

# Biotic and abiotic determinants of finescale dace distribution at the southern edge of their range

Evan C. J. Booher<sup>1</sup>  | Annika W. Walters<sup>2</sup> 

<sup>1</sup>Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA

<sup>2</sup>U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA

## Correspondence

Evan C. J. Booher, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166, USA.  
Email: evan.c.booher@gmail.com

## Funding information

Wyoming Game and Fish Department; U.S. Fish and Wildlife Service State Wildlife, Grant/Award Number: 1003586

Editor: Chris Burridge

## Abstract

**Aim:** The factors that set range limits for animal populations can inform management plans aimed at maintaining regional biodiversity. We examine abiotic and biotic drivers of the distribution of finescale dace (*Chrosomus neogaeus*) in two Great Plains basins to identify limiting factors for a threatened freshwater fish population at the edge of their range.

**Location:** Great Plains, Nebraska, South Dakota and Wyoming, USA.

**Methods:** We investigated abiotic and biotic factors influencing the contemporary distribution of finescale dace in the Belle Fourche and Niobrara River basins with Random Forests classification models using fish surveys from multiple agencies spanning 2008–2019 and GIS-derived environmental data.

**Results:** In both basins, finescale dace occurrence exhibited a nonlinear response to mean August water temperature. Abiotic covariates, including streamflow, water temperature and channel slope, were important limiting factors in the final model fit with Belle Fourche River basin surveys ( $n = 131$ ). In contrast, a biotic covariate, native minnow richness, was the most important predictor of finescale dace occurrence in the Niobrara River basin model ( $n = 27$ ). In the Niobrara River, native minnow richness was lower at sites with non-native northern pike (*Esox lucius*).

**Main conclusions:** Basin-specific analyses revealed context dependencies for species–environment relationships, which can inform targeted restoration actions. Similar relationships between water temperature and finescale dace occurrence across both basins suggest summer thermal habitat as a regional limiting factor. The importance of biotic interactions in the Niobrara River highlights an emergent threat from invasive predators to a distinct assemblage of native prairie fishes.

## KEYWORDS

abiotic–biotic interactions, biological invasions, *Chrosomus neogaeus*, climate relict, *Esox lucius*, finescale dace, Great Plains, native fish, northern pike

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

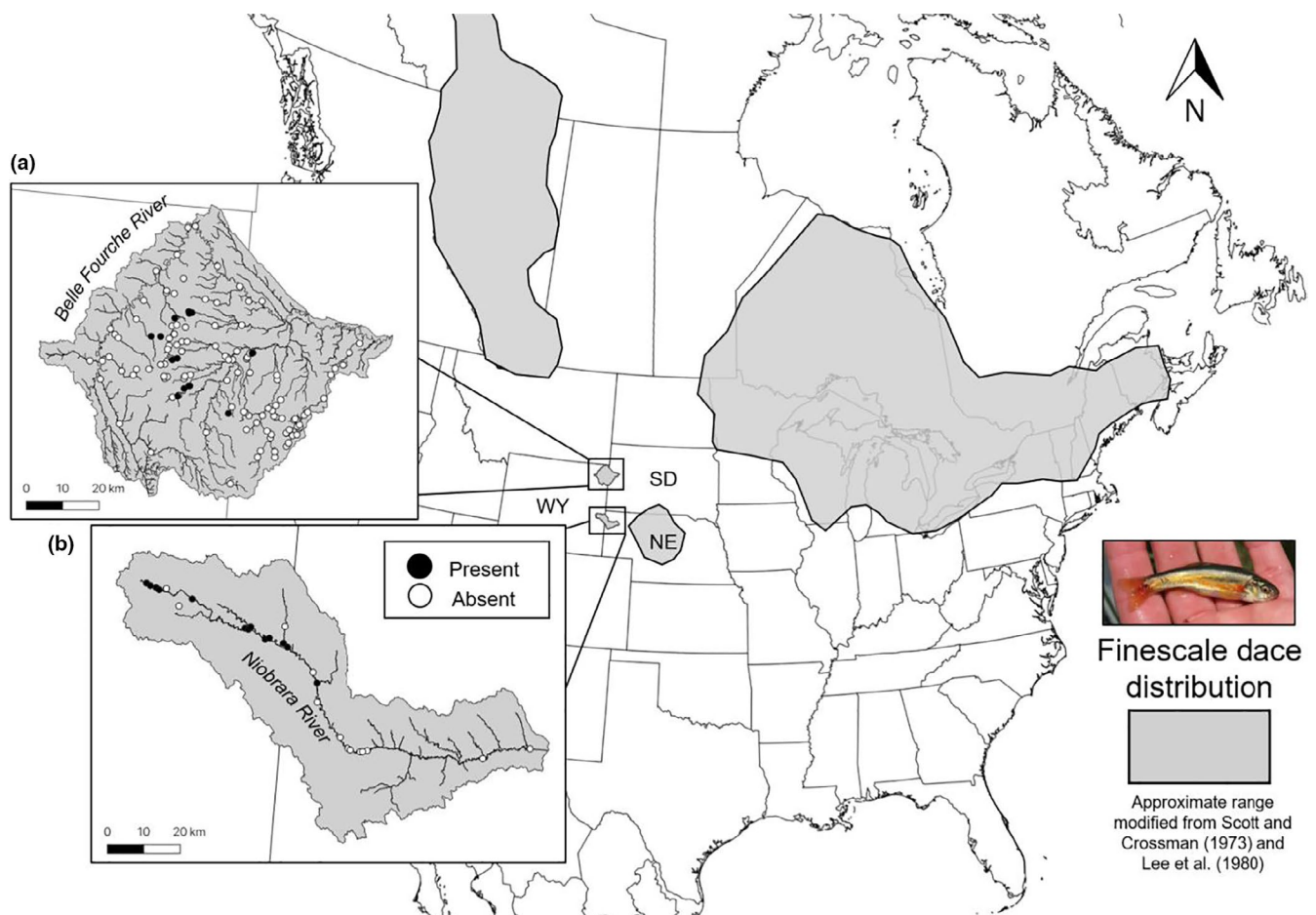
© 2021 This article has been contributed to by US Government employees and their work is in the public domain in the USA. *Diversity and Distributions* published by John Wiley & Sons Ltd.

## 1 | INTRODUCTION

Understanding the factors that create species' range limits is a central goal of biogeography and can inform fisheries and wildlife management. Constraints on the distribution of animal populations have been conceptualized as a series of abiotic and biotic filters operating over multiple spatial and temporal scales (Poff, 1997; Smith & Powell, 1971; Tonn, 1990). Long-term environmental change (e.g. Pleistocene glaciation) and modern disturbances such as biological invasions and habitat destruction can interact to increase extirpation risk, particularly for rare and threatened species (Brook et al., 2008). The global proliferation of invasive species threatens native biodiversity and emphasizes the importance of identifying where physical factors or biotic interactions exert more influence on populations (Clavero & García-Berthou, 2005; Louthan et al., 2015). A key challenge to such efforts are sparse occurrence records for many species of conservation concern (Elith et al., 2006). Studies that leverage new and existing survey data in modelling efforts for these populations will be better positioned to inform their conservation and management.

Many studies employ physical climate data in species distribution modelling efforts, while applications assessing where abiotic or biotic factors will dominate are less common (Franklin, 2013; Louthan et al., 2015). The latter approach may be particularly useful in the study of climate relicts, which constitute fauna isolated due to environmental change in locally suitable areas, often near the edge of longitudinal or elevational thresholds for range-wide distributions (Hampe & Jump, 2011; Woolbright et al., 2014). Key threats to climate relict populations include limitations on available habitat and loss of genetic diversity (Hampe et al., 2005; Rabinowitz, 1981). Studies of relicts are often challenged by their geographic rarity and lack of previous study (McDonald, 2004; Wisz et al., 2013), yet could yield insight into species–environment relationships which differ from those in a core distribution (Gross & Price, 2000; Tarkan, 2006).

Relict fish populations in the Great Plains, USA, are members of an understudied biotic community in the prairie biome (Fausch & Bestgen, 1997). Finescale dace (*Chrosomus neogaeus*) (Cope, 1869) is a North American freshwater fish species that occurs in the Great Plains in isolated populations at the southern edge of their range in Wyoming, South Dakota and Nebraska (Lee et al., 1980; Scott



**FIGURE 1** Distribution of finescale dace (*Chrosomus neogaeus*) across North America and within the study area at the southern edge of their range in the (a) Belle Fourche River ( $n_{present} = 16$ ;  $n_{absent} = 115$ ) and (b) Niobrara River ( $n_{present} = 13$ ;  $n_{absent} = 14$ ) basins of Nebraska (NE), South Dakota (SD) and Wyoming (WY), USA. Locations where finescale dace were detected (black) and were not detected (white) were determined from field surveys by multiple state agencies and the authors from 2008 to 2019. The map projection is North America Albers Equal Area

& Crossman, 1973) (Figure 1). Their regional habitat associations are linked to cool-water environments (i.e. headwater streams and groundwater seeps), which may enable persistence under localized conditions more similar to cooler, wetter palaeo-climatic conditions that prevailed several thousand years ago (McPhail, 1963; Stasiak & Cunningham, 2006). The low prevalence and spatially disjunct pattern of finescale dace occurrence in the Great Plains (Hoagstrom & Berry, 2006) account for their designation as a species of conservation concern in this region (Schneider et al., 2011; *South Dakota Wildlife Action Plan. Wildlife Division Report 2014-03, 2014*; Wyoming State Wildlife Action Plan, 2017).

The fish community associations of finescale dace are not well-understood, but studies in north temperate lakes indicate that native cyprinids in the genus *Chrosomus* are highly sensitive to introductions of non-native predators, including bass and sunfish in the family Centrarchidae and northern pike (*Esox lucius*) (Findlay et al., 2000; MacRae & Jackson, 2001; Tonn & Magnuson, 1982; Whittier et al., 1997). Scaling up from lakes to the landscape, Jackson and Mandrak (2002) predicted the loss of a substantial number (>25,000) of local cyprinid populations in Ontario by 2,100 due to climate-mediated northward range expansion of smallmouth bass (*Micropterus dolomieu*). Threats to cyprinid biodiversity from invasive predators are likely exacerbated at edge populations (Hickerson et al., 2019), highlighting the need for distributional data that can inform analyses of limiting factors.

Our objective in this study was to identify drivers of the contemporary distribution of relict finescale dace in the headwaters of two Great Plains river basins. We assessed potential abiotic and biotic

pathways affecting finescale dace occurrence by fitting classification models with (a) abiotic-only and (b) combined abiotic and biotic variables. Given our location at the southern edge of their range, we hypothesized abiotic factors (e.g. stream size and temperature, channel slope) to exert a strong filtering effect on finescale dace occurrence within both river basins (Quist et al., 2005). For biotic factors, we expected that finescale dace occurrence would be positively correlated with the presence of other small-bodied native fishes, as higher native minnow richness could be indicative of habitat quality or a lack of influence from non-native species. Conversely, we expected a negative relationship between finescale dace occurrence and the presence of non-native, predatory fish species, which forage in nearshore, littoral environments. By incorporating ecologically relevant variables into our basin-specific analysis, we aim to better understand the environmental context under which limiting factors prevail for finescale dace in the Great Plains. These insights could inform broader actions to safeguard imperilled aquatic species and conserve regional biodiversity.

## 2 | METHODS

### 2.1 | Study area

Our study occurred within the Belle Fourche River and Niobrara River basins of Wyoming, South Dakota and Nebraska (Figure 1). These focal basins constitute headwater systems of the Missouri River drainage and represent the only known occurrence of finescale

**TABLE 1** Predictor variables, group (A = abiotic; B = biotic), descriptions and data sources for study sites in the Belle Fourche River and Niobrara River basins of Wyoming, Nebraska and South Dakota, USA

Variable	Group	Description	Source
Baseflow index	A	Baseflow index, estimated proportion of groundwater comprising streamflow (%)	Environmental Protection Agency StreamCat Dataset (Hill et al., 2016)
Channel slope	A	Channel gradient (%), flow line length divided by the change in elevation from upstream to downstream end points of a reach	National Hydrography Dataset (NHD)
Habitat condition index	A	Degradation risk to catchments ranging from 1 (high risk) to 5 (low risk) by integrating multiple disturbance metrics (e.g. road length density, impervious surface, crop land use) for 2010	National Fish Habitat Partnership (Crawford et al. 2016)
Streamflow	A	Estimated mean annual streamflow (m <sup>3</sup> /s) from 1971 to 2000	NHD
Littoral predator occurrence	B	Occurrence of non-native littoral predatory fish species	Nebraska Game and Parks Commission; South Dakota Game, Fish and Parks; Wyoming Game and Fish Department; surveys by the authors (2018, 2019)
Mean August water temperature	A	Mean August water temperature from 1999 to 2019 (°C)	Modelled by the authors using data from Chandler et al. (2016) and field observations (2018, 2019)
Native minnow richness	B	Sum of unique observations of small-bodied native fish species (excluding finescale dace)	Same as littoral predator occurrence
Open water and wetlands	A	Per cent cover (%) of open water and wetlands in catchments	National Landcover Dataset (2011)

dace in Wyoming. Our study sites within the Belle Fourche River basin were located in the Black Hills of north-eastern Wyoming and western South Dakota. Tributary streams to the Belle Fourche River flow across mixed-grass prairie from forested areas in the Bear Lodge Mountains and Black Hills, which encompass the Black Hills National Forest (Knight et al., 2014). Total watershed area of the study area is 3,711 km<sup>2</sup>, with elevation ranging from 943 m to 2,024 m. Land use in the area includes livestock grazing, logging, mining and recreation (Beck et al., 2010). The section of the Niobrara River in our study area (watershed area = 2,400 km<sup>2</sup>) is in the High Plains of eastern Wyoming and western Nebraska and exhibits less topographic diversity than the Belle Fourche River basin (elevation range = 1,343–1,615 m). Land use in the basin is primarily agricultural, with livestock grazing and pivot irrigation being predominant uses (Bradshaw, 1996). The Niobrara River is largely intermittent in Wyoming and becomes perennial near its confluence with Van Tassell Creek near the Wyoming–Nebraska state line. Across both basins, groundwater is an important source of surface water for fish-bearing streams and small lakes (Naus et al., 2001; Szilagyi et al., 2003).

## 2.2 | Fish surveys

Given a paucity of fish survey data in our region of interest, we compiled a dataset from years 2008 to 2019 from multiple state agencies (Table 1). Fish collection methods included seining, single-pass electrofishing and passive gears including minnow traps, fyke nets and trammel nets. Given the variability in methods employed across multiple studies, we filtered these data to binary response metrics of finescale dace presence and pseudo-absence. To account for pseudo-replication of surveys within each sample unit reaches (National Hydrography Dataset (NHD) flow lines; range = 0.03–7.64 km; mean = 1.94 ± 1.54 km (mean ± SD)), we retained only the most recent observation of finescale dace presence/absence within each sample unit.

We conducted targeted surveys for finescale dace during the summer seasons of 2018–2019. Fish collection methods included single-pass backpack electrofishing in 150-metre stream reaches and standardized gear sets with minnow traps and mini-hoop nets in standing waters. Our aim in these surveys was to (a) update the status of finescale dace in historical localities and (b) characterize fish community and habitats under consideration for restoration activities by managers. Given the rarity of finescale dace in the study area and lack of data, we sampled non-random lentic and lotic sites ( $n = 29$ ) in historical localities to refine distributions and evaluate limiting factors (Egley & Larson, 2018). We also randomly sampled lotic sites ( $n = 33$ ) within drainages with known finescale dace occurrence, translocation history or as recommended by managers for restoration potential. We jointly used these surveys and synthesized data from managers to assemble a dataset representative of contemporary basin-wide fish occurrence in the study area. While we used this 11-year snapshot of fish surveys as a representation

of contemporary fish occurrence, we acknowledge that aggregating surveys over time limit our ability to examine potentially important shifts in species distributions during the study period.

We used fish community data comprised of 36 species (25 native and 11 non-native) across nine families (Table 2) to calculate native minnow richness and classify the occurrence of littoral predatory fish at study sites. Native minnow richness was calculated as the sum of unique occurrences of native, small-bodied fishes. We then subtracted finescale dace from these totals at sites where they occurred. We also calculated a binary presence/absence variable for multiple non-native, predatory fish species (Table 2) that are known to forage in littoral, nearshore habitats and have negative effects on native cyprinid communities as introduced or invasive species (He & Kitchell, 1990; Jackson & Mandrak, 2002).

## 2.3 | Environmental data

We retrieved data from multiple sources to describe environmental factors with a known filtering effect on freshwater fishes at the basin scale (e.g. channel gradient, stream size, water temperature) or literature-derived relationship to finescale dace (Lyons et al., 2010; Quist et al., 2005; R. Stasiak & Cunningham, 2006) (Table 1, Table 3). We extracted mean annual streamflow, a proxy for stream size, in cubic metres per second (m<sup>3</sup>/s) (1971–2000) and channel slope (%) for flow lines from the National Hydrography Dataset (NHDPlus High Resolution, accessed December 17, 2020, at <https://www.usgs.gov/core-science-systems/ngp/national-hydrography/nhdplus-high-resolution>), a digital database of surface water features in the United States. We retrieved baseflow index (%) values at the catchment scale (i.e. the local landscape that directly contributes water to a stream), a ratio representing an estimate of the amount of streamflow comprised of groundwater discharge, from the Environmental Protection Agency StreamCat dataset (Hill et al., 2016, <https://www.epa.gov/national-aquatic-resource-surveys/streamcat>). We used catchment-scale habitat condition index (HCI) scores from National Fish Habitat Partnership (Crawford et al., 2016, <http://assessment.fishhabitat.org/>), which assign degradation risk to catchments ranging from 1 (high risk) to 5 (low risk) by integrating multiple disturbance metrics (e.g. road length density, impervious surface, crop land use) into a metric of watershed disturbance. We calculated the percentage of open water and wetlands (%) within catchments from the 2011 National Land Cover Dataset (Multi-Resolution Land Characteristics Consortium, <https://www.mrlc.gov/>).

Using geostatistical network models, we developed predictions of mean August stream temperature (°C) for stream networks in each basin using continuous water temperature observations spanning 2004–2019 (Chandler et al., 2016; Isaak et al., 2017; Ver Hoef et al., 2006). To account for interannual variability in climate, we fit these models with mean August values of air temperature (°C) (PRISM Climate Group, accessed September 25, 2019, at <http://www.prism.oregonstate.edu/>) and streamflow (m<sup>3</sup>/s) (Homer et al., 2015, USGS water data for the Nation: U.S. Geological Survey National

**TABLE 2** Common and scientific names, taxonomic family, status (N = native; E = non-native), categorization as native minnow or non-native littoral predator, and study basin (Belle Fourche or Niobrara) of fish species sampled during fish surveys in the Belle Fourche River and Niobrara River basins of Wyoming, Nebraska and South Dakota, USA, from 2008 to 2019

Common name	Scientific name	Family	Species code	Status	Native minnow	Non-native littoral predator	Belle Fourche	Niobrara
Bigmouth shiner	<i>Notropis dorsalis</i>	Cyprinidae	BMS	N	x			x
Black bullhead	<i>Ameiurus melas</i>	Ictaluridae	BLB	N			x	
Bluegill	<i>Lepomis macrochirus</i>	Centrarchidae	BLG	E		x	x	
Brassy minnow	<i>Hybognathus hankinsoni</i>	Cyprinidae	BMN	N	x			x
Brook stickleback	<i>Culaea inconstans</i>	Gasterosteidae	STK	E			x	
Brook trout	<i>Salvelinus fontinalis</i>	Salmonidae	BKT	E			x	
Brown trout	<i>Salmo trutta</i>	Salmonidae	BNT	E			x	
Central stoneroller	<i>Campostoma anomalum</i>	Cyprinidae	STR	N	x			x
Channel catfish	<i>Ictalurus punctatus</i>	Ictaluridae	CCF	N			x	
Common carp	<i>Cyprinus carpio</i>	Cyprinidae	CRP	E			x	
Common shiner	<i>Luxilus cornatus</i>	Cyprinidae	CSH	N	x			x
Creek chub	<i>Semotilus atromaculatus</i>	Cyprinidae	CKC	N	x		x	x
Fathead minnow	<i>Pimephales promelas</i>	Cyprinidae	FHM	N	x		x	x
Finescale dace	<i>Chrosomus neogaeus</i>	Cyprinidae	FSD	N	x		x	x
Flathead chub	<i>Platygobio gracilis</i>	Cyprinidae	FHC	N	x		x	
Green sunfish	<i>Lepomis cyanellus</i>	Centrarchidae	GSF	E		x	x	x
Iowa darter	<i>Etheostoma exile</i>	Percidae	IDT	N	x			x
Lake chub	<i>Couesius plumbeus</i>	Cyprinidae	LKC	N	x		x	
Largemouth bass	<i>Micropterus salmoides</i>	Centrarchidae	LMB	E		x	x	x
Longnose dace	<i>Rhinichthys cataractae</i>	Cyprinidae	LND	N	x		x	x
Longnose sucker	<i>Catostomus catostomus</i>	Catostomidae	LNS	N			x	
Mountain sucker	<i>Catostomus platyrhynchus</i>	Catostomidae	MTS	N			x	
Northern pearl dace	<i>Margariscus margarita</i>	Cyprinidae	NPD	N	x			x
Northern pike	<i>Esox lucius</i>	Esocidae	NOP	E		x		x
Northern redbelly dace × finescale dace hybrid	<i>Chrosomus eos</i> × <i>Chrosomus neogaeus</i>	Cyprinidae	NRD × FSD	N	x			x
Plains topminnow	<i>Fundulus sciadicus</i>	Fundulidae	PTM	N	x			x
Rainbow trout	<i>Oncorhynchus mykiss</i>	Salmonidae	RBT	E			x	
Red shiner	<i>Cyprinella lutrensis</i>	Cyprinidae	RDS	N	x		x	
River carsucker	<i>Carpionodes carpio</i>	Catostomidae	RCS	N			x	
Sand shiner	<i>Notropis stramineus</i>	Cyprinidae	SDS	N	x		x	x
Sauger	<i>Sander canadensis</i>	Percidae	SAR	N			x	
Shorthead redhorse	<i>Moxostoma macrolepidotum</i>	Catostomidae	NRH	N			x	
Smallmouth bass	<i>Micropterus dolomieu</i>	Centrarchidae	SMB	E		x	x	
Stonecat	<i>Noturus flavus</i>	Ictaluridae	STC	N			x	
White sucker	<i>Catostomus commersonii</i>	Catostomidae	WHS	N			x	x
Yellow perch	<i>Perca flavescens</i>	Percidae	YEP	E		x	x	x



**TABLE 3** Abiotic and biotic predictors (mean  $\pm$  SD for continuous variables) derived from GIS layers for fish surveys in the Belle Fourche River and Niobrara River basins of Wyoming, Nebraska and South Dakota, USA, from 2008 to 2019

Basin	Baseflow index (%)	Channel slope	Habitat condition index	Littoral predator occurrence (1/0)	Mean August water temperature 1999–2019 (°C)	Native minnow richness	Open water and wetlands	Streamflow (m <sup>3</sup> /s)
Belle Fourche	71.68 (5.85)	0.02 (0.02)	3.05 (1.06)	24/131 (18%)	15.85 (4.10)	1 (1)	0.04 (0.09)	0.75 (1.53)
Niobrara	67.70 (6.10)	0.00 (<0.01)	3.66 (0.98)	12/27 (44%)	18.59 (1.64)	3 (3)	0.12 (0.08)	0.52 (0.47)

Note: Littoral predator occurrence (presence = 1; absence = 0; prevalence (%)) was a categorical predictor variable.

Water Information System database, accessed February 20, 2020, at <https://doi.org/10.5066/F7P55KJN>) that were cross-referenced to the matching year for each observation dataset (Appendix S1) (Isaak et al., 2017). We then used a prediction dataset with mean air temperature and streamflow values from 1999 to 2019 to produce a composite 20-year mean stream temperature metric, analogous to a project-specific climate normal (Jarnevich & Young, 2019). We joined environmental data to NHD flow lines using the spatial join tool in ArcMap version 10.5 (Esri, Redlands, California). Fish survey sites were joined to NHD flow lines using package “rgeos” in Program R (Bivand et al., 2019; R Core Team, 2019).

## 2.4 | Statistical analyses

We used Random Forests classification models to examine potential relationships among abiotic and biotic factors that influence the occurrence of finescale dace in our study area. Random Forests are a type of classification and regression tree (CART) model that are generated by bootstrapping data to create a large number of decision trees, which converge on a prediction and rank covariates by their importance in explaining variation in the response (Breiman, 2001; Breiman et al., 1984). This modelling approach is well-suited for ecological studies as it assumes no underlying distribution of the data, is invariant to predictor variable transformations, can fit nonlinear relationships and is relatively insensitive to autocorrelation (Cutler et al., 2007). Finescale dace occurrence (present (1) or absent (0)) was the binary response variable, and unstandardized abiotic and biotic variables were used as predictors (Table 1). To maintain model parsimony, we used the model improvement ratio (MIR) method, which minimizes the number of retained predictors and model mean-squared error while maximizing the percentage of variation explained (Murphy et al., 2010). We fit models separately for each river basin to examine potential context-specific drivers of fish occurrence and provide interpretable information for regional fisheries managers.

For each basin, we fit two groups of models. In the initial model, (a) we used only abiotic covariates as predictors of finescale dace occurrence. We then fit (b) a subsequent model with added biotic variables to examine their effects on model performance (Veza et al., 2015). We applied the MIR procedure to each model for covariate selection. We used packages “randomForest” and “rfUtilities” in Program R for model fitting, selection and performance assessment (Evans & Cushman, 2009; R Core Team, 2019; Wiener & Andy, 2002). For datasets with excessive zeros ( $\geq 30\%$  of the response variable), we used zero-inflated models, which combine independent ensembles of models fit with random subsets of the majority class (Evans & Cushman, 2009).

To assess model performance, we calculated the percentage of correctly classified instances (CCI) with confusion matrices (Buckland & Elston, 1993), evaluated predictive performance with area under each curve (AUC) measures from receiver operator characteristic plots (Manel et al., 2001) and evaluated cross-classification error using Cohen's Kappa statistic (K) (Cohen, 1968). We also assessed error

**TABLE 4** Random Forest classification models for finescale dace occurrence fit with fish surveys from the Belle Fourche River ( $n = 131$ ) and Niobrara River ( $n = 27$ ) basins of Wyoming, Nebraska and South Dakota, USA, from 2008 to 2019 and abiotic and biotic covariates (Table 1)

Basin	Group	Model	OOB error	CCI	AUC	Kappa
Belle Fourche	Abiotic-only	Baseflow index, channel slope, habitat condition index, open water and wetlands, streamflow, water temperature	0.20	0.79	0.75	0.52
Belle Fourche	Abiotic + biotic	Baseflow index, channel slope, native minnow richness, open water and wetlands, streamflow, water temperature	0.24	0.77	0.73	0.48
Niobrara	Abiotic-only	Open water and wetlands, water temperature	0.30	0.70	0.71	0.41
Niobrara	Abiotic + biotic	Littoral predators, native minnow richness, open water and wetlands, water temperature	0.07	0.93	0.93	0.85

Note: Groups represent models with abiotic-only or combined abiotic-biotic covariate sets. The model improvement ratio (MIR) technique was applied for covariate selection in all cases. Model classification accuracy was assessed with error estimates for out-of-bag data (OOB error), correctly classified instances (CCI), area under each curve (AUC) and cross-classification error using Cohen's Kappa ( $K$ ).

estimates for out-of-bag (OOB) data (observations withheld from the training dataset), which function as cross-validated accuracy estimates (Veza et al., 2015). Model significance ( $p$ ;  $\alpha = .05$ ) was computed with a randomization test with 999 permutations (Murphy et al., 2010). Intercorrelation among predictor variables was calculated using generalized variance inflation factor (GVIF), and highly correlated variables (GVIF > 3) were not included in the same model (Dormann et al., 2013). We used partial dependence plots of the marginal effect of covariates on the predicted probability of finescale dace occurrence to visualize species-environment relationships (Cutler et al., 2007).

### 3 | RESULTS

#### 3.1 | Contemporary distribution of finescale dace

Finescale dace were observed at 16 of 131 (12%) surveyed stream reaches in the Belle Fourche River basin and 13 of 27 (48%) sites in the Niobrara River basin from 2008 to 2019 (Figure 1). In surveys conducted from 2018 to 2019, we detected finescale dace at sites throughout the Wyoming portion of the Niobrara River ( $n = 7$ ), but not within the mainstem Niobrara River in Nebraska ( $n = 3$ ). We did, however, detect finescale dace in the Lakotah Canal, an off-channel irrigation ditch sourced from the Niobrara River in Nebraska. During this same period, we documented finescale dace occurrence in the Belle Fourche River basin in nine distinct drainages, including Blacktail Creek, Cox Lake, Cub Creek, Medicine Flat Creek, Middle Fork Hay Creek, Middle Redwater Creek, Mud Lake, Spotted tail Reservoir and Sundance Creek.

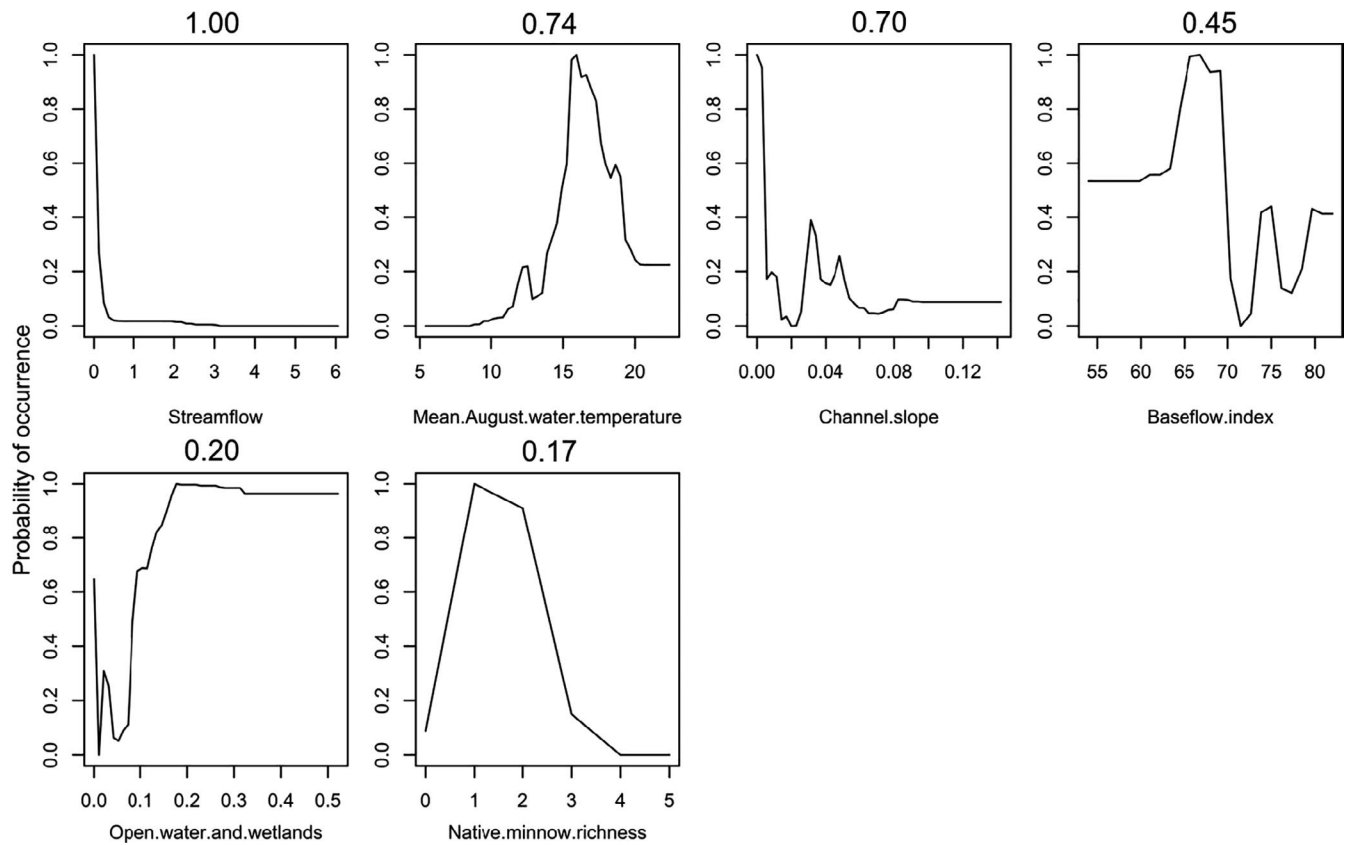
#### 3.2 | Random Forests classification models

Covariates supported in basin-specific classification models exhibited both similarities and differences in their relationships to

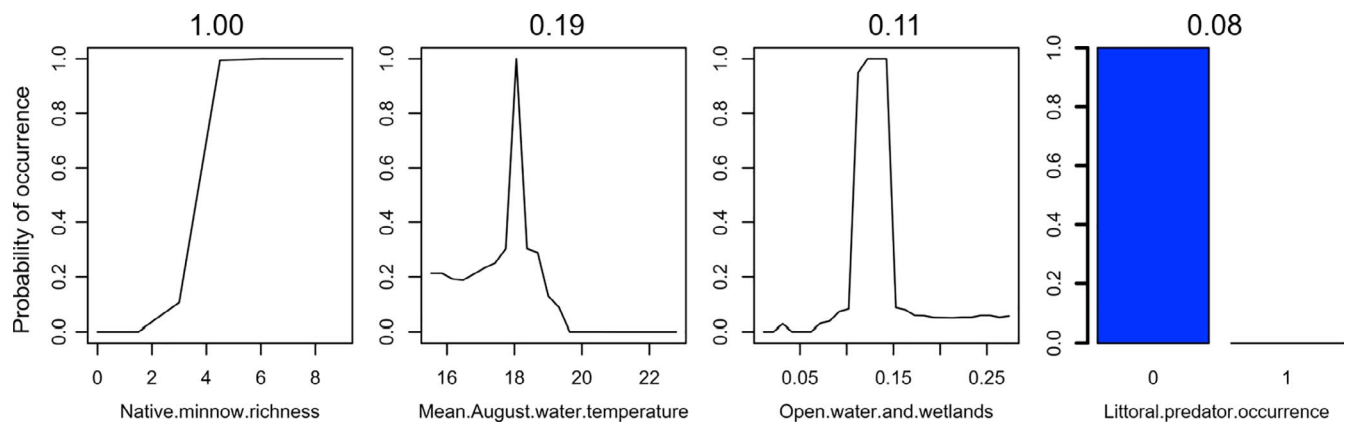
finescale dace occurrence across basins. No significant intercorrelation was found among predictor variables in the Belle Fourche River basin, while streamflow (GVIF = 6.73) and baseflow index (GVIF = 5.27) were removed from further consideration in Niobrara River basin models (Appendix S2).

In Belle Fourche River basin models, the addition of biotic variables (native minnow richness and littoral predator occurrence) to the initial abiotic-only model resulted in a slight decrease in performance ( $\Delta$ OOB error rate = +0.03;  $\Delta$ CCI = -0.02;  $\Delta$ AUC = -0.01;  $\Delta$ K = -0.04) (Table 4). Classification accuracy measures indicated moderate predictive performance (OOB error rate = 0.24; CCI = 0.77; AUC = 0.73;  $K = 0.48$ ). The final model was a good fit to the data based on the randomization test ( $p = .001$ ). Abiotic variables were more important than biotic variables in the final model for the Belle Fourche. Variables in the final model, listed in descending order of importance, included mean annual streamflow (1.00), mean August water temperature (0.74), channel slope (0.70), baseflow index (0.45), per cent open water and wetlands (0.20) and native minnow richness (0.17). Streamflow exhibited a negative relationship to finescale dace occurrence, while all other covariates exhibited nonlinear relationships with both positive and negative trends in relation to the response variable (Figure 2).

In Niobrara River basin models, inclusion of biotic variables improved model performance ( $\Delta$ OOB error rate = -0.22;  $\Delta$ CCI = +0.22;  $\Delta$ AUC = +0.22;  $\Delta$ K = +0.51) (Table 4). Classification accuracy measures indicated good predictive performance (OOB error rate = 0.07; CCI = 0.92; AUC = 0.92;  $K = 0.85$ ). Variables in the final model, listed in descending order of importance, included native minnow richness (1.00), mean August water temperature (0.19), open water and wetlands (0.11) and littoral predator occurrence (0.08). The final model was a good fit to the data based on the randomization test ( $p < .001$ ). Relationships between finescale dace occurrence and covariates were positive for native minnow richness, nonlinear for mean August water temperature and open water and wetlands, and negative for littoral predator occurrence (Figure 3).



**FIGURE 2** Partial dependence plots from Random Forests models depicting finescale dace occurrence as a response to covariates from the best supported model fit with Belle Fourche River basin surveys. Abiotic factors were the most important variables in the model, as finescale dace occurrence was negatively associated with streamflow ( $\text{m}^3/\text{s}$ ) and exhibited a nonlinear relationship to other covariates. Variable importance (range = 1.00–0.17) is listed for each covariate in descending order



**FIGURE 3** Partial dependence plots from Random Forests models depicting finescale dace occurrence as a response to covariates from the best supported model from the Niobrara River basin. Finescale dace were positively associated with a biotic covariate, native fish minnow richness, exhibited nonlinear relationships to mean August water temperature ( $^{\circ}\text{C}$ ) and open water and wetlands (%), and were not predicted to occur at sites with littoral predators. Variable importance (range = 1.00–0.08) is listed for each covariate in descending order

## 4 | DISCUSSION

Differential drivers of occurrence between the two basins highlight the importance of context dependency, including environmental heterogeneity and recent biological invasions, when evaluating the relative importance of abiotic and biotic covariates in species

occurrence models. Abiotic factors were the most important predictors of finescale dace occurrence in the Belle Fourche River basin, where the Black Hills and Bear Lodge Mountains provide topographic diversity creating distinct environmental gradients. By contrast, low-gradient stream channels and seasonal wetlands characterize the more homogenous high prairie environment of the



Niobrara River basin. In addition, the Niobrara River is experiencing the arrival of a novel non-native predator, northern pike. In this environmental context, biotic factors were important drivers of occurrence. This result adds to a body of work highlighting the utility of biotic interactions in models used for fisheries and wildlife conservation planning (Chamberlain et al., 2014; MacDougall et al., 2018). Consistency in the relationship between August water temperature and finescale dace occurrence across both basins suggests summer thermal habitat as a potential limiting factor at the regional level.

#### 4.1 | Drivers of finescale dace occurrence

Abiotic drivers of finescale dace occurrence in the Belle Fourche River basin suggest that geomorphic and climatic filters limit their habitat breadth. The negative relationship between finescale dace occurrence and mean annual streamflow (Figure 2) suggests an orientation towards headwaters for this population. The effect of stream size as a distributional constraint on small-bodied freshwater fishes has been documented in Wyoming (Quist et al., 2004) and other locations in North America (Taylor et al., 2006; Zorn et al., 2002). The nonlinear relationship between finescale dace occurrence and base-flow index in the partial dependence plot indicates a lower probability of occurrence at sites with the highest estimated groundwater influence. This unexpected result could reflect the coarse resolution of the source data (1-km raster grid), which is unlikely to capture locally important features such as springs and seeps. The negative relationship to channel slope and positive relationship to per cent open water and wetlands align with literature-derived expectations that finescale dace inhabit low-gradient streams, bogs and lakes (Rahel, 1984; Stasiak, 1972). These patterns are likely indicative of hierarchical relationships between landscape position and important local habitat characteristics for finescale dace, such as vegetation cover (Stasiak, 1978).

The nonlinear response of finescale dace occurrence to a biotic covariate, native minnow richness, in the Belle Fourche model, may reflect less diverse fish assemblages, and historic management of finescale dace, in this part of the study area. Managed translocations, beginning in the late 1970s, established conservation populations in several headwater drainages in the Belle Fourche River basin. We documented present-day persistence at a subset of these localities. Native fish species richness at finescale dace-occupied sites in these drainages is comparatively lower than sites in the Niobrara River basin ( $\bar{x}_{\text{Belle Fourche}} = 2$ ,  $\bar{x}_{\text{Niobrara}} = 6$ ). Consequently, these data may not exhibit sufficient variation to explain finescale dace occurrence, or outperform abiotic covariates, in Random Forest models. In two locations in the Belle Fourche River basin, upper Middle Redwater Creek and Cub Creek, finescale dace was the only detected fish species. Segments of these drainages may have been naturally fishless prior to the establishment of translocated populations. This history cannot be resolved without a better understanding of past fish occurrence and management actions in the study area. While littoral predators, including bluegill (*Lepomis macrochirus*), green

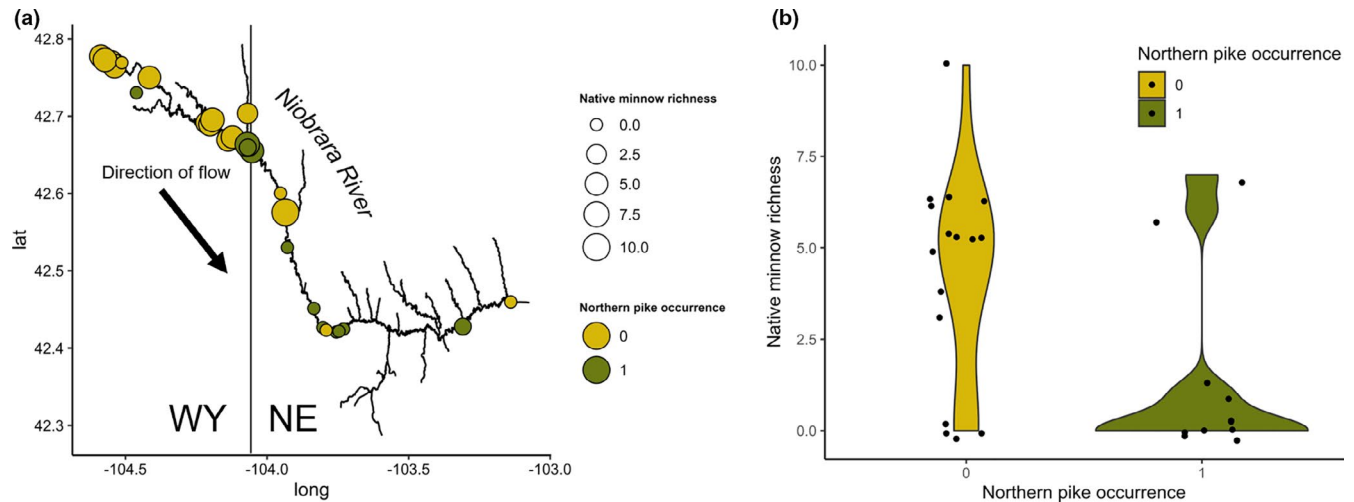
sunfish, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*), occur in the Belle Fourche River basin, their potential interactions with finescale dace could be mediated by habitat partitioning related to stream morphology, fragmentation and water temperature (Matthews & Hill, 1980). We observed predation of finescale dace by smallmouth bass during one survey in Middle Fork Hay Creek ( $n = 1$ ). This encounter provides highly limited yet direct evidence of a negative biotic interaction in the Belle Fourche River basin and suggests the need for further research into the effects of non-native species on native fish distributions in the Belle Fourche River basin.

The relative importance of biotic drivers in the Niobrara River provides an insightful contrast to modelled fish-habitat relationships in the Belle Fourche River basin. Native minnow richness was by far the most important variable in the Niobrara River, while a negative association between finescale dace and littoral predatory fish, driven by northern pike, was also a retained covariate in the model (Appendix S3). Abiotic variables retained included water temperature and percentage of open water and wetlands within catchments. A nonlinear, yet positive, relationship to the percentage of open water and wetlands suggests an environmental optimum between 10% and 15% and an association with a habitat type reflecting the low-gradient geomorphic setting of this basin (Figure 3).

The nonlinear relationship between mean August water temperature and finescale dace occurrence across both basins suggests that summer thermal habitat is a limiting factor for these populations. The nonlinear relationship between finescale dace occurrence and mean August water temperature suggests similar thermal optima (15–20°C) for finescale dace in the Belle Fourche River and Niobrara River basins. The Niobrara River basin contains waterbodies with cool (19–22°C) thermal regimes, while the Belle Fourche basin also contains cold waters (<19°C) (Wehrly et al., 2003). Water temperature is known to limit the dispersal ability and geographic range of ectothermic species (Recoder et al., 2018; Turlure et al., 2010). Future warming trends may further restrict finescale dace distribution at lower latitudes. However, groundwater-influenced headwater streams which currently support finescale dace will likely experience slower warming rates, potentially allowing them to serve as climate refugia (Isaak et al., 2016).

#### 4.2 | Fish community patterns in the Niobrara River

In the Niobrara River, finescale dace co-occurred with each species from the native minnow group in at least one survey, demonstrating their ubiquity within the global fish fauna in the headwaters of the Niobrara River and their potential utility as an indicator species of ecological perturbation. Our inability to detect finescale dace at mainstem Niobrara River sites in Nebraska may reflect temporal shifts in fish assemblages, suggesting potential threats to fish diversity in this system. Native cyprinid species, including brassy minnow (*Hybognathus hankinsoni*), central stoneroller (*Camptostoma anomalum*), creek chub (*Semotilus*



**FIGURE 4** (a) Spatial patterns of native minnow richness at sites with and without the occurrence of invasive northern pike (*Esox lucius*) in the Niobrara River basin from 2008 to 2019. The most recent survey was retained among replicates within National Hydrography Dataset flow lines. (b) Counts of native minnow species (see Table 2 for species list) were lower at sites where northern pike were detected (Mann–Whitney  $U$  test,  $W = 126$ ,  $p = .054$ ; Fligner–Killeen test,  $\chi^2 = 0.46$ ,  $p = .499$ )

*atromaculatus*) and fathead minnow (*Pimephales promelas*), were detected in surveys within Agate Fossil Beds National Monument in 1979 and 1989, but not in subsequent sampling events in 2008 and 2011 (Spurgeon et al., 2014). Spurgeon et al. (2014) observed relatively intact native fish assemblages, including finescale dace, on two properties located upstream of Agate Fossil Beds National Monument in 2011, but in 2018 we did not detect finescale dace, or any native small-bodied fish, at sites in close proximity to those sites.

Non-native predatory game species such as northern pike were historically stocked in the lower segment of the Niobrara basin at Box Butte Reservoir, Nebraska, between 1949 and 1989 (Spurgeon et al., 2014), and colonization of areas farther upstream has been documented in recent monitoring efforts (B. Compton & N. Hogberg, Wyoming Game and Fish Department, personal communication, 2017). Negative effects of northern pike on finescale dace could be attributed to mechanisms such as displacement of habitat use, competition or predation. Stasiak et al. (2011) suggested that northern pike predation on native fishes was potentially causing the absence of small-bodied native fishes during 2011 surveys in the Niobrara River within Agate Fossil Beds National Monument, Nebraska. Diet samples from northern pike taken near the Wyoming–Nebraska state line in 2015 contained finescale dace and other native minnows, providing additional evidence that predation could be an important mechanism driving biotic interactions in the Niobrara River (N. Hogberg, Wyoming Game and Fish Department, personal communication, 2017). Collectively, spatial patterns in minnow diversity and a negative trend of association between northern pike occurrence and native minnow richness (Mann–Whitney  $U$  test,  $W = 126$ ,  $p = .054$ ; Fligner–Killeen test,  $\chi^2 = 0.46$ ,  $p = .499$ ; Figure 4) suggest potential displacement of native species by an invasive predatory species. These data are indicative of novel biotic interactions that could alter or eliminate entire assemblages of native freshwater fishes.

### 4.3 | Conservation and management implications

We expected abiotic factors to be dominant drivers of finescale dace occurrence in our study system, as relict populations tend to occupy areas in close proximity to abiotically stressful conditions (Woolbright et al., 2014). This was supported by (a) a shared response to August water temperature in both basins, indicating that summer thermal habitat is a regional limiting factor for finescale dace in the Great Plains, and (b) the importance of abiotic drivers in the Belle Fourche River basin (Figure 2, Figure 3). The importance of biotic interactions in the Niobrara River highlights a scenario where biotic interactions may further constrain populations with naturally low prevalence. Collectively, these results suggest that potential mitigation efforts for finescale dace will benefit greatly from basin-specific management plans.

Our surveys revealed greater finescale dace occurrence in the Belle Fourche River basin than had been documented in previous sampling efforts (B. Bradshaw, Wyoming Game and Fish Department, personal communication, 2015). Notably, we documented persistence in six distinct drainages with a history of managed translocation in Wyoming and South Dakota, providing further documentation of the potential viability of this restoration strategy for increasing the redundancy of finescale dace populations within the Belle Fourche River basin (Amiotte et al., 2015). Studies that assessed the quality of candidate translocation sites (Hickerson & Walters, 2019) and success of past translocation efforts (Harig et al., 2000; Novinger & Rahel, 2003) for freshwater fishes could guide future management actions for finescale dace.

Belle Fourche River basin models indicate that low-gradient, cool-water environments are important for finescale dace. These characteristics could be strongly influenced by current and future management of North American beaver (*Castor canadensis*) in the study area. Habitat modelling by Beck et al. (2010) identified areas in the Black

Hills National Forest with perennial water and low stream gradients as two factors affecting site suitability for beaver. Areas with suitable geomorphology, vegetation and hydrology could be targeted for active beaver reintroduction (Macdonald et al., 2000) or restoration using beaver dam analogs—structures which simulate beaver dams and promote recovery of degraded streams (Pollock et al., 2014). Ecosystem benefits stemming from beaver-influenced landscapes, including increased habitat complexity, streamflow duration and invertebrate production (Kemp et al., 2012), could benefit finescale dace and the greater biotic community of the Belle Fourche River basin.

Leveraging biological data, such as the distribution and abundance of competing and predatory species, can yield insight into emergent threats to native taxa. We highlight the importance of such an approach with fish survey data from the Niobrara River basin, where biotic interactions substantially improved performance of classification models (Table 4). An apparent reduction in native minnow richness at sites with non-native littoral predators adds to previous studies examining incursions of invasive species into hotspots of native species diversity (Light & Marchetti, 2007; Stohlgren et al., 1999). Invasions of northern pike are particularly alarming, as they exhibit trophic adaptability in prey selection between fish and invertebrates, indicating their potential to alter or eliminate native fish communities as novel apex predators (Beaudoin et al., 1999; Chapman & Mackay, 1984; Sepulveda et al., 2013). Their profound impact on aquatic systems alludes to dim ecological futures for native small-bodied fishes of the Great Plains in the absence of effective predator control or containment. The Niobrara River's fragmented nature due to headwater intermittency provides opportunities for slowing northern pike invasion, but is also a challenge for the long-term fitness of native fishes (Pavlova et al., 2017). Safeguarding remaining native fish diversity in the Niobrara River will likely require measures, which both suppress predators and use hydrologic and structural fish passage barriers to control non-native colonization of remaining native fish refugia (Kruse et al., 2001).

Studies that effectively integrate new and existing datasets can inform future actions aimed at maintaining distinct assemblages of native fishes in an increasingly uncertain future of invasions and environmental change. Our results highlight the importance of basin-specific approaches due to the potential for high context dependence, as we found explanatory factors that were useful for evaluating the relative importance of biotic versus abiotic drivers. In a topographically diverse watershed such as the Belle Fourche abiotic drivers can strongly influence fish distributions, while biotic drivers are likely to be especially important in basins with recent biological invasions. In this context, novel species interactions present a more pressing risk to persistence than abiotic stressors often linked to climate relict distributions. Conservation plans that incorporate mutual and synergistic threats will improve efforts to safeguard rare species at the edge of range-wide distributions.

#### ACKNOWLEDGEMENTS

We are deeply grateful to the private landowners of Crook County and Niobrara County, Wyoming, Nebraska Chapter of The Nature

Conservancy and the Prairie Plains Resource Institute for providing site access. We thank seasonal technicians Andrew Kaneb and Taren Giberti and fisheries management biologists in Wyoming, Nebraska and South Dakota who provided data, assistance in the field or advice in project planning. Historic survey data were provided by the Wyoming Game and Fish Department, South Dakota Natural Heritage Database and Department of Game, Fish and Parks, and Nebraska Game and Parks Commission Rivers and Streams Program. This project was funded by the Wyoming Game and Fish Department through U.S. Fish and Wildlife Service State Wildlife Grant #1003586. Field data from 2018 to 2019 were collected under Chapter 33 Permit 1177 from the Wyoming Game and Fish Department, Scientific Collector's Permit 41 and an Endangered Species Permit from the State of South Dakota, Department of Game Fish and Parks, and Scientific and Educational Permit 1094 from the Nebraska Game and Parks Commission. The study was performed under the auspices of University of Wyoming Institutional Animal Care and Use Committee Protocol #20180625AW00316-01. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

#### CONFLICT OF INTEREST

There is no conflict of interest declared in this article.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13227>.

#### DATA AVAILABILITY STATEMENT

Data supporting the results are available from the Dryad Digital Repository [<https://doi.org/10.5061/dryad.q573n5th9>; Booher and Walters 2020].

#### ORCID

Evan C. J. Booher  <https://orcid.org/0000-0003-4353-9113>

Annika W. Walters  <https://orcid.org/0000-0002-8638-6682>

#### REFERENCES

- Amiotte, J., Simpson, G., & Barnes, M. E. (2015). Re-establishment of Finescale Dace (*Phoxinus neogaeus*) in Mud lake, Lawrence County, South Dakota. *Proceedings of the South Dakota Academy of Science*, 94, 195–200.
- Beaudoin, C. P., Tonn, W. M., Prepas, E. E., & Wassenaar, L. I. (1999). Individual specialization and trophic adaptability of northern pike (*Esox lucius*): An isotope and dietary analysis. *Oecologia*, 120(3), 386–396. <https://doi.org/10.1007/s004420050871>
- Beck, J. L., Dauwalter, D. C., Gerow, K. G., & Hayward, G. D. (2010). Design to monitor trend in abundance and presence of American beaver (*Castor canadensis*) at the national forest scale. *Environmental Monitoring and Assessment*, 164(1–4), 463–479. <https://doi.org/10.1007/s10661-009-0907-8>
- Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K., Giraudoux, P., Davis, M., & Santilli, S. (2019). *Package "rgeos"*. Retrieved from <https://cran.rstudio.com/web/packages/rgeos/rgeos.pdf>

- Bradshaw, B. (1996). *Niobrara River basin management plan*. Sheridan, Wyoming: Wyoming Game and Fish Department.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32. <https://doi.org/10.1023/A:1010933404324>
- Breiman, L., Friedman, J. H., Olshen, R. A., & Stone, C. J. (1984). *Classification and regression trees* (1st ed.). Chapman & Hall.
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, 23(8), 453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Buckland, S. T., & Elston, D. A. (1993). Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology*, 30(3), 478–495. <https://doi.org/10.2307/2404188>
- Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17(7), 881–890. <https://doi.org/10.1111/ele.12279>
- Chandler, G. L., Wollrab, S. P., Horan, D. L., Nagel, D. E., Parkes, S. L., Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Hostetler, S. W., Luce, C. H., Dunham, J. B., Kershner, J. L., & Roper, B. B. (2016). *NorWeST stream temperature data summaries for the western U.S.* Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2016-0032>
- Chapman, C. A., & Mackay, W. C. (1984). Versatility in habitat use by a top aquatic predator, *Esox lucius* L. *Journal of Fish Biology*, 25(1), 109–115. <https://doi.org/10.1111/j.1095-8649.1984.tb04855.x>
- Clavero, M., & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, 20(3), 110. <https://doi.org/10.1016/j.tree.2005.01.003>
- Cohen, J. (1968). Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit. *Psychological Bulletin*, 70(4), 213–220. <https://doi.org/10.1037/h0026256>
- Cope, E. D. (1869). Synopsis of the Cyprinidae of Pennsylvania with supplement on some new species of American and African fishes. *Transactions of the American Philosophical Society*, 13(3), 351–410.
- Crawford, S., Whelan, G., Infante, D., Blackhart, K., Wesley, D., Fuller, P. L., Birdsong, T., Wieferich, D. J., McClees-Funinan, R., Stedman, S. M., Herreman, K., & Ruhl, P. (2016). *Through a fish's eye: The status of fish habitats in the United States 2015*. National Fish Habitat Partnership. <http://assessment.fishhabitat.org/>
- Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, 88(11), 2783–2792. <https://doi.org/10.1890/07-0539.1>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Egley, R. M., & Larson, E. R. (2018). Distribution, habitat associations, and conservation status updates for the pilose crayfish *Pacifastacus gambelii* (Girard, 1852) and Snake River pilose crayfish *Pacifastacus connectens* (Faxon, 1914) of the western United States. *PeerJ*, 9, e5668. <https://doi.org/10.7717/peerj.5668>
- Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., ... E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Evans, J. S., & Cushman, S. A. (2009). Gradient modeling of conifer species using random forests. *Landscape Ecology*, 24(5), 673–683. <https://doi.org/10.1007/s10980-009-9341-0>
- Fausch, K. D., & Bestgen, K. R. (1997). Ecology of fishes indigenous to the central and southwestern great plains. In F. B. Knopf, & F. L. Samson (Eds.), *Ecology and conservation of Great Plains Vertebrates* (pp. 131–166). Springer. [https://doi.org/10.1007/978-1-4757-2703-6\\_6](https://doi.org/10.1007/978-1-4757-2703-6_6)
- Findlay, C. S., Bert, D. G., & Zheng, L. (2000). Effect of introduced piscivores on native minnow communities in Adirondack lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(3), 570–580. <https://doi.org/10.1139/cjfas-57-3-570>
- Franklin, J. (2013). Species distribution models in conservation biogeography: Developments and challenges. *Diversity and Distributions*, 19(10), 1217–1223. <https://doi.org/10.1111/ddi.12125>
- Gross, S. J., & Price, T. D. (2000). Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography*, 27(4), 869–878. <https://doi.org/10.1046/j.1365-2699.2000.00440.x>
- Hampe, A., & Jump, A. S. (2011). Climate relicts: Past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, 42, 313–333.
- Hampe, A., My, R., & Petit, J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, 8, 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Harig, A. L., Fausch, K. D., & Young, M. K. (2000). Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management*, 20(4), 994–1004. [https://doi.org/10.1577/1548-8675\(2000\)020<0994:fisogc>2.0.co;2](https://doi.org/10.1577/1548-8675(2000)020<0994:fisogc>2.0.co;2)
- He, X., & Kitchell, J. F. (1990). Direct and indirect effects of predation on a fish community: A whole-lake experiment. *Transactions of the American Fisheries Society*, 119, 825–835. [https://doi.org/10.1577/1548-8659\(1990\)119<0825:DAIEOP>2.3.CO;2](https://doi.org/10.1577/1548-8659(1990)119<0825:DAIEOP>2.3.CO;2)
- Hickerson, B. T., Maitland, B. M., & Walters, A. W. (2019). Effects of multiple nonnative fish on an imperiled cyprinid, hornyhead chub. *Transactions of the American Fisheries Society*, 148(6), 1132–1145. <https://doi.org/10.1002/tafs.10203>
- Hickerson, B. T., & Walters, A. W. (2019). Evaluation of potential translocation sites for an imperiled cyprinid, the h hornyhead chub. *North American Journal of Fisheries Management*, 39(1), 205–218. <https://doi.org/10.1002/nafm.10261>
- Hill, R. A., Weber, M. H., Leibowitz, S. G., Olsen, A. R., & Thornbrugh, D. J. (2016). The Stream-Catchment (StreamCat) dataset: A database of watershed metrics for the conterminous United States. *Journal of the American Water Resources Association*, 52(1), 120–128. <https://doi.org/10.1111/1752-1688.12372>
- Hoagstrom, C. W., & Berry, C. R. (2006). Island biogeography of native fish faunas among great plains drainage basins: Basin scale features influence composition. *American Fisheries Society Symposium*, 48(November), 221–264.
- Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N., Wickham, J., & Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States—Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, 81(5), 345–354. <http://www.ingentaconnect.com/content/asprs/pers/2015/00000081/00000005/art00002>
- Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Nagel, D. E., Luce, C. H., Hostetler, S. W., Dunham, J. B., Roper, B. B., Wollrab, S. P., Chandler, G. L., Horan, D. L., & Parkes-Payne, S. (2017). The NorWeST summer stream temperature model and scenarios for the Western U.S.: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resources Research*, 53(11), 9181–9205. <https://doi.org/10.1002/2017WR020969>
- Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 113(16), 4374–4379. <https://doi.org/10.1073/pnas.1522429113>
- Jackson, D. A., & Mandrak, N. E. (2002). Changing fish biodiversity: Predicting the loss of cyprinid biodiversity due to global climate change. *American Fisheries Society Symposium*, 32, 89–98.



- Jarnevich, C. S., & Young, N. E. (2019). Not so normal normals: Species distribution model results are sensitive to choice of climate normals and model type. *Climate*, 7(3), 37. <https://doi.org/10.3390/cli7030037>
- Kemp, P. S., Worthington, T. A., Langford, T. E. L., Tree, A. R. J., & Gaywood, M. J. (2012). Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries*, 13(2), 158–181. <https://doi.org/10.1111/j.1467-2979.2011.00421.x>
- Knight, D., Jones, G., Reiners, W., & Romme, W. D. (2014). Chapter 6: Grasslands. In Knight, D. (Ed.), *Mountains and plains: The ecology of Wyoming landscapes*, Second, (83–84). New Haven, Connecticut: Yale University Press.
- Kruse, C. G., Hubert, W. A., & Rahel, F. J. (2001). An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. *Northwest Science*, 75(1), 1–11.
- Liaw, A., & Wiener, M. (2002). Classification and regression by random forest. *R News*, 2/3, 18–22. [http://cran.r-project.org/doc/Rnews/Rnews\\_2002-3.pdf](http://cran.r-project.org/doc/Rnews/Rnews_2002-3.pdf)
- Lee, D. S., Gilbert, C. R., Hocutt, C. H., Jenkins, R. E., McAllister, D. E., & Stauffer, J. R. J. (1980). *Atlas of North American freshwater fishes*, Raleigh, North Carolina: North Carolina State Museum of Natural History.
- Light, T., & Marchetti, M. P. (2007). Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, 21(2), 434–446. <https://doi.org/10.1111/j.1523-1739.2006.00643.x>
- Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, 30(12), 780–792. <https://doi.org/10.1016/j.tree.2015.09.011>
- Lyons, J., Stewart, J. S., & Mitro, M. (2010). Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, U.S.A. *Journal of Fish Biology*, 77(8), 1867–1898. <https://doi.org/10.1111/j.1095-8649.2010.02763.x>
- Macdonald, D. W., Tattersall, F. H., Rushton, S., South, A. B., Shaila, R., Maitland, P., & Strachan, R. (2000). Reintroducing the beaver (*Castor fiber*) to Scotland: A protocol for identifying and assessing suitable release sites. *Animal Conservation*, 3(2), 125–133. <https://doi.org/10.1017/S1367943000000822>
- MacDougall, A. S., Harvey, E., McCune, J. L., Nilsson, K. A., Bennett, J., Firn, J., Bartley, T., Grace, J. B., Kelly, J., Tunney, T. D., McMeans, B., Matsuzaki, S. I. S., Kadoya, T., Esch, E., Cazelles, K., Lester, N., & McCann, K. S. (2018). Context-dependent interactions and the regulation of species richness in freshwater fish. *Nature Communications*, 9(1), 1–9. <https://doi.org/10.1038/s41467-018-03419-1>
- MacRae, P. S. D., & 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(2), 342–351. <https://doi.org/10.1139/cjfas-58-2-342>
- Manel, S., Williams, H. C., Ormerod, S. J., Manel, S., Williamst, H. C., & Ormerod, S. J. (2001). Evaluating presence-absence models in ecology: The need to account for prevalence published by : British Ecological Society *Journal of Applied Ecology*, 38, 921–931 the need to account for prevalence. *Journal of Applied Ecology*, 38(5), 921–931.
- Matthews, W. J., & Hill, L. G. (1980). Habitat partitioning in the fish community of a southwestern river. *The Southwestern Naturalist*, 25(1), 51–66. <https://doi.org/10.2307/3671211>
- McDonald, L. (2004). Sampling Rare Populations. In W. Thompson (Ed.), *Sampling rare or elusive species: Concepts, designs, and techniques for estimating population parameters*, (11–21). Washington D.C.: Island Press.
- McPhail, J. D. (1963). *The postglacial dispersal of freshwater fishes in northern North America*. McGill University.
- Murphy, M. A., Evans, J. S., & Storfer, A. (2010). Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology*, 91(1), 252–261. <https://doi.org/10.1890/08-0879.1>
- Naus, C. A., Driscoll, D. G., & Carter, J. M. (2001). *Geochemistry of the Madison and Minnelusa Aquifers in the Black Hills Area, South Dakota*, Water-Resources Investigations Report 01-4129(63–65). Rapid City, South Dakota: U.S. Geological Survey. [https://pubs.usgs.gov/wri/wri014129.pdf](https://pubs.usgs.gov/wri/wri014129/pdf/wri014129.pdf)
- Novinger, D. C., & Rahel, F. J. (2003). Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology*, 17(3), 772–781. <https://doi.org/10.1046/j.1523-1739.2003.00472.x>
- Pavlova, A., Beheregaray, L. B., Coleman, R., Gilligan, D., Harrison, K. A., Ingram, B. A., Kearns, J., Lamb, A. M., Lintermans, M., Lyon, J., Nguyen, T. T. T., Sasaki, M., Tonkin, Z., Yen, J. D. L., & Sunnucks, P. (2017). Severe consequences of habitat fragmentation on genetic diversity of an endangered Australian freshwater fish: A call for assisted gene flow. *Evolutionary Applications*, 10(6), 531–550. <https://doi.org/10.1111/eva.12484>
- 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.
- Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *BioScience*, 64(4), 279–290. <https://doi.org/10.1093/biosci/biu036>
- PRISM Climate Group (2019). Oregon State University. Retrieved from <http://prism.oregonstate.edu>, created September 29, 2019.
- Quist, M. C., Hubert, W. A., & Rahel, F. J. (2004). Elevation and stream-size thresholds affect distributions of native and exotic warmwater fishes in Wyoming. *Journal of Freshwater Ecology*, 19(2), 227–236. <https://doi.org/10.1080/02705060.2004.9664536>
- Quist, M. C., Rahel, F. J., & Hubert, W. A. (2005). Hierarchical faunal filters: An approach to assessing effects of habitat and nonnative species on native fishes. *Ecology of Freshwater Fish*, 14(1), 24–39. <https://doi.org/10.1111/j.1600-0633.2004.00073.x>
- R Foundation for Statistical Computing (2019). *R: A language and environment for statistical computing* (3.6.1 (2019-07-05)). R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Rabinowitz, D. (1981). Seven forms of rarity. In F. N. Hepper, & H. Syge (Eds.), *The biological aspects of rare plant conservation* (pp. 205–217). Somerset, New Jersey: John Wiley & Sons. <https://doi.org/10.2307/4110060>
- Rahel, F. J. (1984). Factors structuring fish assemblages along a Bog lake successional gradient. *Ecology*, 65(654), 1276–1289. <https://doi.org/10.2307/1938333>
- Recoder, R. S., Magalhães-Júnior, A., Rodrigues, J., de Pinto, H. B. A., Rodrigues, M. T., & Camacho, A. (2018). Thermal constraints explain the distribution of the climate relict lizard *Colobosauroides carvalhoi* (Gymnophthalmidae) in the semiarid Caatinga. *South American Journal of Herpetology*, 13(3), 248–259. <https://doi.org/10.2994/sajh-d-17-00072.1>
- Schneider, R., Stoner, K., Steinauer, G., Panella, M., & Humpert, M. (Eds.) (2011). In *The Nebraska Natural Legacy Project: State Wildlife Action Plan*, (2nd ed.) (121–123). The Nebraska Game and Parks Commission. <https://outdoornebraska.gov/wp-content/uploads/2015/09/NebraskaNaturalLegacyProject2ndEdition.pdf>
- Scott, W., & Crossman, E. (1973). *Freshwater Fishes of Canada*, Bulletin 184 (pp. 396–399). Ottawa: Fisheries Research Board of Canada.
- Sepulveda, A. J., Rutz, D. S., Ivey, S. S., Dunker, K. J., & Gross, J. A. (2013). Introduced northern pike predation on salmonids in south-central Alaska. *Ecology of Freshwater Fish*, 22(2), 268–279. <https://doi.org/10.1111/eff.12024>
- Smith, C. L., & Powell, C. R. (1971). The summer fish communities of Brier Creek, Marshall County, Oklahoma. *American Museum Novitates*, 2458, 1–30.
- South Dakota Wildlife Action Plan (2014). *Wildlife division report 2014-03*. South Dakota Wildlife Action Plan. Retrieved from [https://gfp.sd.gov/UserDocs/nav/SD\\_Wildlife\\_Action\\_Plan\\_Revision\\_Final.pdf](https://gfp.sd.gov/UserDocs/nav/SD_Wildlife_Action_Plan_Revision_Final.pdf)

- Spurgeon, J. J., Stasiak, R. H., Cunningham, G. R., Pope, K. L., & Pegg, M. A. (2014). Status of native stream fishes within selected protected areas of the Niobrara river in western Nebraska. *Great Plains Research*, 24(1), 71–78. <https://doi.org/10.1353/gpr.2014.0009>
- Stasiak, R. H. (1972). *The morphology and life history of the finescale dace, Pfrille neogaea, in Itasca State Park*. University of Minnesota.
- Stasiak, R. H. (1978). Reproduction, age, and growth of the finescale dace, *Chrosomus neogaeus*, in Minnesota. *Transactions of the American Fisheries Society*, 107(5), 720–723. [https://doi.org/10.1577/1548-8659\(1978\)107<720:RAAGOT>2.0.CO;2](https://doi.org/10.1577/1548-8659(1978)107<720:RAAGOT>2.0.CO;2)
- Stasiak, R., & Cunningham, G. R. (2006). *Finescale Dace (Phoxinus neogaeus): A technical conservation assessment*, (19–20). USDA Forest Service, Rocky Mountain Region. <http://www.fs.fed.us/r2/projects/scp/assessments/finescaledace.pdf>
- Stasiak, R. H., Cunningham, G. R., Flash, S., Wagner, A., & Barela, A. (2011). *Fishes of the Niobrara River at Agate Fossil Beds National Monument 2011 Survey*. Retrieved from <http://npshistory.com/publications/agfo/niobrara-river-fishes-2011.pdf>
- Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan, M. A., Schell, L. D., Bull, K. A., Otsuki, Y., Newman, G., Bashkin, M., & Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, 69(1), 25. <https://doi.org/10.2307/2657193>
- Szilagyi, J., Harvey, F. E., & Ayers, J. F. (2003). Regional estimation of base recharge to ground water using water balance and a base-flow index. *Ground Water*, 41(4), 504–513. <https://doi.org/10.1111/j.1745-6584.2003.tb02384.x>
- Tarkan, A. S. (2006). Reproductive ecology of two cyprinid fishes in an oligotrophic lake near the southern limits of their distributions range. *Ecology of Freshwater Fish*, 15(2), 131–138. <https://doi.org/10.1111/j.1600-0633.2006.00133.x>
- Taylor, C. M., Holder, T. L., Fiorillo, R. A., Williams, L. R., Thomas, R. B., & Warren, M. L. (2006). Distribution, abundance, and diversity of stream fishes under variable environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(1), 43–54. <https://doi.org/10.1139/f05-203>
- Tonn, W. M. (1990). Climate change and fish communities: A conceptual framework. *Transactions of the American Fisheries Society*, 119(2), 337–352. [https://doi.org/10.1577/1548-8659\(1990\)119<0337:ccafta>2.3.co;2](https://doi.org/10.1577/1548-8659(1990)119<0337:ccafta>2.3.co;2)
- Tonn, W. M., & Magnuson, J. J. (1982). Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology*, 63(4), 1149–1166. <https://doi.org/10.2307/1937251>
- Turlure, C., Chouff, J., Bague, M., & Van Dyck, H. (2010). Microclimatic buffering and resource-based habitat in a glacial relict butterfly: Significance for conservation under climate change. *Global Change Biology*, 16, 1883–1893. <https://doi.org/10.1111/j.1365-2486.2009.02133.x>
- U.S. Geological Survey. (2016). National Water Information System data available on the World Wide Web (USGS Water Data for the Nation). Retrieved from <http://dx.doi.org/10.5066/F7P55KJN>
- Ver Hoef, J. M., Peterson, E., & Theobald, D. (2006). Spatial statistical models that use flow and stream distance. *Environmental and Ecological Statistics*, 13(4), 449–464. <https://doi.org/10.1007/s10651-006-0022-8>
- Veza, P., Muñoz-Mas, R., Martínez-Capel, F., & Mouton, A. (2015). Random forests to evaluate biotic interactions in fish distribution models. *Environmental Modelling and Software*, 67, 173–183. <https://doi.org/10.1016/j.envsoft.2015.01.005>
- Wehrly, K. E., Wiley, M. J., & Seelbach, P. W. (2003). Classifying regional variation in thermal regime based on stream fish community patterns. *Transactions of the American Fisheries Society*, 132(1), 18–38. [https://doi.org/10.1577/1548-8659\(2003\)132<0018:crvitr>2.0.co;2](https://doi.org/10.1577/1548-8659(2003)132<0018:crvitr>2.0.co;2)
- Whittier, T. R., Halliwell, D. B., & Paulsen, S. G. (1997). Cyprinid distributions in Northeast U.S.A. lakes: Evidence of regional-scale minnow biodiversity losses. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(7), 1593–1607. <https://doi.org/10.1139/cjfas-54-7-1593>
- Wis, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann, C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K., Høye, T. T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N. M., ... Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews*, 88(1), 15–30. <https://doi.org/10.1111/j.1469-185X.2012.00235.x>
- Woolbright, S. A., Whitham, T. G., Gehring, C. A., Allan, G. J., & Bailey, J. K. (2014). Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends in Ecology and Evolution*, 29(7), 406–416. <https://doi.org/10.1016/j.tree.2014.05.003>
- Wyoming State Wildlife Action Plan (2017). Wyoming Game and Fish Department. <https://wgfd.wyo.gov/Habitat/Habitat-Plans/Wyoming-State-Wildlife-Action-Plan>
- Zorn, T. G., Seelbach, P. W., & Wiley, M. J. (2002). Distributions of stream fishes and their relationship to stream size and hydrology in Michigan's Lower Peninsula. *Transactions of the American Fisheries Society*, 131(1), 70–85. [https://doi.org/10.1577/1548-8659\(2002\)131<0070:dosfat>2.0.co;2](https://doi.org/10.1577/1548-8659(2002)131<0070:dosfat>2.0.co;2)

#### BIOSKETCHES

**Evan C. J. Booher** is a master's student at the University of Wyoming. His research interests include fisheries ecology and management. His work focuses on the distribution and conservation of native fishes in Great Plains basins of Eastern Wyoming.

**Annika Walters** is the Assistant Unit Leader for fisheries at the Wyoming Cooperative Fish and Wildlife Research Unit of the United States Geological Survey and an associate professor at the University of Wyoming. Her primary research focuses on population and community ecology, fisheries and conservation biology.

**Author contributions:** E.C.J.B. led the writing and subsequent manuscript reviews and edits, contributed to study conceptualization, and collected and analysed the data. A.W.W. conceptualized the study, acquired funding, provided resources and project supervision, and reviewed and edited the manuscript.

#### SUPPORTING INFORMATION

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

**How to cite this article:** Booher ECJ, Walters AW. Biotic and abiotic determinants of finescale dace distribution at the southern edge of their range. *Divers Distrib*. 2021;00:1–14. <https://doi.org/10.1111/ddi.13227>