



Landscape-scale determinants of native and non-native Great Plains fish distributions

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ABSTRACT

Aim Landscape-scale factors may have differential effects on the distribution of native and non-native fishes and may help explain invasion success and species declines.

Location Great Plains, Wyoming, USA

Methods We used hierarchical Bayesian mixture models and constrained ordination techniques to evaluate associations between landscape-scale factors on native and non-native fish species richness, reproductive guilds and individual species distributions.

Results Predicted responses between landscape-scale factors and native and non-native fish species richness were similar, except non-native fish species richness that was positively associated with density of oil and gas wells. Non-native fish species richness was also positively associated with native fish species richness. Spawning guild composition differed between native and non-native fishes. Canonical correspondence analysis revealed that the most abundant non-native and only a few native species were positively associated with oil and gas wells.

Main conclusions The similar relationships between native and non-native fish species richness are likely evidence that they share similar ecological rules, which supports that non-native species become naturalized and they may be affected by the same environmental factors that determine distribution of native species.

Keywords

Bayesian multilevel models, landscape-scale factors, native and non-native fish species richness, reproductive guild

INTRODUCTION

Understanding factors influencing the distribution of species is a principal goal of ecology (Olden *et al.*, 2010). Landscape-scale factors affecting the distribution of individual species, communities and ecosystems operate across both fine and coarse scales (Peterson *et al.*, 2005). Given that the landscape strongly influences ecological processes and spatial complexity of streams, information from both fine and coarse scale factors must be considered to understand the organization of fish assemblages (Peterson *et al.*, 2005). Thus, identifying this hierarchy of factors is also critical to developing model-based hypotheses that help us to explain

invasion success of non-native species and declines of native species (Gido *et al.*, 2004).

Historically, streams in the North American Great Plains were highly dynamic systems that exhibited wide fluctuations in physical conditions, and native fishes evolved unique life history strategies to persist in these environments (Matthews, 1998). These same life history strategies have made many species vulnerable to the synergistic effects of habitat modification, climate change and introduced species (Olden *et al.*, 2006). Impoundments, diversions, increased agriculture and water demand, and low-head dams have stabilized and reduced flows, simplified channel complexity and fragmented streams (Perkin & Gido, 2011). As a result, Great Plains streams are among the

most imperilled habitats in North America and have experienced declines for 41 of the 49 fish species endemic to this ecoregion (Hoagstrom *et al.*, 2011). Understanding how geographic and anthropogenic factors shape the distribution of native species is of central importance to conserving these freshwater ecosystems (Saunders *et al.*, 2002).

Reproductive ecology can provide insight into factors driving success and declines of groups of species (Perkin *et al.*, 2011). Life history strategies reflect physiological adaptations to environmental constraints or trade-offs made in response to environmental conditions and biotic interactions (Olden *et al.*, 2010). For example, stream fragmentation and reduced discharge are two factors reducing the distribution and abundance of pelagic broadcast spawners, which produce semi-buoyant, non-adhesive eggs (Hoagstrom & Turner, 2015). It is unclear how anthropogenic impacts and habitat features influence distribution and abundance of other reproductive guilds, including non-native species. However, identifying factors influencing functionally similar species may highlight processes shaping species composition and determine community-wide consequences of human alterations (Perkin *et al.*, 2011).

Ecologists typically use species distribution models to determine species responses with environmental factors (Peterson *et al.*, 2005). Both classical maximum likelihood estimation and Bayesian modelling techniques are used to evaluate these responses (Latimer *et al.*, 2006), but several factors could result in poor characterizations, given that most species distribution models do not account for scale and spatial autocorrelation (Wenger *et al.*, 2008). Within a Bayesian framework, spatial scale and autocorrelation can easily be incorporated into a hierarchical model, where uncertainty is described for all parameters (fixed and random effects) and spatial patterns that can reduce the predictive power of simple species distributions is addressed (Latimer *et al.*, 2006). Additionally, hierarchical Bayesian models allow for the hierarchical organization of parameters being functions of other parameters (Snijders & Bosker, 1999), which may allow us to more accurately test our model-based hypotheses as it relates to spatial scale.

The objective of this study was to determine which landscape-scale factors affect distributions of native and non-native fish distributions in the Great Plains drainage of Wyoming. Unlike other studies that focus on either species-specific relationships (Perkin & Gido, 2011), guild(s) analysis or richness (Gido *et al.*, 2004), we sought to use a comprehensive model-based strategy that used all three methods to determine how native and non-native fish species distributions relate to urban land coverage, stream context and landscape geology. Our secondary objectives sought to determine whether native and non-native species shared similar ecological rules by identifying how landscape-scale factors relate to native and non-native species richness, and evaluating reproductive guild mechanisms. Lastly, we used multivariate ordination techniques to quantify species-specific habitat relationships.

METHODS

Study area

The fish collection locations were within the Missouri River drainage of Wyoming, the largest (186,000 km²) river system in the Great Plains drainage (Quist *et al.*, 2004; Fig. 1). Many streams in Wyoming exhibit a gradient of environmental factors that vary from small headwater streams to larger rivers at lower elevations. Headwater streams (>2000 m elevation) are smaller and shallower, have large rocky substrate and are dominated by a trout assemblage (Quist *et al.*, 2004). Further downstream, streams are larger and deeper and have a lower gradient, and the fish community is dominated by a minnow–sucker assemblage (Rahel & Hubert, 1991). Streams within this region are often affected by anthropogenic activities such as water development, fragmentation, land use, grazing activities and energy development (Davis *et al.*, 2010).

Fish surveys

Fish community data were obtained from the Wyoming Game and Fish Department database. Fish collections were made between 1993 and 2009 at 478 reaches located throughout the Missouri River drainage (Fig. 1). Because we were interested in Great Plains fishes found in non-montane

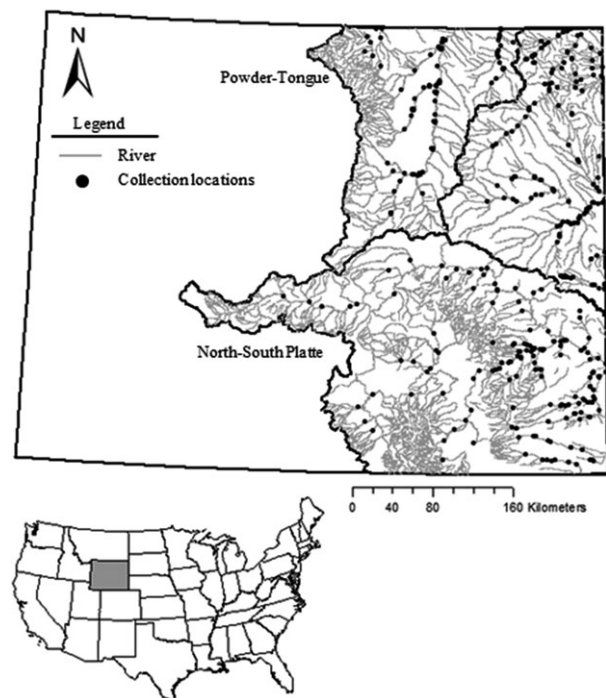


Figure 1 Map of fish survey locations ($n = 478$) in the Missouri River drainage, Wyoming. Shown are the three HUC2 waters within the Missouri River drainage [North–South Platte, Cheyenne (top right corner) and Powder–Tongue]. HUC, hydrologic unit code.

regions, we used data collected from reaches <2300 m in elevation and did not use data from surveys targeting specific species (e.g. sport fish surveys). Fish communities were sampled using seining and pulsed DC electrofishing (single pass), where a backpack electrofisher was used to sample small streams and larger streams were sampled using a bank unit or raft electrofishing (Quist *et al.*, 2004). Sampled reaches were at least 200 m in length, and relative abundance was represented as the number of fish per 200 m. Collected fish were identified, and voucher specimens were preserved in 10% formalin to corroborate identifications made in the field.

Landscape data

One of our primary objectives was to draw inferences between landscape-scale factors and species origin (native and non-native) and reproductive strategy. Therefore, we used environmental data from online sources to develop model-based hypotheses by measuring stream size and context variables and land cover at the reach scale, and geology and watershed size and disturbance variables like density of oil and gas wells at the watershed scale [hydrologic unit code (HUC) 10; Muellner *et al.*, 2013].

Stream context variables such as elevation, aspect and stream gradient were derived using 30-m resolution digital elevation models (DEMs; <http://ned.usgs.gov/>). Stream size variables such as stream order, link and downstream-link (d-link) magnitude were calculated using 1:24,000 scale maps to determine stream position and size. Land cover surrounding each study reach was summarized using a 300-m buffer around each sampling location from the latest 30-m resolution land cover data (2006) from the Multi-Resolution Land Characteristics Consortium (Fry *et al.*, 2011). We considered the fish collections were contemporaneous with the 'current' land cover data because land use has changed <1% over the last 10 years in Wyoming (Hulme *et al.*, 2009). Land cover types were grouped into the following classes: barren, forest, shrub, grassland, agriculture, wetland and residential development. We developed the following model-based hypotheses for stream size and context variables: that native species would occur more often at higher elevations than non-native species because many of the non-native fishes that have been introduced into Wyoming are warm-water species (Bozek & Hubert, 1992), and predicting that native and non-native species richness would show a positive correlation with stream size (stream order, link, and d-link) based on the principles of the river continuum concept (Vannote *et al.*, 1980; Wenger *et al.*, 2011). We hypothesized that factors facilitating non-native species would include land cover variables such as agriculture and residential development (Rahel, 2002).

Watershed (HUC 10) variables such as those related to human alterations were collected from the National Inventory of Dams (United States Army Corps of Engineers, 2013), Wyoming State Water Plan, Wyoming State

Geological Survey and the 2010 Tiger road database to calculate the density of dams, diversions, coal-bed methane mines (Biewick, 2011), oil and gas wells (Kirkaldie *et al.*, 2007) and roads (US Census Bureau, 2002) for each watershed (Table 1). Landscape geology was summarized and characterizes conditions relevant to the physiochemical properties of streams. Landscape geology was summarized by the major classes: alluvium, limestone–dolomite, sandstone and gravel using 1:500,000 statewide digital geology data for Wyoming (WSGS, 2013). We hypothesized that the physical and chemical disturbance associated with energy development, and road density are related to factors facilitating non-native species (an index of urbanization; Trombulak & Frissell, 2000). We also hypothesized that non-native species would show a positive correlation and native species a negative correlation with dams and diversions (Rahel, 2002). Finally, we hypothesized that reproductive strategists like open-water spawners would be negatively related to dams and diversions, whereas benthic spawners would exhibit a positive relationship due to increased substrate size and stabilized flows (Matthews, 1998). Additionally, we hypothesized that stream bed geology would be an important factor controlling where native and non-native species occur, where benthic-spawning non-native species would occur less often in sandy substrate streams and more often in cobble–bedrock streams (Matthews, 1998).

Statistical analysis

We classified each species origin as either native or introduced. Reproductive guild and behaviour were classified according to Balon (1975) and Simon (1999; Appendix S1). We classified species as either pelagic or benthic, each of which has two subsections based on their reproductive behaviour as guarders or non-guarders. Based on the spawning substrate, species were either ariadnophilic (deposit adhesive eggs within nests), lithophilic (deposit eggs over or in gravel), lithopelagophilic (deposit eggs over or within rock, and have pelagic larvae), phytophilic (deposit eggs over plants and submerged woody debris), phytolithophilic (deposit eggs released over plants and rock), polyphilic (deposit eggs over nests of various substrates) or speleophilic (deposit eggs in crevices, or in cavities), or if a species produces semi-buoyant eggs, they were classified as being pelagophilic (Appendix S1). To classify species, we used life history descriptions from Etnier & Starnes (1993), Boschung & Mayden (2004), Frimpong & Marcinek (2009), Hoagstrom & Turner (2013) and the Kansas Fish Committee (2014).

We used a hierarchical Bayesian framework to evaluate relationships between habitat and species richness (native and non-native) and reproductive guild groupings (Terörde & Turpie, 2013). We accounted for multiscale patterns and spatial autocorrelation, where spatial autocorrelation violates assumptions of independent model errors, leading to biased variance estimates and an increased type I error rate (Snijders & Bosker, 1999). We used a two-level hierarchical Bayesian mixture model representing y_{ik} as species richness or

Table 1 Watershed and reach variables for rivers and watersheds in Great Plains rivers of Wyoming, USA.

Scale	Variable Group	Variable	Mean (SD)	Range
Reach	Stream size and context	Downstream-link magnitude (d-link)	47.15 (87.15)	1.00–764.00
		Link magnitude	1,966.82 (1,373.17)	15.00–4,581.00
		Aspect	175.86 (0.21)	0.45–359.82
		Gradient (%)	4.09 (5.30)	0.00–38.93
		Elevation (m; elev)	1,363 (263)	953–2,288
	Land use (%)	Residential development	2.56 (2.32)	0.00–100.00
		Barren	0.33 (1.26)	0.00–10.32
		Forest	1.74 (1.27)	0.00–9.45
		Shrub land	24.15 (8.48)	0.00–93.18
		Grass land	41.79 (22.37)	0.00–100.00
		Agriculture	6.25 (14.17)	0.00–94.84
		Wetland	22.73 (14.20)	0.00–89.84
	Richness	Native	6 (3)	0–15
		Non-native	1 (1)	0–6
Watershed	Landscape geology (%)	Alluvium (alluv)	57.94 (36.79)	0.00–100.00
		Limestone–dolomite (lime)	1.16 (6.93)	0.00–100.00
		Sandstone (sand)	36.16 (38.30)	0.00–100.00
		Gravel	3.68 (10.44)	0.00–100.00
	Watershed context	Dams (dams km ⁻²)	0.01 (0.01)	0.00–0.04
		Road density (km m ⁻² ; road)	10.34 (3.69)	3.16–32.88
		Oil and gas (No. per km ² ; oil)	0.01 (0.01)	0.00–0.03
		Coal–bed mines (No. per km ² ; mines)	0.02 (0.04)	0.00–0.31
		Diversions (No. per km ²)	1.97 (2.01)	0.21–11.53
		Area (km ² ; area)	786.33 (198.97)	284.77–1,267.97
		Impervious surface (%; imp)	0.28 (0.35)	0.06–3.32

guild abundance (i.e. the combined abundance of all species within a spawning guild, for guilds having at least three species) from reach i and watershed k . Abundance was estimated by assuming a negative binomial error distribution by adding a hierarchical component ε_i to the likelihood of a Poisson distribution to account for overdispersion:

$$y_{ik} \sim \text{Poisson}(\lambda_{ik}\varepsilon_i)$$

where $\varepsilon_i \sim \text{gamma}(\theta, \theta)$ and λ_{ik} is expressed in level one (reach-level effects) of the model as

$$\text{Level 1: } \log(\lambda_{ik}) = \gamma_{0k} + \sum_{v=1}^n \beta_v x_{v,ik} + \varepsilon_{ik},$$

$$\text{Level 2: } \gamma_{0k} = \gamma_0 + \sum_{s=1}^m \gamma_s w_{s,k} + \delta_k,$$

where

$$\begin{bmatrix} \varepsilon_{ik} \\ \delta_k \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_\varepsilon^2 \\ \sigma_\delta^2 \end{bmatrix}\right)$$

where $x_{v,ik}$ are predictors $v = 1, 2, \dots, n$ measured for reach i within watershed k , and the intercept γ_{0k} was modelled in level two (watershed-level effects) as a function of watershed characteristics where $w_{s,k}$ are the $s = 1, 2, \dots, m$ predictors for watershed k , and δ_k is the reach nested within watershed random effect. The β 's and γ 's are the fixed effect coefficients that relate richness or guild abundance to the landscape-scale

factors, and ε 's and δ 's are the random effect coefficients. Also of interest was dealing with a large number of zeros in the data; excessive zeros are either structural (species not occurring at reach) or sampling related (species was present but not detected; Arab *et al.*, 2008). In instances of excessive zeros ($\geq 30\%$ of the data), we considered a zero-inflated mixture model by adding an additional term $\text{pres}_i \sim \text{Bernoulli}(\psi_i)$ which is the latent suitability state that describes the probability that the species is present to the mean count that is negatively binomially distributed $y_{ik} \sim \text{Poisson}(\lambda_{ik}\varepsilon_i)$ so that the model is explicitly defined by a latent abundance state expressed as $\lambda_{ik} = \text{pres}_i \times c_{ik}$ following Wenger & Freeman (2008), and c_{ik} is a log-linear function of environmental variables and ε_i is the overdispersion parameter.

Predictor variables were standardized with mean zero and standard deviation of one, and only predictor variables that had a correlation coefficient (r) < 0.60 were used in the same model to reduce intercorrelation (Esselman *et al.*, 2011). Models were implemented in WINBUGS software, version 1.4 (Spiegelhalter *et al.*, 2003), using Markov chain Monte Carlo (MCMC) algorithms to generate posterior distributions of the parameters. Diffuse priors (non-informative) were used, and models were fit using three parallel chains simulated for 500,000 iterations with a burn-in of the first 200,000 iterations. Gelman–Rubin diagnostics, examination of chain histories and the posterior density plots were used to determine convergence (Gelman & Rubin, 1992). We identified 13 candidate models of native and non-native species richness and

guild abundance related to stream and watershed size and context, land cover, geology and disturbance variables. Candidate models were ranked using an information theoretic approach (Burnham & Anderson, 2002). We ranked models using the deviance information criterion (DIC), an analogue to the Akaike information criterion (AIC; Plummer, 2007). We assumed models with $\Delta\text{DIC} \leq 6$ were considered plausible, and the degree of evidence of one model over another was calculated from deviance weights (i.e. Akaike weights based on DIC statistics; Burnham & Anderson, 2002). Because model-theoretic approaches do not depict model fit, we calculated the marginal ($R^2_{\text{GLMM}(m)}$) and conditional ($R^2_{\text{GLMM}(c)}$) r^2 values for mixed-effects models to determine the amount of variation explained by the fixed effect components (predictor variables) and the entire model that includes variation explained by the random effects (reach- and watershed-level variation; Nakagawa & Schielzeth, 2013). Credible intervals (95%) of fixed effect parameters that contained zero were considered weak relationships.

Lastly, we used canonical correspondence analysis (CCA) to evaluate species-specific relationships (VEGAN in R program; Dixon, 2003; R Development Core Team 2011). CCA is a multivariate technique that uses direct gradient analysis by constraining axes to be linearly related, given reach variation between the species abundance and environmental matrices (ter Braak, 1986). Because of spatial autocorrelation, we used partial CCA (pCCA), a modified canonical ordination technique, to factor out the effect of spatial dependence by using ten-digit HUC (HUC 10) as a conditional covariate (Dauwalter, 2013). Species abundances were $\log_{10}(x + 1)$ -transformed, and only those species that occurred at >3% of all reaches sampled were considered (Dauwalter, 2013). Environmental variables were selected in a stepwise forward selection. We used permutation tests with 9999 permutations to assess the significance ($P \leq 0.05$) of environmental variables and pCCA axes based on the hypothesis that the species and environmental matrices were not related.

RESULTS

Fish composition

Overall, 49 species were caught from 478 reaches in 120 watersheds between 1993 and 2009 (Table 2). Of the 49 fishes caught, 33 (67%) were native fishes and 16 (33%) were non-native to Wyoming. Four families were represented by only native fishes (Catostomidae, Fundulidae, Hiodontidae and Ictaluridae), and four families were represented by only non-native fishes (Centrarchidae, Clupeidae, Gasterosteidae and Salmonidae). The Cyprinidae family was the most dominant (21 fish species out of 48), and the majority of species (86%) were native to Wyoming. The most commonly collected species were Fathead Minnow *Pimephales promelas* (67% occurrence), White Sucker *Catostomus commersonii* (67% occurrence), Longnose Dace *Rhinichthys cataractae* (62% occurrence) and Sand Shiner *Notropis stramineus* (62%

occurrence) which occurred in almost every drainage. The Hornyhead Chub *Nocomis biguttatus*, Northern Pearl Dace *Margariscus margarita* and Spottail Shiner *Notropis hudsonius* were the least common species, occurring in one or two drainages.

Species richness

Results from the Spearman rank correlation revealed few correlations greater than the pre-defined 0.60 value; in model development, elevation and link magnitude ($r = 0.75$) and downstream-link magnitude and stream order ($r = 0.94$) were not included in the same model.

The model selection procedure identified six models relating native fish species richness to reach and watershed context variables (Table 3). Density of dams and stream position (i.e., stream order and downstream-link magnitude) were the most commonly represented variables in the top models, both positively related to native fish species richness (Figs 2 and 3a,b). The best model was 1.08 times better in support than the second model. The fixed effect components of the best supported model accounted for 51% of the variance, due to the large effect of stream order (30%), whereas the combined effect of density of dams, stream gradient and watershed area accounted for 21.05% of the variance. Thirty-two percentage of the variability in the data was explained by the random effects. Native fish species richness showed a unimodal relationship with downstream-link magnitude, positive relationship with non-native species richness, and negative responses to impervious surface and density of oil and gas wells (Figs 2 and 3d,e).

The model selection procedure identified eight models relating non-native fish species richness to reach and watershed context variables (Table 3). Models based on land cover (percentage residential development, shrub land and agriculture) hypothesis were over 44 DIC values worse (not shown in tables) than the lowest supporting model in the DIC confidence set. The model selection criterion identified seven models, and the top three differed by only 0.20 DIC values. The fixed effect components of the top two equally supported models accounted for 27.49% and 22.70% of the variance. The effects of elevation and random effect components accounted for >10% of the variance in both models. Density of dams and downstream-link magnitude were the most common variables, where non-native species exhibited a positive and a unimodal relationship (Figs 2 and 3a,b), respectively. Non-native species richness showed a negative relationship with elevation (Fig. 3c), a positive response to native species richness (Fig. 2) and density of oil and gas wells (Fig. 3e).

Reproductive guild

Native and non-native fish were divided among 11 reproductive guilds, though native and non-native species belonged to different spawning guild groups. Sixty-four percentage (21 of

Table 2 Common and scientific names of fishes, species code, origin (N = native; E = non-native), and reproductive guild (ONL, open-water non-guarding lithophilic; ONLP, open-water non-guarding lithopelagophilic; ONP, open-water non-guarding pelagophilic; ONPH, open-water non-guarding phytohilic; ONPHL, open-water non-guarding phytolithophilic; BGA, benthic-guarding ariadnophilic; BGPH, benthic-guarding phytophilic; BGPL, benthic-guarding polyphilic; BGS, benthic-guarding speleophilic; BNL, benthic non-guarding lithophilic; BNS, benthic non-guarding speleophilic) of the 49 fish species used in analyses.

Scientific name	Common name	Species code	Origin	Guild
<i>Rhinichthys cataractae</i>	Longnose Dace	LND	N	ONL
<i>Margariscus margarita</i>	Northern Pearl Dace	NPD	N	ONL
<i>Fundulus zebrinus</i>	Northern Plains Killifish	PKF	N	ONL
<i>Moxostoma macrolepidotum</i>	Shorthead Redhorse	NRH	N	ONL
<i>Phenacobius mirabilis</i>	Suckermouth Minnow	SMM	N	ONL
<i>Dorosoma cepedianum</i>	Gizzard Shad	GZS	E	ONLP
<i>Couesius plumbeus</i>	Lake Chub	LKC	N	ONLP
<i>Catostomus catostomus</i>	Longnose Sucker	LNS	N	ONLP
<i>Catostomus platyrhynchus</i>	Mountain Sucker	MTS	N	ONLP
<i>Carpoides cyprinus</i>	Quillback	QBK	N	ONLP
<i>Carpoides carpio</i>	River Carpsucker	RCS	N	ONLP
<i>Notropis hudsonius</i>	Spottail Shiner	STS	E	ONLP
<i>Sander vitreus</i>	Walleye	WAE	E	ONLP
<i>Catostomus commersonii</i>	White Sucker	WHS	N	ONLP
<i>Notropis dorsalis</i>	Bigmouth Shiner	BMS	N	ONP
<i>Notropis atherinoides</i>	Emerald Shiner	EMS	E	ONP
<i>Platygobio gracilis</i>	Flathead Chub	FHC	N	ONP
<i>Hiodon alosoides</i>	Goldeye	GDE	N	ONP
<i>Hybognathus placitus</i>	Plains Minnow	PMN	N	ONP
<i>Macrhybopsis gelida</i>	Sturgeon Chub	SGC	N	ONP
<i>Hybognathus argyritus</i>	Western Silvery Minnow	SMN	N	ONP
<i>Hybognathus hankinsoni</i>	Brassy Minnow	BMN	N	ONPH
<i>Fundulus sciadicus</i>	Plains Topminnow	PTM	N	ONPH
<i>Cyprinus carpio</i>	Common Carp	CRP	E	ONPHL
<i>Phoxinus neogaeus</i>	Finescale Dace	FSD	N	ONPHL
<i>Notropis stramineus</i>	Sand Shiner	SDS	N	ONPHL
<i>Perca flavescens</i>	Yellow Perch	YEP	E	ONPHL
<i>Pomoxis nigromaculatus</i>	Black Crappie	BLC	E	BGA

Table 2 Continued.

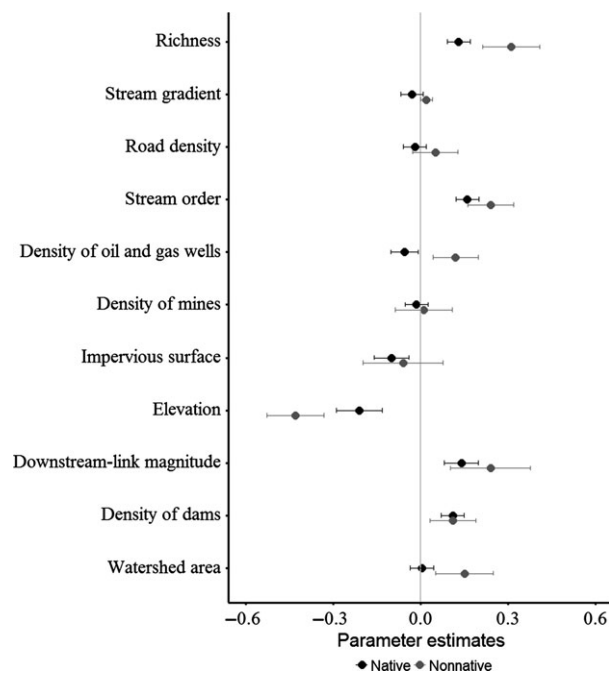
Scientific name	Common name	Species code	Origin	Guild
<i>Culaea inconstans</i>	Brook Stickleback	STK	E	BGA
<i>Pomoxis annularis</i>	White Crappie	WHC	E	BGA
<i>Etheostoma exile</i>	Iowa Darter	IDT	N	BGPH
<i>Lepomis cyanellus</i>	Green Sunfish	GSF	E	BGPL
<i>Micropterus salmoides</i>	Largemouth Bass	LMB	E	BGPL
<i>Ambloplites rupestris</i>	Rock Bass	RKB	E	BGPL
<i>Micropterus dolomieu</i>	Smallmouth Bass	SMB	E	BGPL
<i>Ameiurus melas</i>	Black Bullhead	BLB	N	BGS
<i>Ictalurus punctatus</i>	Channel Catfish	CCF	N	BGS
<i>Pimephales promelas</i>	Fathead Minnow	FHM	N	BGS
<i>Etheostoma nigrum</i>	Johnny Darter	JDT	N	BGS
<i>Noturus flavus</i>	Stonecat	STC	N	BGS
<i>Salvelinus fontinalis</i>	Brook Trout	BKT	E	BNL
<i>Salmo trutta</i>	Brown Trout	BNT	E	BNL
<i>Campostoma anomalum</i>	Central Stoneroller	STR	N	BNL
<i>Luxilus cornutus</i>	Common Shiner	CSH	N	BNL
<i>Semotilus atromaculatus</i>	Creek Chub	CKC	N	BNL
<i>Nocomis biguttatus</i>	Hornyhead Chub	HHC	N	BNL
<i>Etheostoma spectabile</i>	Orangethroat Darter	OTD	N	BNL
<i>Oncorhynchus mykiss</i>	Rainbow Trout	RBT	E	BNL
<i>Cyprinella lutrensis</i>	Red Shiner	RDS	N	BNS

33 species) of native species were classified as open-water spawners (Fig. 4a), half identified as non-guarding pelagophilic and lithopelagophilic spawners (Fig. 4b). Benthic-guarding and non-guarding spawners represented 18% of the remaining native species, whereas non-native species were mostly comprised of benthic-guarding spawners (7 of 16 species), consisting of mostly polyphilic spawning fishes. However, 38% (6 of 16 species) of non-native species were also classified as open-water spawners.

Only three open-water spawning guilds had greater than three species, all native, and they were considered for analysis (Table 4; Fig. 5). Open-water spawners were best predicted by both landscape geology and watershed context models, albeit the responses within this guild were different. Density of dams was represented in the best supporting models for all open-water spawning species (except lithophilic), showing an inverse relationship (pelagophilic, negatively related; lithopelagophilic, positively related; and lithophilic, positively related) in which the effect of dams accounted for >10% of the variance for both pelagophilic and lithopelagophilic

Table 3 Results of the hierarchical Bayesian multilevel negative binomial mixture models predicting species richness in relation to reach- and watershed-level habitat variables.

Origin	Model	Deviance information criterion (DIC)	Δ DIC	w_i	$R^2_{\text{GLMM}(m)}$	$R^2_{\text{GLMM}(c)}$
Native	– area + dam + order – gradient	233.61	0.00	0.28	51.31%	82.72%
	+ non-native + dam – oil – imp	233.74	0.13	0.26		
	+ dam + dlink – elev – imp – gradient	234.34	0.73	0.20		
	– elev – elev2 + dlink – dlink2 – gradient	235.34	1.73	0.12		
	+ dam + dlink – elev – road	235.70	2.09	0.10		
Nonnative	+ dam – imp – mines – oil	237.59	3.98	0.04	27.49%	37.08%
	– elev + elev2 – dlink – dlink2 + gradient	125.03	0.00	0.25		
	+ dam + dlink – elev – imp + gradient	125.06	0.03	0.25		
	+ dam + dlink – elev + road	125.23	0.20	0.23		
	+ native + dam + oil – imp	126.28	1.25	0.14		
	+ area + dam + order + gradient	127.64	2.61	0.07		
	+ area + aspect + dam + dlink	129.16	4.13	0.03		
	+ dam – imp + mines + oil	130.12	5.09	0.02		
	+ oil + dlink – dlink2	130.61	5.58	0.02		

**Figure 2** Parameter estimates ($\pm 95\%$ credibility intervals) for the best supported hierarchical Bayesian multilevel negative binomial mixture models relating reach- and watershed-level landscape characteristics to native and non-native species richness. Richness indicates native versus non-native richness. Credible intervals (95%) of fixed effect parameters that contained zero were considered weak relationships.

spawners. The effect of dams explained $<5\%$ of the variance for lithophilic spawners. Sandstone geology explained 21.05% of the variance for pelagophilic spawners, where both sandstone and gravel geology accounted for only 5% of the variance for lithophilic spawners. The modelled response for oil and gas density demonstrated a decrease in abundance for all

open-water spawners, explaining 20% of the variance for lithophilic species and much less for pelagophilic and litho-pelagophilic spawners ($<5\%$).

Four benthic-spawning guilds, two of which were non-native, had greater than three species for analysis (Table 4; Fig. 5). The relationships between benthic non-guarding lithophilic species and landscape-scale factors were similar for native and non-natives. Both native and non-native species were negatively associated with oil and gas well densities and positively associated with density of dams. Native benthic-guarding speolophilic species showed a positive response to oil and gas well densities (although not significant) and negative responses to coal-bed methane mine densities and were inversely related to both sandstone geology and road density. The fixed effect components (predictor variables) from the best models explained 50% and 85% of the variance in both cases. Polyphilic spawners (considered as a generalist spawning group) response was described by four models, and none of the landscape-scale factors were significant, which likely explains why the fixed effects accounted for a small amount of the variance (29.30%).

Fish community response

The first CCA axis explained 39.55% of the variance between fish composition and environmental variables (permutation $F = 20.53$, $P < 0.01$). Density of dams, road density, sandstone geology, alluvium and down-stream link magnitude were significant contributors to the first CCA axis (Appendix S2a). Channel Catfish *Ictalurus punctatus*, Goldeye *Hiodon alosoides*, River Carpsucker *Carpionodes carpio*, Bigmouth Shiner *Notropis dorsalis* and Flathead Chub *Platygobio gracilis* abundance tended to be higher at reaches in larger streams and in watersheds with high density of dams, whereas Brassy Minnow *Hybognathus hankinsoni*, Creek

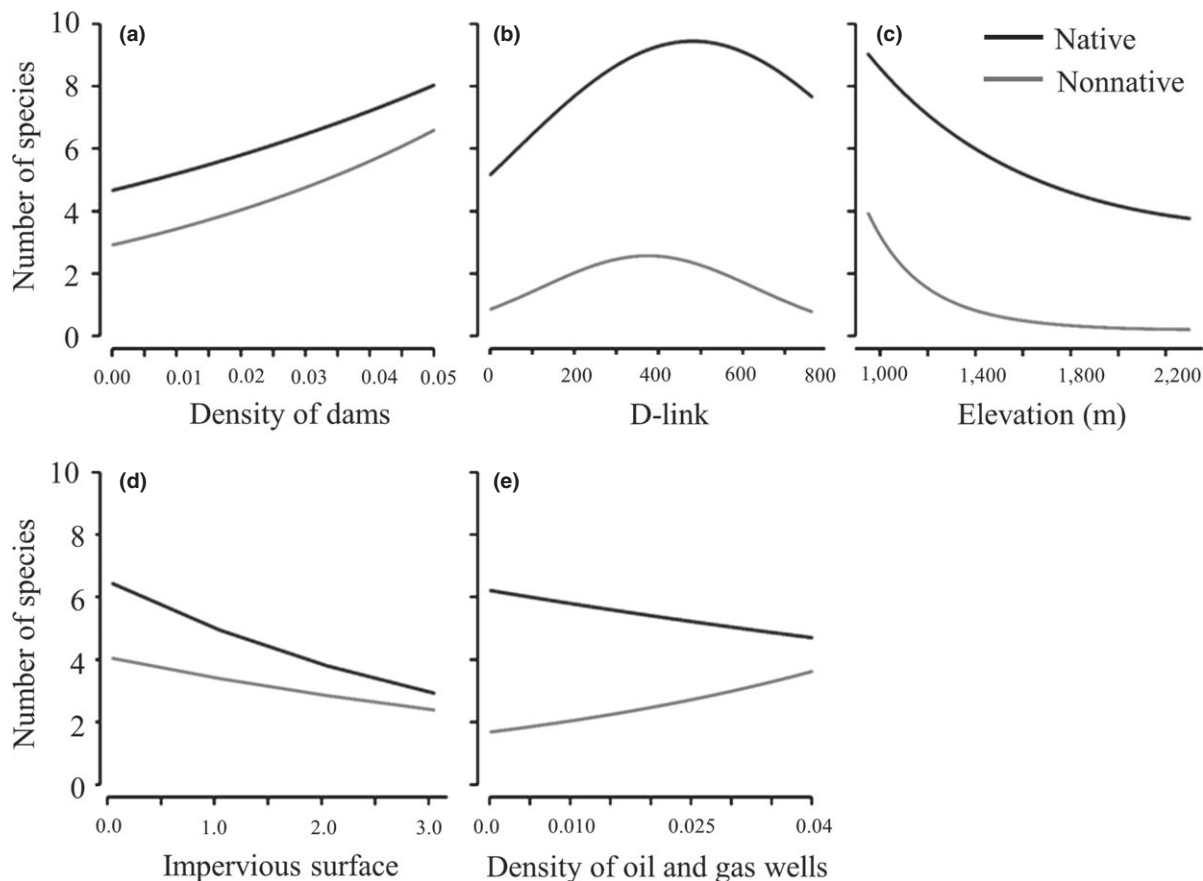


Figure 3 Species richness response to reach- and watershed-level habitat features from the best supported models.

Chub *Semotilus atromaculatus*, Iowa Darter *Etheostoma exile*, Longnose Dace *Rhinichthys cataractae*, Longnose Sucker *Catostomus catostomus*, Mountain Sucker *Catostomus platyrhynchus*, Shorthead Redhorse *Moxostoma macrolepidotum* and White Sucker *Catostomus commersonii* were most abundant at reaches with alluvial-based geology (Appendix S2b). Density of oil and gas wells was the next significant factor influencing fish assemblage structure (pCCA Axis 2; permutation $F = 16.10$, $P < 0.01$), explaining 32.15% of the variance, with native species such as Black Bullhead *Ameiurus melas*, Fathead Minnow, Plains Killifish *Fundulus zebrinus*, Plains Minnow *Hybognathus placitus*, Plains Topminnow *Fundulus sciadicus* and Red Shiner *Cyprinella lutrensis* being more abundant at reaches within watersheds with high density of oil and gas wells and roads. The non-native species positively associated with oil and gas wells and road densities were Brook Stickleback *Culaea inconstans*, Common Carp *Cyprinus carpio*, Gizzard Shad *Dorosoma cepedianum* and Green Sunfish *Lepomis cyanellus*. Stream gradient and landscape geology explained 12.87% of the variance (pCCA Axis 3; permutation $F = 6.01$, $P < 0.01$). Brown Trout *Salmo trutta*, Longnose Sucker, Smallmouth Bass *Micropterus dolomieu* and Stonecat *Noturus flavus* were most abundant in high-gradient, gravel-bed streams.

DISCUSSION

Multilevel models provided further insight into the way landscape-scale factors affected the distribution of native and non-native fish species. This approach improves on the typical approach that estimates the role of reach and watershed-level variables using separate estimation techniques (Steenbergen & Jones, 2002). Our modelling approach used an estimation strategy that uses both reach-level variables and watershed-level variables in a multilevel framework that essentially incorporates spatial scale explicitly in the analysis. The fixed effect components of models developed for spawning guild analysis often explained more of the variance in the data than models developed for species richness, likely related to the reduced variation that occurs when grouping species that exploit similar resources (Landers 1983). Overall, the amount of variation explained by the fixed and random components ranged between 23 and 97% for both richness and guild analysis, which is similar or greater (21–33%) than the variance explained by other studies (Tomcko & Pierce, 2001; Wagner *et al.*, 2007).

This study contributes to the growing body of ecological literature about whether the distributions of native and non-native species follow similar ecological rules (Lockwood

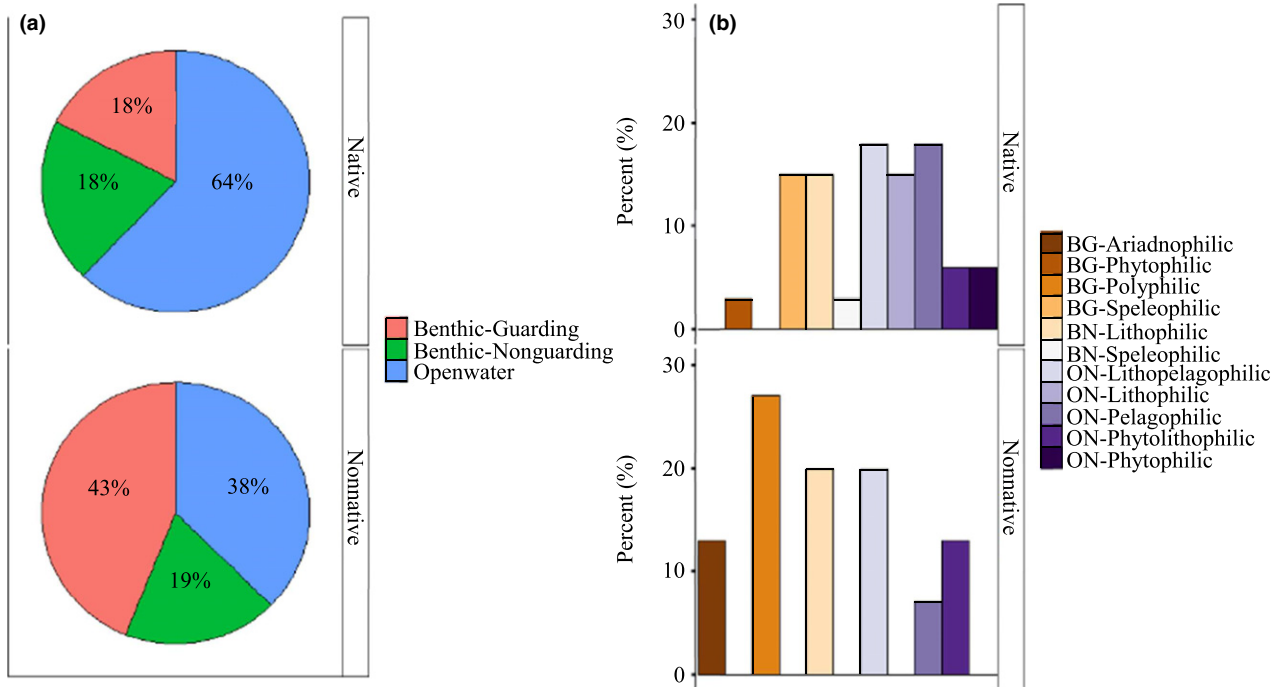


Figure 4 Reproductive guild composition (%) of the number of native and non-native fish collected from the Missouri River drainage, Wyoming. Codes are: BG, benthic guarding; BN, benthic non-guarding; ON, open water. Reproductive behaviour is referenced in Appendix S1.

et al., 2007; Sax *et al.*, 2007; Cucherousset & Olden, 2011). Many studies have found contrasting differences in biogeographical patterns between native and non-native species, hypothesizing that these differences were a result of native species distributions being predominantly influenced by environmental filtering, while the distribution and invasion success of non-native species are related to human-mediated processes (Leprieur *et al.*, 2009). Unlike these studies, we found that the predicted responses between native and non-native fish species richness and landscape-scale factors were similar, suggesting that native and non-native species may share similar ecological rules (Sax 2001). In our study, the richness of both native and non-native species was positively associated with density of dams, downstream-link magnitude, native–non-native richness and stream order and negatively associated with impervious surface and elevation.

The one landscape factor relationship that differed between native and non-native species richness was oil and gas development. Oil and gas development was negatively related to native fish species richness and positively related to non-native fish species richness. One reason for this difference may be that systems affected by oil and gas development typically exhibit elevated ionic concentrations (e.g., aluminium, iron, manganese), surface disturbance due to road construction and stabilized flow regimes that may create physiological stress on native fishes or degrade spawning conditions (Davis *et al.*, 2010). Four of the most abundant non-native species (Brook Stickleback, Common Carp, Gizzard Shad, and Green Sunfish) showed positive associations

to oil and gas development. With the exception of Brook Stickleback, three of these four species were found in Wyoming since the beginning of these surveys, although the range of Brook Stickleback has increased during the sampling period. The increased expansion of Brook Stickleback and positive association between all four non-native species and energy development might be related to the physiological tolerances that these species possess. These non-native species are all highly tolerant to salinity-related stress and changing pH, and their introductions may likely be associated with increased introduction opportunities created by oil and gas development (Dauwalter, 2013), whereas 70% of the most abundant native species were negatively related to oil and gas well development. The seven native species positively associated with oil and gas development (Black Bullhead, Fathead Minnow, Plains Killifish, Plains Minnow, Plains Topminnow, Red Shiner and Sand Shiner) are tolerant of a wide range of water quality conditions and are thus able to persist in areas affected by oil and gas development (Boschung & Mayden, 2004; Davis *et al.*, 2010; Dauwalter, 2013).

Another benefit of this analysis is that it allowed us to determine which guild(s) of fishes were most sensitive to landscape-scale factors. The benthic-guarding guild has been associated with invasiveness in regulated rivers where embryos and larval behaviour require stabilized flows and coarse substrate to survive (Quist *et al.*, 2004; Olden *et al.*, 2006). As a result of dams, rocky substrate types such as gravel, cobble and boulder have replaced fine substrates that would have otherwise degraded spawning grounds and

Table 4 Results of the hierarchical Bayesian multilevel negative binomial mixture models predicting spawning guild abundance for native and non-native species in relation to habitat variables.

Origin	Guild	Type	Model	Deviance information criterion (DIC)	Δ DIC	w_i	$R^2_{\text{GLMM}(m)}$	$R^2_{\text{GLMM}(c)}$
Native	<i>Open-water</i> Non-guarders	Pelagophilic	– dam + gravel + sand + road	1700.64	0.00	0.49	55.67%	91.18%
			– dam – mines + gravel + sand	1700.76	0.12	0.46		
			– dam + gravel + sand + road – alluv – oil – dlink	1705.40	4.76	0.05		
		Lithopelagophilic	+ dam – oil + dlink + elev – elev2	3729.84	0.00	1.00	24.57%	35.78%
		Lithophilic	– oil – gravel + sand – alluv – ag	4170.14	0.00	0.91	31.45%	80.66%
			– road – alluv – sand + elev – elev2	4174.76	4.62	0.09		
	<i>Benthic</i> Non-guarders	Lithophilic	+ dam – oil + dlink + elev – elev2	4170.52	0.00	0.88	50.00%	57.47%
			+ dam – imp – road + elev – elev2	4174.56	4.04	0.12		
		Speleophilic	+ oil – mines – alluv – gravel + sand	4558.28	0.00	0.67	85.44%	97.65%
			+ oil – gravel + sand + alluv – ag	4561.02	2.74	0.17		
			– dam + oil – dlink – elev – elev2	4562.40	4.12	0.09		
			– dam + oil + road – alluv – gravel + sand – dlink	4562.86	4.58	0.07		
Non-native	<i>Benthic</i> Non-guarders	Lithophilic	+ dam – oil – dlink – elev + elev2	339.27	0.00	0.26	80.90%	87.27%
			+ dam – mines – oil – road	339.93	0.66	0.19		
			– oil – mines + gravel + alluv + sand	340.50	1.23	0.14		
			– oil + gravel + sand + alluv + ag	340.95	1.68	0.11		
			– oil + gravel + alluv + road	340.95	1.68	0.11		
			– oil – gravel – sand – road	341.36	2.09	0.09		
			+ dam – oil + road – dlink + alluv + gravel + sand	344.45	2.18	0.09		
			– dam + oil – dlink – elev – elev2	1519.06	0.00	0.47	29.30%	65.58%
			– dam – imp + road – elev – elev2	1519.56	0.50	0.37		
			– dam – mines – gravel – sand	1521.91	2.85	0.11		
			+ oil – mines – alluv + gravel + sand	1523.91	4.85	0.04		
	<i>Benthic</i> Guarders	Polyphilic						

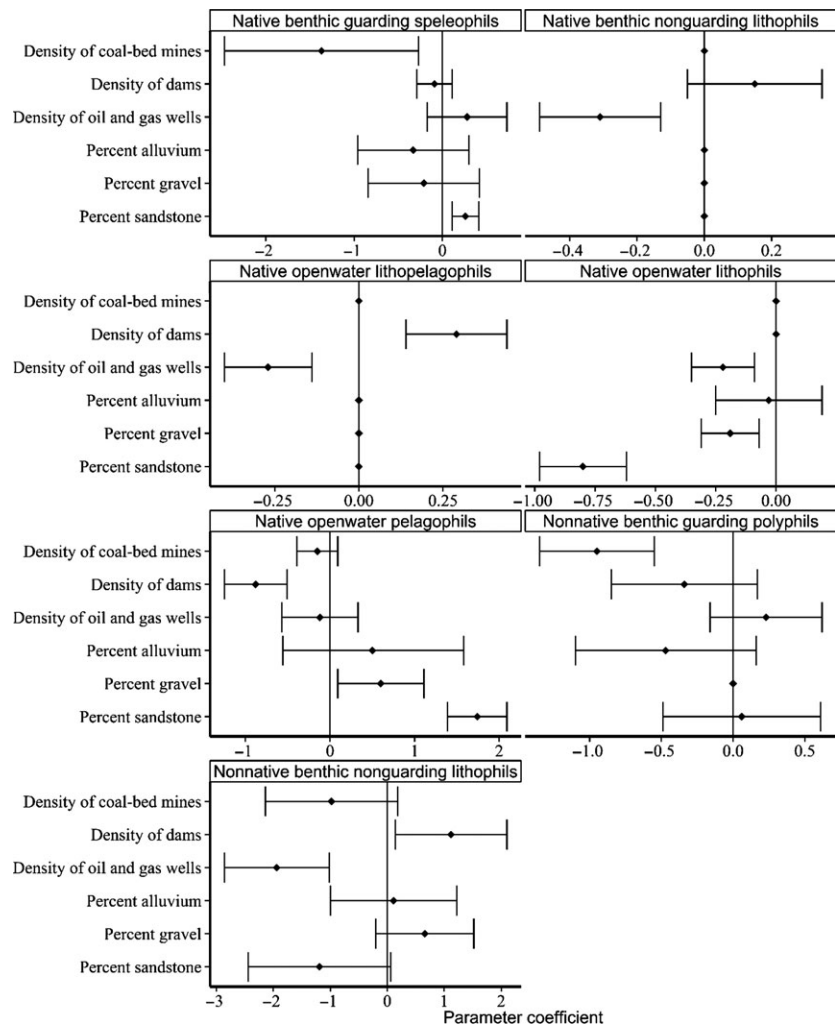
reproductive success of benthic-spawning, lithophilic species (Pulg *et al.*, 2013). Additionally, dams alter prairie streams by fragmenting habitats, increasing substrate size, lowering turbidity and eliminating intermittent flow conditions (Quist *et al.*, 2004; Perkin & Gido, 2011). These environmental changes could benefit benthic-spawning species but be especially problematic for native open-water spawning species that have sensory systems specially adapted to forage in highly turbid systems (Bonner & Wilde, 2002; Dieterman & Galat, 2014), and reproductive mechanisms that require fluvial conditions and natural flow regimes to complete their life cycle (Perkin & Gido, 2011). Habitats altered by dams are no longer suitable for native species that produce buoyant eggs that must have long stretches of free-flowing conditions to hatch successfully (Perkin & Gido, 2011). Thus, our guild analysis corroborates recent studies that have illustrated species-specific declines in native open-water spawners to human alterations such as dams (Perkin *et al.*, 2014), while identifying the habitat alterations like coarser substrate, flow alterations and increased water clarity that may increase

invasion success in Great Plains streams (Bonner & Wilde, 2002; Dieterman & Galat, 2014; Olden *et al.*, 2006).

Geological variables were not an important predictor for native and non-native species richness but did influence the relative abundance of spawning guilds. Of particular note is the consistent association of native species belonging to the open-water, non-guarding pelagophilic spawning guild with sandstone geology in the watershed. Sandstone streams are characterized as having low summer flows, fine substrate, lower gradients, more pool habitat and riffle habitats that are vulnerable to desiccation with reductions in discharge (Hicks & Hall, 2003). Open-water, non-guarding pelagophilic spawners are adapted to these dynamic flow regimes and shifting sand substrate.

Our land-cover models performed poorly in comparison with models developed using stream and watershed context variables. This does not imply that land cover has little effect on streams. A number of studies have found that streams near urban and agriculture land cover areas were associated with increased nitrogen concentrations, substrate embeddedness,

Figure 5 Parameter estimates for the best supported hierarchical Bayesian multilevel negative binomial mixture models for the most significant variables that relate reach- and watershed-level characteristics to reproductive guild abundance. Reproductive guild descriptions: Benthic-guarding speleophils = eggs deposited within crevices; benthic non-guarding lithophils = demersal or adhesive eggs deposited over gravel or rock; open-water lithopelophils = pelagic larvae, eggs deposited over gravel or rock; open-water lithophils = eggs deposited over gravel or rock; open-water pelagophils = broadcast spawners with semi-buoyant eggs; benthic-guarding polyphils = eggs deposited on nests of various substrates. Credible intervals (95%) of fixed effect parameters that contained zero were considered weak relationships. Road density was not a significant effect and was not included in the figure.



reduced riparian habitat and homogenized in-stream habitat (Wang *et al.*, 2008). Based on our available data, reach-specific urban and agriculture land use comprised a small proportion of the available habitat (on average was <9%) compared to other more predominant land cover types such as grassland, barren and wetland habitats. Therefore, the lack of effect in our analysis may be related to the lack of urban-dominated watersheds in Wyoming.

We found a very strong relationship between native–non-native richness that is consistent with invasion and coexistence theories, where positive relationships illustrate the patterns of successful establishment of non-native species (Stohlgren *et al.*, 2006). For instance, some studies have evaluated native–non-native richness relationships at fine scales and found negative relationships between native and non-native marine invertebrates and reptiles (Case and Bolger 1991; Stachowicz *et al.*, 1999), while positive relationships have been found at larger scales (Burger *et al.*, 2001; Jeschke and Genovesi 2011). The contradictory observations at different spatial scales illustrate ‘biotic resistance’ at fine scales and ‘biotic acceptance’ at large scales, where coexistence rather than competitive exclusion drives community assembly at a large scale (Stohlgren *et al.*, 2006). In our study we found a posi-

tive relationship between native–non-native richness at the watershed scale, potentially reflecting the biotic acceptance hypothesis (Fridley *et al.*, 2007), where watersheds that have higher native species richness also support high numbers of non-native species. The idea is that ‘the rich get richer’ because of ‘good’ habitats that are desirable and ‘bad’ habitats that necessitate costly physiological adaptations to overcome stressful conditions (Fridley *et al.*, 2007).

We demonstrated a comprehensive model-based strategy that specifically measured landscape-scale factors that spanned the full range of possible responses across ecological scales. Our results show that no single model strategy can be designated as ecologically representative of all fish–habitat relationships. For example, species richness described coarse-level responses related to landscape-scale factors and these results suggests that native and non-native species share similar ecological rules, but richness was insensitive to changing relative abundances across sites relative to landscape factors. Because our richness models failed to demonstrate known relationships between factors like density of dams and declining numbers of native species (Perkin & Gido, 2011), other approaches like guild analysis should be considered to compliment the richness analysis to better define community

function and landscape factors at a fine scale (Mithcell *et al.*, 2006). Using a guild approach indicated a few differences and illustrates some variability between native and non-native species based on guild composition, but even with these few differences, native and non-native species guilds typically responded similarly to landscape-scale factors because the differences were specific to one or two guilds. Lastly, our individual-based models complemented the richness and guild associations by indicating which of the most abundant species might underlie the observed patterns. Overall, our comprehensive model-based strategy could easily be used to evaluate fine and course relationships with landscape factors when considering management alternatives.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Reproductive guild classifications and descriptions included in analysis of community structure. Guild descriptions are based on Balon (1975) and Simon (1999).

Appendix S2. Plots of the first two axis from partial canonical correspondence analysis (pCCA) summarizing native and nonnative (denoted by underline and italics) fish community structure in relation to landscape characteristics of the Missouri River drainage, Wyoming.

BIOSKETCH

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