., … Vonesh, J. R. (2010). Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, *119*(4), 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x

Sowa, S. P., & Rabeni, C. F. (1995). Regional evaluation of the relation of habitat to distribution and abundance of smallmouth bass and largemouth bass in Missouri streams. *Transactions of the American Fisheries Society*, *124*(2), 240–251. https://doi.org/10.1577/1548-8659(1995)124%3C0240:REOTRO%3E2.3.CO;2

Stasiak, R. H. (2007). *Southern redbelly dace* (Phoxinus erythrogaster)*: A technical conservation assessment*. USDA Forest Service, Rocky Mountain Region.

Stefferud, J. A., Gido, K. B., & Propst, D. L. (2011). Spatially variable response of native fish assemblages to discharge, predators and habitat characteristics in an arid-land river. *Freshwater Biology*, *56*(7), 1403–1416. https://doi.org/10.1111/j.1365-2427.2011.02577.x

Turner, A. M., & Mittelbach, G. G. (1990). Predator avoidance and community structure: Interactions among piscivores, planktivores, and plankton. *Ecology*, *71*(6), 2241–2254. https://doi.org/10.2307/1938636

US Census Bureau (2001). *Topologically Integrated Geographic Encoding and Referencing (TIGER) database*. Retrieved from https://www.census.gov/programs-surveys/geography/guidance/tiger-data-products-guide.html

[USFWS] U.S. Fish and Wildlife Service (2018). *National Wetlands Inventory Version 2.0*. Retrieved from https://www.fws.gov/wetlands/arcgis/services/Wetlands/MapServer/WMSServer

[USGS] U.S. Geological Survey (2002). *[NED] National Elevation Dataset*. Retrieved from https://www.sciencebase.gov/catalog/item/505a61cde4b0c8380cd71b8d

[USGS] U.S. Geological Survey (2016). *National hydrography dataset*. Retrieved from https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

Vander Zanden, M. J., Olden, J. D., Thorne, J. H., & Mandrak, N. E. (2004). Predicting occurrences and impacts of smallmouth bass introductions in North Temperate lakes. *Ecological Applications*, *14*(1), 132–148. https://doi.org/10.1890/02-5036

Vanhaecke, D., Garcia de Leaniz, C., Gajardo, G., Dunham, J., Giannico, G., & Consuegra, S. B. (2015). Genetic signatures of historical dispersal of fish threatened by biological invasions: The case of galaxiids in South America. *Journal of Biogeography*, *42*(10), 1942–1952. https://doi.org/10.1111/jbi.12568

Vanni, M. J., Arend, K. K., Bregmigan, M. T., Bunnell, D. B., Garbey, J. E., González, M. J., & Renwick, W. H. (2005). Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. *BioScience*, *55*(2), 155–167. https://doi.org/10.1641/0006-3568(2005)055[0155:LLAFWE]2.0.CO;2

Walsworth, T. E., Budy, P., & Thiede, G. P. (2013). Longer food chains and crowded niche space: Effects of multiple invaders on desert stream food web structure. *Ecology of Freshwater Fish*, *22*(3), 439–452. https://doi.org/10.1111/eff.12038

Wang, L., Lyons, J., Kanehl, P., & Gatti, R. (1997). Influences of catchment land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries*, *22*(6), 6–12. https://doi.org/10.1577/1548-8446(1997)022%3C0006:IOWLUO%3E2.0.CO;2

Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). mvabund–an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, *3*(3), 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Warton, D. I., & Hui, F. K. C. (2022). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, *91*(1), 3–10. https://doi.org/10.1890/10-0340.1

Welcomme, R. L. (1988). *International introductions of inland aquatic species*. Food and Agriculture Org.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*, *30*(5), 377–392. https://doi.org/10.1086/622910

White, J. L., & Harvey, B. C. (2001). Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. *Freshwater Biology*, *46*(7), 987–995. https://doi.org/10.1046/j.1365-2427.2001.00724.x

Winemiller, K. O., Humphries, P., & Pusey, B. J. (2016). Protecting apex predators. In G. P. Bloss, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 361–398). Cambridge University Press.

Woodford, D. J., & McIntosh, A. R. (2010). Evidence of source–sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout. *Ecological Applications*, *20*(4), 967–977. https://doi.org/10.1890/08-1909.1

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bruckerhoff LA, Gido KB, Estey M, Moore PJ. Disentangling effects of predators and landscape factors as drivers of stream fish community structure. *Freshwater Biology*. 2021;66:656–668. https://doi.org/10.1111/fwb.13668