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PRIMARY RESEARCH PAPER

Invasive Brook Stickleback *Culaea inconstans* occurrence, habitat drivers, and spatial overlap with native fishes in Wyoming, USA

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Abstract A central focus of modern fisheries management is eradicating invaders that threaten imperiled native fishes. However, vast landscapes and limited funding and personnel resources demand a prioritized approach to management. Brook Stickleback *Culaea inconstans* (Kirtland, 1840) is an aquatic invasive species in Wyoming, USA, that may pose a risk to native biodiversity. Our aim was to evaluate Brook Stickleback's invasive potential in the North Platte River drainage. We updated the current distribution of Brook Stickleback, evaluated for possible range expansion, and determined landscape-level habitat drivers and occurrence potential for streams across the North Platte River drainage. Additionally, we examined Brook Stickleback's spatial overlap with native nongame fishes. At the landscape scale, Brook Stickleback preferred low-gradient streams with moderate disturbance risk. Though we did not find evidence of current Brook Stickleback range expansion 61% of streams in the drainage have landscape-level environmental characteristics that are likely suitable for Brook Stickleback, creating potential for future expansion. Brook Stickleback overlapped spatially with 13 native nongame species, though spatial overlap was less common than expected for species with similar habitat preferences. Our work serves as a case study of the factors to consider when assessing a species' invasive potential in a previously unstudied region.

Keywords Brook Stickleback *Culaea inconstans* · Distribution · Random forest · Non-native species · Range expansion · Spatial overlap

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Introduction

Declines in native fish biodiversity are commonly linked to invasive species introductions, particularly in freshwater systems which are characterized by high degrees of isolation and speciose endemic communities (Richter et al., 1997; Parker et al., 1999; Mills et al., 2004; Dudgeon et al., 2006; Vander Zanden & Olden, 2008). Unfortunately, such introductions are increasingly common because of human activities (Rahel, 2002; Dudgeon et al., 2006). Environmental gradients that historically served as barriers to species movement (e.g., mountain ranges) have been dissolved by human-mediated transport, making freshwater systems more vulnerable to invasive species introductions (Elton, 1958; Rahel, 2002; Vander Zanden & Olden, 2008). In response, invasive species control has become a common management tool, with managers relying on an understanding of the species' habitat and community associations to evaluate its invasive potential in a region and select sites where management actions will have the greatest positive effect. However, our understanding of these metrics is complicated by the context dependency of species–environment relationships (Booher & Walters, 2021) and the phenotypic plasticity of invaders (Daehler, 2003; Engel et al., 2011; Kovalenko et al., 2021). These challenges highlight the need for studies that contribute to our understanding of invasive species in previously unstudied regions.

Native fish communities can be affected by invasive fishes through various mechanisms, including predation and competition for food and space resources (Rahel, 2002; Mills et al., 2004). The direct consumptive effects of large-bodied piscivorous species have been well documented. For example, predation by non-native Nile Perch *Lates niloticus* (Linnaeus, 1758) led to the loss of approximately 200 species of endemic haplochromine cichlids in Lake Victoria, Africa (Witte et al., 1992). Further, population declines of western North American native fishes have been linked to predation by non-native Northern Pike *Esox lucius* Linnaeus, 1758 and Smallmouth Bass *Micropterus dolomieu* Lacepède, 1802 (Johnson et al., 2008; Zelasko et al., 2016; Hickerson et al., 2019; Booher & Walters, 2021). Competition for food and space resources between native and introduced species also occurs; a phenomenon that has been documented globally. In North America, one prominent example is the introduction of competitively dominant Bigheaded carps *Hypophthalmichthys* spp. to the Mississippi River basin, which depleted food resources and caused reductions in body condition and abundance of native Bigmouth Buffalo *Ictiobus cyprinellus* (Valenciennes, 1844) and Gizzard Shad *Dorosoma cepedianum* (Lesueur, 1818) (Irons et al., 2007; Phelps et al., 2017). In Brazil, Gois et al. (2015) found evidence of competitive interactions between an invasive Amazonian cichlid fish *Geophagus proximus* (Castelnau, 1855) and the closely related native Pantanal eartheater *Satanoperca pappaterra* (Heckel, 1840).

Though the effects of non-native fishes are well documented for large-bodied species, it is easy to overlook small-bodied fish invaders. Despite their minimalistic morphometry, these invaders are capable of the same magnitude of ecosystem effects as their more charismatic counterparts. Species such as the Round Goby *Neogobius melanostomus* (Pallas, 1814) and Eastern Mosquitofish *Gambusia holbrooki* Girard, 1859, for example, have been shown to have deleterious effects on populations of native fishes, causing species declines and even extirpations (Janssen & Jude, 2001; Lauer et al., 2004; Pyke, 2008). In addition to their ability to affect native fish communities, small-bodied fish invaders present distinct challenges to managers as they are generally more difficult to detect, are commonly sold and used as bait species for angling, and are often incidentally transported during stocking operations for other species (Rahel, 2002; Rahel & Smith, 2018). Therefore, evaluating and monitoring small-bodied fish invaders in invaded environments is important for managers attempting to contain their spread and protect at-risk populations of sensitive native species.

Brook Stickleback *Culaea inconstans* (Kirtland, 1840) is a small-bodied invasive fish in Wyoming, USA. Native to the northern latitudes of the United States and Canada, Brook Stickleback has invaded south in the last three decades (Fig. 1) (Scholz et al., 2003; McAllister et al., 2010). Early records of Brook Stickleback expansion date back to the 1990s when the species was detected outside its native range in Colorado, Utah, and California (Modde & Haines, 1996). In Wyoming, Brook Stickleback was first detected in 1993 (Wyoming Game and Fish Department, Fish Division, 1994). Though exact sources of introduction and propagule pressure are unknown, it is widely thought that contaminated shipments of live baitfish and human transport contributed to Brook Stickleback's spread (Ludwig & Leitch, 1996; Fuller et al., 1999; Gunselman, 2017). The species thrives in clear, spring-fed, and heavily vegetated systems, but is also known for its generalist nature which allows it to occupy a wide range of habitats (Winn, 1960; Stewart et al., 2007). Brook Stickleback is believed to cause population declines in sympatric fishes through predation on eggs and early life stages (Woodling, 1985), and studies from other invaded regions show

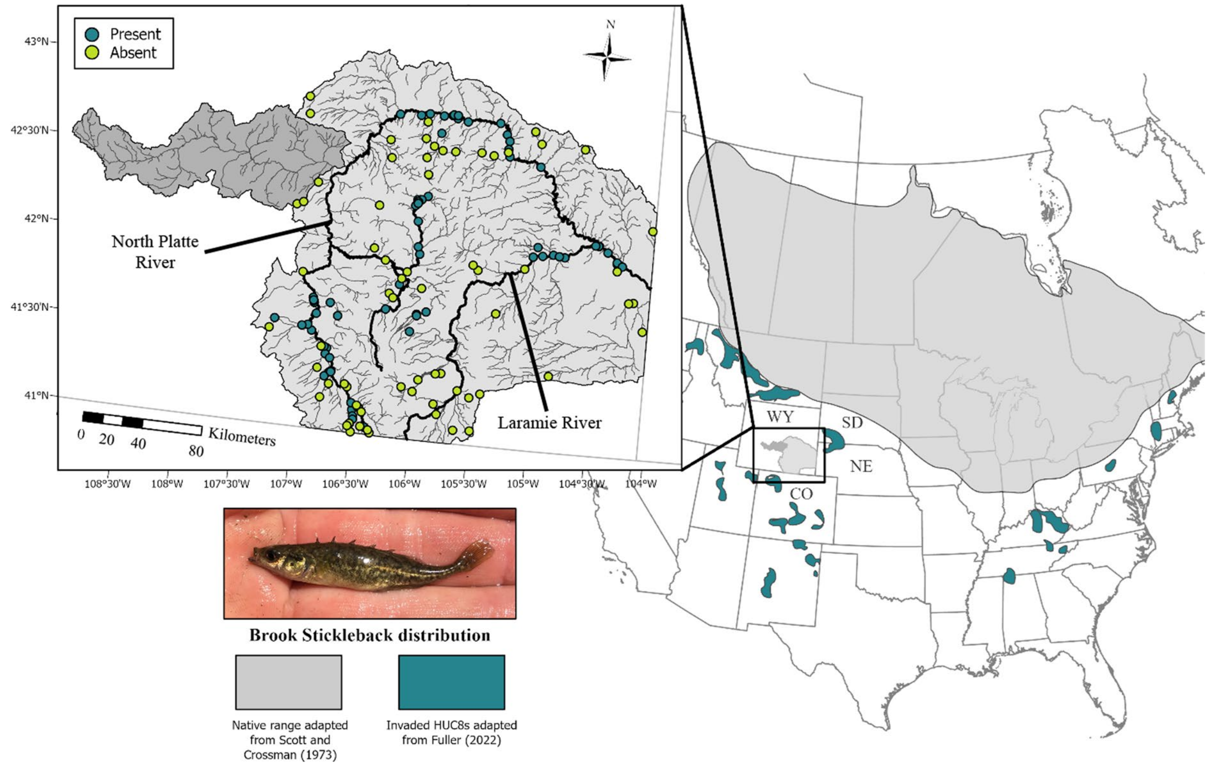

Fig. 1 Brook Stickleback distribution in the Wyoming portion of the North Platte River basin, USA. The Sweetwater sub-basin (dark gray) was excluded from our study area due to a lack of Brook Stickleback presences in historical data. Presences and absences in the study area were documented by sampling conducted by the authors in 2020 and 2021, as well as historical sampling data dating back to 1995. The species' native range (adapted from Scott & Crossman, 1973) is shown in gray and invaded sub-basin level Hydrologic Unit Codes (HUC8s) across the United States (adapted from Fuller, 2022) are shown in blue (Scott & Crossman, 1973; Fuller, 2022). Despite being similarly colored, the North Platte River drainage is not part of Brook Stickleback's native range

that the species may have negative effects on migrating waterfowl by reducing aquatic macroinvertebrate density (Wieker et al., 2016). In Wyoming, concerns center on native nongame fishes with similar literature-derived habitat preferences to Brook Stickleback (Baxter & Stone, 1995), two of which, Brassy Minnow *Hybognathus hankinsoni* Hubbs, 1929 and Iowa Darter *Etheostoma exile* (Girard, 1859), are classified as species of greatest conservation need.

Our study objectives were to (1) update the current known distribution of Brook Stickleback in the North Platte River drainage, Wyoming, and evaluate for range expansion, (2) determine the species' habitat drivers and basin-wide occurrence potential, and (3) determine the degree of spatial overlap with native nongame fishes. We hypothesized that Brook Stickleback would be found primarily in low-gradient, slow-moving streams with cooler temperatures and high groundwater input. We also hypothesized they would occupy disturbed habitats given their ability to survive in a wide range of conditions. Finally, we hypothesized that Brook Stickleback would be found in sympatry most frequently with Iowa Darter and Brassy Minnow given their similar habitat preferences and range in Wyoming. We updated the species' distribution in the North Platte River drainage, Wyoming area and evaluated for range expansion. We then constructed a distribution model to evaluate the species' landscape-level habitat drivers and occurrence potential for streams across the study area. Finally, we used assemblage-intensive data, collected across two years, to evaluate Brook Stickleback's spatial overlap with native nongame fishes. Our work provides baseline knowledge necessary to guide prioritized management of Brook Stickleback in Wyoming, and serves as a case study of the factors to consider when assessing a species' invasive potential in a previously unstudied region.

Materials and methods

Study area

The North Platte River drainage, located in the southeast corner of Wyoming, covers approximately 25% of the land area in the state (Fig. 1). Supported primarily by snowmelt and groundwater input, many tributaries in the drainage are intermittent and become dry during the late summer months (Bear & Barrineau, 2007). Land and water use throughout the drainage is primarily driven by agriculture, including livestock production and crop irrigation (Bear & Barrineau, 2007). The North Platte River drainage has diverse native fish assemblages for the region, with previous studies capturing more than 12 species (Brunger Lipsey et al., 2005; Bear & Barrineau, 2007). Simultaneously, the drainage has the highest prevalence of invasive Brook Stickleback in historical sampling data collected by the Wyoming Game and Fish Department (WGFD) and datasets collated by researchers at the University of Wyoming. Our study area was confined to the Wyoming portion of the drainage; we omitted the Sweetwater sub-basin from the study area due to a lack of Brook Stickleback occurrences in historical sampling data (Fig. 1).

Site selection

Sampling locations were divided into three categories: targeted sites, random sites, and lentic sites. We selected targeted sites ($n=34$) from previous sampling data provided by the WGFD and datasets collated by researchers at the University of Wyoming. Assemblage-intensive surveys conducted at these sites provided initial data on Brook Stickleback presence and absence in our study area. To select random sites ($n=47$), we applied Balanced Acceptance Sampling (BAS, Robertson et al., 2013) in Program R (version 1.4.1103, R Core Team, 2020) to flowlines in the National Hydrography Dataset (NHDPlusV2, accessed January 31, 2022, at https://www.epa.gov/waterdata/get-nhdplus-national-hydrography-dataset-plus-data). Balanced Acceptance Sampling mitigates spatial autocorrelation by selecting locations that are evenly distributed across the extent of the study area (Robertson et al., 2013). We limited random site selection to flowlines with an elevation below 2,590-m as Brook Stickleback has not been documented at higher elevations in Wyoming (Quist et al., 2004). We selected lentic sites ($n=7$) based on known occurrences of Iowa Darter and Brassy Minnow given their similar habitat preferences to Brook Stickleback (Baxter & Stone, 1995) and importance to managers as species of greatest conservation need in Wyoming.

Fish sampling

Sampling occurred from July to October 2020, and June to September 2021. Sampling in 2020 was delayed due to the COVID-19 Pandemic. For streams with a wetted width less than 5-m we selected a sampling reach of 150-m; otherwise, a sampling reach of 200-m was sampled (Patton et al., 2000). We measured sampling reaches using the line distance tool in a global positioning system (onX Hunt version 20.4.0). We used two backpack electrofishing units (Smith-Root LR-24) to capture fish with pulsed DC current; we conducted a single pass in the upstream direction to collect fish and did not use block nets. At lentic sites, we used miniature fyke nets, minnow traps (un-baited), and bag seines to capture fish. We set miniature fyke nets and minnow traps overnight in littoral habitats, and conducted seining parallel to the shoreline in similar areas if no fish were captured in the passive gears. In both lentic and lotic habitats, we identified all individuals to species and enumerated them before release. Given its status as an invasive species, we euthanized all Brook Stickleback in accordance with WGFD Chapter 33 permit requirements and University of Wyoming Institutional Animal Care and Use Committee protocols.

Environmental data—reach scale

We collected instantaneous surface temperature (°C) and turbidity (nephelometric turbidity units, NTU) measurements at all sites, as well as discharge measurements at lotic sites. We collected instantaneous surface temperature measurements with an YSI Professional Plus instrument and turbidity measurements with an Oakton T-100 turbidity meter. We collected three turbidity samples at each site and retained the average value. To estimate discharge at lotic sites, we measured velocity (meters/second) at 60% of the depth (Fitzpatrick et al., 1998) at 10 equidistant points along a transect which was selected to be representative of the sampling reach.

Environmental data—landscape scale

We used literature-derived habitat preferences of Brook Stickleback (Winn, 1960; Reisman & Cade, 1967; Stewart et al., 2007) and general habitat metrics known to limit the distribution of fishes (Baxter & Stone, 1995; Quist et al., 2005) to select relevant variables from multiple sources. Channel slope (meters/meter) and mean annual gage-adjusted flow (cubic feet per second, cfs) values were extracted from the NHDPlusV2 dataset. Baseflow index values at the catchment scale (i.e., the area immediately surrounding a stream that contributes water) and mean annual stream temperature data (averaged across 2008, 2009, 2013, and 2014) were downloaded from the EPA StreamCat dataset (Hill et al., 2016, https://www.epa.gov/national-aquatic-resource-surveys/streamcat-dataset-0). We also included habitat condition index scores from the National Fish Habitat Partnership for reaches in our study area, a metric that incorporates various measures of disturbance (e.g., road density, dam density) to rank the risk of degradation for a stream reach from 1 (high risk) to 5 (low risk) (Crawford et al., 2016, http://assessment.fishhabitat.org/). All variables were joined to NHD flowlines, and then to fish sampling data, using the spatial join feature in package 'sf' in program R (Pebesma, 2018; R Core Team, 2020).

Data analysis

To evaluate Brook Stickleback expansion, we conducted sampling at a subset of targeted sites where the species had been detected previously. We then compared the presence/absence status from our sampling to that of the oldest available data point for a given site, allowing us to infer changes in Brook Stickleback occurrence through time. We then combined Brook Stickleback presence/absence data from targeted sites with data from random and lentic sites to update the map of Brook Stickleback's current distribution in the North Platte River drainage.

We used a random forest classification model to determine Brook Stickleback habitat associations in lotic environments at the landscape scale. Random forest models are less sensitive to spatial autocorrelation and are good for modeling ecological data which often do not meet the underlying assumptions of other modeling approaches (Evans & Cushman, 2009). We used landscape-scale environmental variables for random and targeted lotic sites to predict binary Brook Stickleback presence (1) or absence (0); for sites with repeated sampling, we retained only the most recent fish assemblage data. We did not include lentic sites in the model due to lack of representation in the NHDPlusV2 dataset.

We constructed a single model for the North Platte River drainage and used packages 'rfUtilities' and 'randomForest' in Program R for model selection, fitting, and evaluation (Liaw & Wiener, 2002; Evans & Cushman, 2009; Murphy et al., 2010; R Core Team, 2020). We evaluated collinearity among predictor variables using generalized variance inflation factor (VIF) scores; all variables had VIF scores less than 3 and were retained for model selection (Zuur et al., 2010). We then used the model improvement ratio method, which maximizes the explanatory power of the model while minimizing predictors and mean squared error, to select covariates and ensure a parsimonious model (Murphy et al., 2010). Environmental predictor variables were scaled prior to analysis to account for differences in value ranges. To mitigate potential effects of class imbalance in the response variable we used the sample-downscaling approach developed by Evans & Cushman (2009). We used out-of-bag error, which is derived from application of the model to data not used in fitting (Cutler et al., 2007), as well as area under the curve (AUC) and the percentage of correctly classified instances (CCI), to evaluate model performance (Manel et al., 2001). We then used the 'predict' function in package 'stats' to estimate occurrence potential in lotic sites across the North Platte River drainage (R Core Team, 2020). Partial probability plots were used to visualize the relationship between each environmental covariate and Brook Stickleback probability of occurrence (Cutler et al., 2007).

To determine the habitat suitability across the study area, we plotted the distributions of predicted

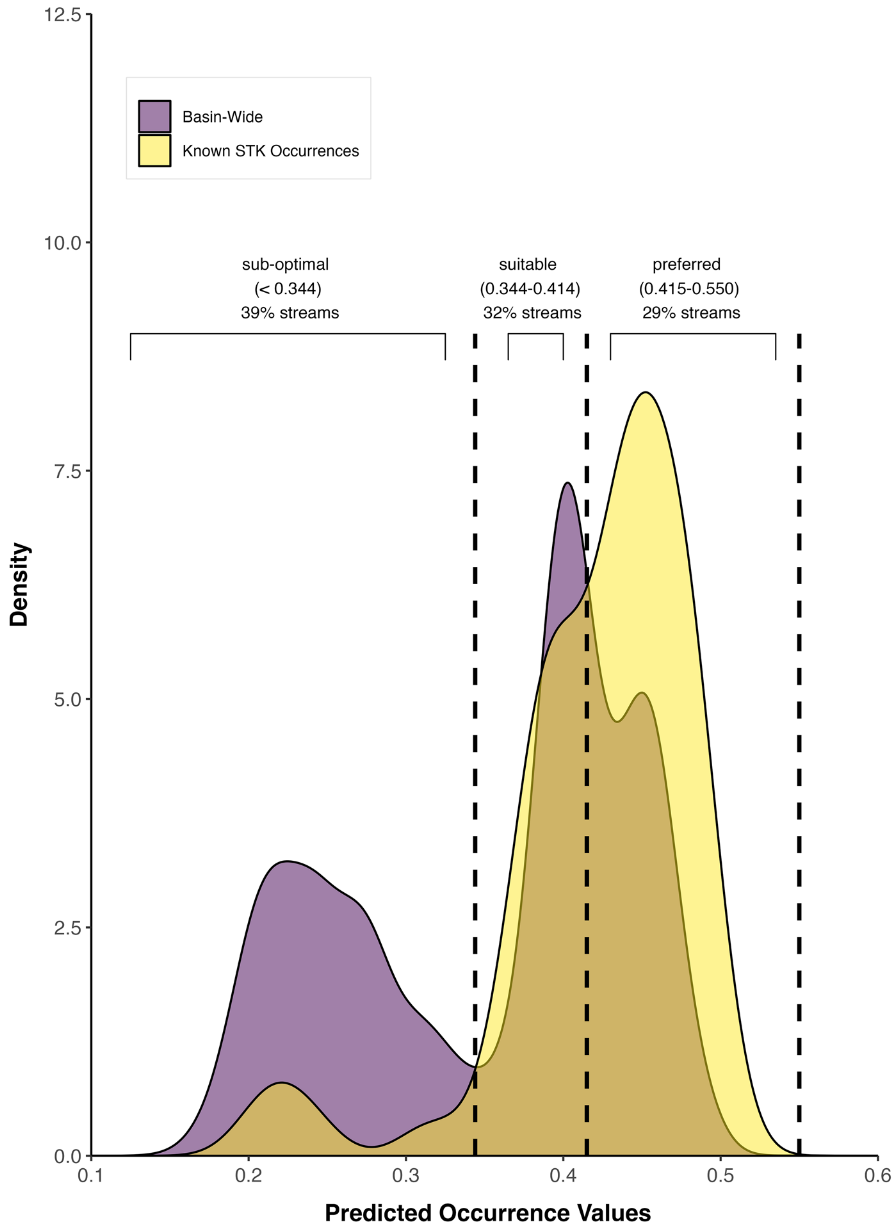

Fig. 2 Predicted probability of occurrence value distributions from the basin-wide random forest model and for sites with known Brook Stickleback (STK) occurrences. Habitat classifications, value ranges, and the percentage of streams in the basin within respective categories are listed at the top of each cell

values from our random forest model for all sites in the basin and for sites with known Brook Stickleback occurrences. We then divided the two distributions into three categories based on predicted values: preferred habitat, suitable habitat, and sub-optimal habitat. Preferred habitat represents streams with predicted occurrence values where density of sites with Brook Stickleback presence was overrepresented relative to overall density of sites, sub-optimal where it was underrepresented, and suitable was the intermediate values where densities were similar (Fig. 2). We then characterized basin-wide occurrence potential using these three predicted value categories. Sites with predicted occurrence values outside the area of overlap between the distributions were not assigned a habitat category.

We used fish relative abundance data to conduct non-metric multidimensional scaling (NMDS) to visualize assemblage associations and qualitatively assess the degree to which Brook Stickleback co-occurred with native fishes. We only used data collected during the 2020 and 2021 field seasons, from both lentic and lotic sites, as historical sampling events oftentimes only noted the presence or absence of Brook Stickleback and excluded other native fishes. We used the 'vegan' package in Program R (Oksanen et al., 2020; R Core Team, 2020) to run the NMDS and fitted landscape- and reach-scale environmental variables to the ordination using vector fitting to better understand the species–environment relationships.

Results

Establishment and expansion

We revisited 34 targeted lotic sites during the 2020 and 2021 field seasons; Brook Stickleback was present at 22 of the 34 sites (65%). Across these 34 sites, Brook Stickleback status changed from present to absent at eight (24%) sites and from absent to present at one (3%) site; the status at the remainder of the sites did not change (21 presences and four absences). Brook Stickleback was also absent at 44 of 47 (94%) lotic random sites and at four of seven (57%) lentic sites. We detected Brook Stickleback in 12 distinct watersheds [Hydrologic Unit Code (HUC) 10] with the species' focal distribution existing in small tributaries along the North Platte River corridor near the town of Saratoga, the mainstem of the North Platte River near Casper, and in the Medicine Bow, Little Medicine Bow, and Laramie River drainages (Fig. 1). Despite increased sampling intensity, we detected Brook Stickleback in fewer HUC 10 watersheds relative to prior survey efforts (89 sampling events and 12 HUC 10 watershed detections 2020–2021; 71 sampling events and 23 HUC 10 watershed detections 2010–2019).

Habitat associations and basin-wide occurrence

Model evaluation metrics indicated strong predictive power for the random forest classification model (OOB error = 0.13, AUC = 0.93, CCI = 0.87) that included slope, habitat condition index, streamflow, baseflow index, and mean annual stream temperature as predictor variables. Slope and habitat condition index were the most important predictors of Brook Stickleback occurrence in the final model (importance = 1.00 and 0.47, respectively). Slope exhibited a strong negative relationship with Brook Stickleback presence and habitat condition index scores showed optimal conditions existing in habitats with moderate disturbance risk (Habitat Condition Index Score = 3, Fig. 3). Streamflow, baseflow index, and mean annual stream temperature (importance = 0.39, 0.21, and 0.18, respectively) showed varying effects on Brook Stickleback presence. Predicted occurrence was higher at sites with more groundwater input but was relatively consistent across a wide range of flow and temperature values (Fig. 3). Basin-wide predictions of occurrence potential from the random forest model suggest that 29% of streams represent preferred habitat, 32% of streams represent suitable habitat, and 39% of streams represent sub-optimal habitat (Figs. 2, 4). Excluding sub-optimal habitat, 61% of streams in the drainage have landscape-level environmental characteristics that are likely suitable for Brook Stickleback.

Spatial overlap with native fishes

Brook Stickleback exhibited a high degree of spatial overlap with native fishes across the study area and co-occurred with 13 species at targeted, random, and lentic sites in 2020 and 2021 sampling (Fig. 5). Our NMDS ordination reached convergence after 39 iterations (stress = 0.13). The first axis (NMDS1) grouped assemblages by water type, with lotic sites at lower values and lentic sites at higher values. The second axis (NMDS2) plotted assemblages along gradients of slope, water temperature, and turbidity. High-gradient, cold water sites with low turbidity were represented at lower values, while higher values represented low-gradient, warm water sites with high turbidity. Brook Stickleback exhibited the lowest centroid score on the second axis, showing fidelity to low-gradient, cold water lentic and lotic habitats with low-turbidity and high groundwater input (baseflow). Brook Stickleback overlapped most frequently with Longnose Sucker *Catostomus catostomus* (Forster, 1773), White Sucker *Catostomus commersonii* (Lacepède, 1803), Johnny Darter *Etheostoma nigrum* Rafinesque, 1820, Fathead Minnow *Pimephales promelas* Rafinesque, 1820, and Creek

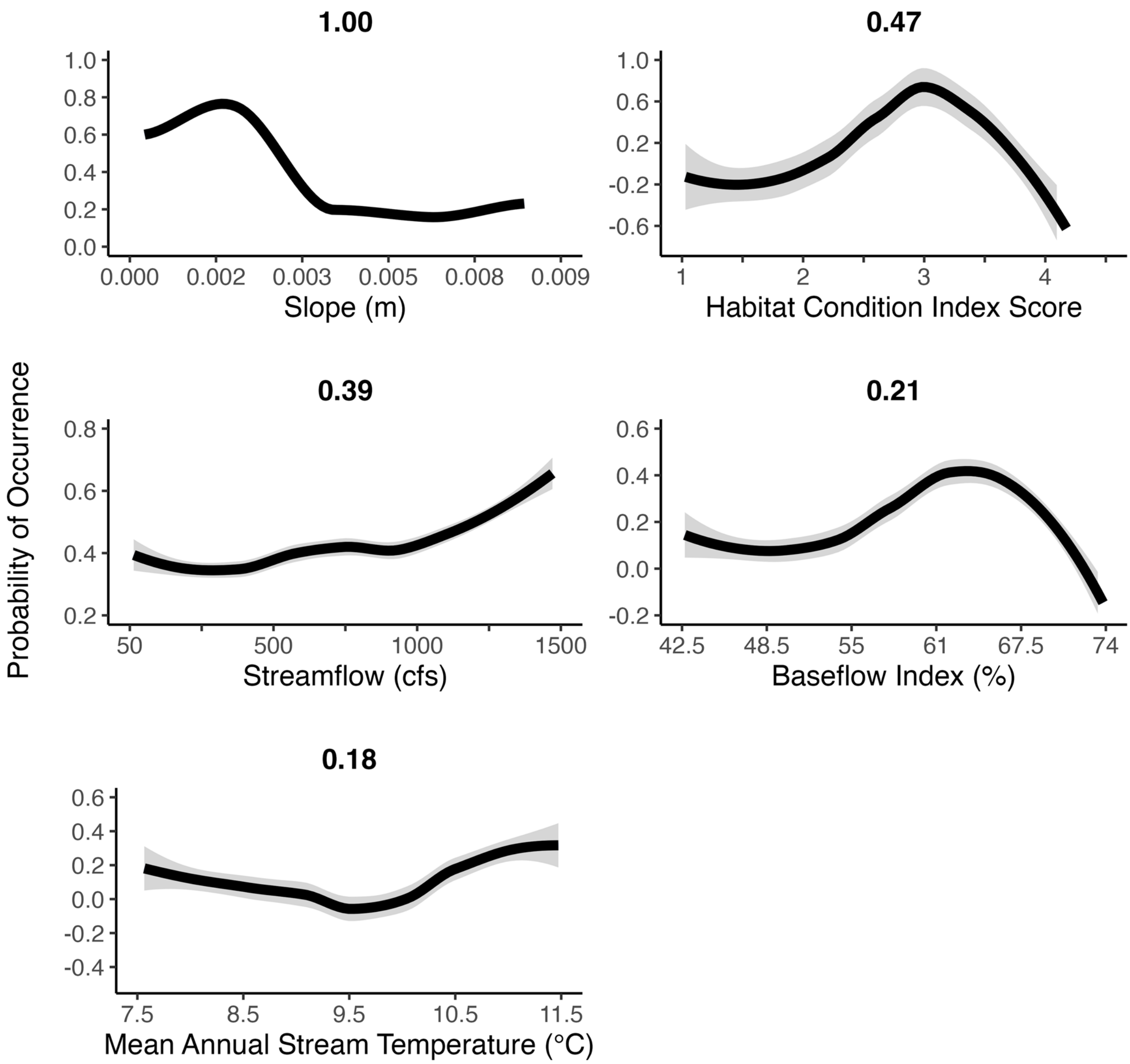

Fig. 3 Partial dependence plots showing Brook Stickleback probability of occurrence (95% confidence level) as a response to landscape-level environmental variables from the random forest model. Slope was the most important predictor of Brook Stickleback occurrence indicated by a strong negative relationship. Model outputs also suggest a preference by Brook Stickleback for moderately disturbed habitats with high groundwater input. Variable importance (range 1.00–0.18) is shown for each variable at top of plot

Chub *Semotilus atromaculatus* (Mitchill, 1818). Iowa Darter and Brassy Minnow were associated with lentic sites lacking Brook Stickleback (Fig. 5).

Discussion

Understanding an invasive species' distribution, habitat drivers, and spatial overlap with native fishes can provide information crucial for prioritizing management efforts across vast landscapes and multiple species. We studied a small-bodied invasive fish to understand its invasive potential and inform future

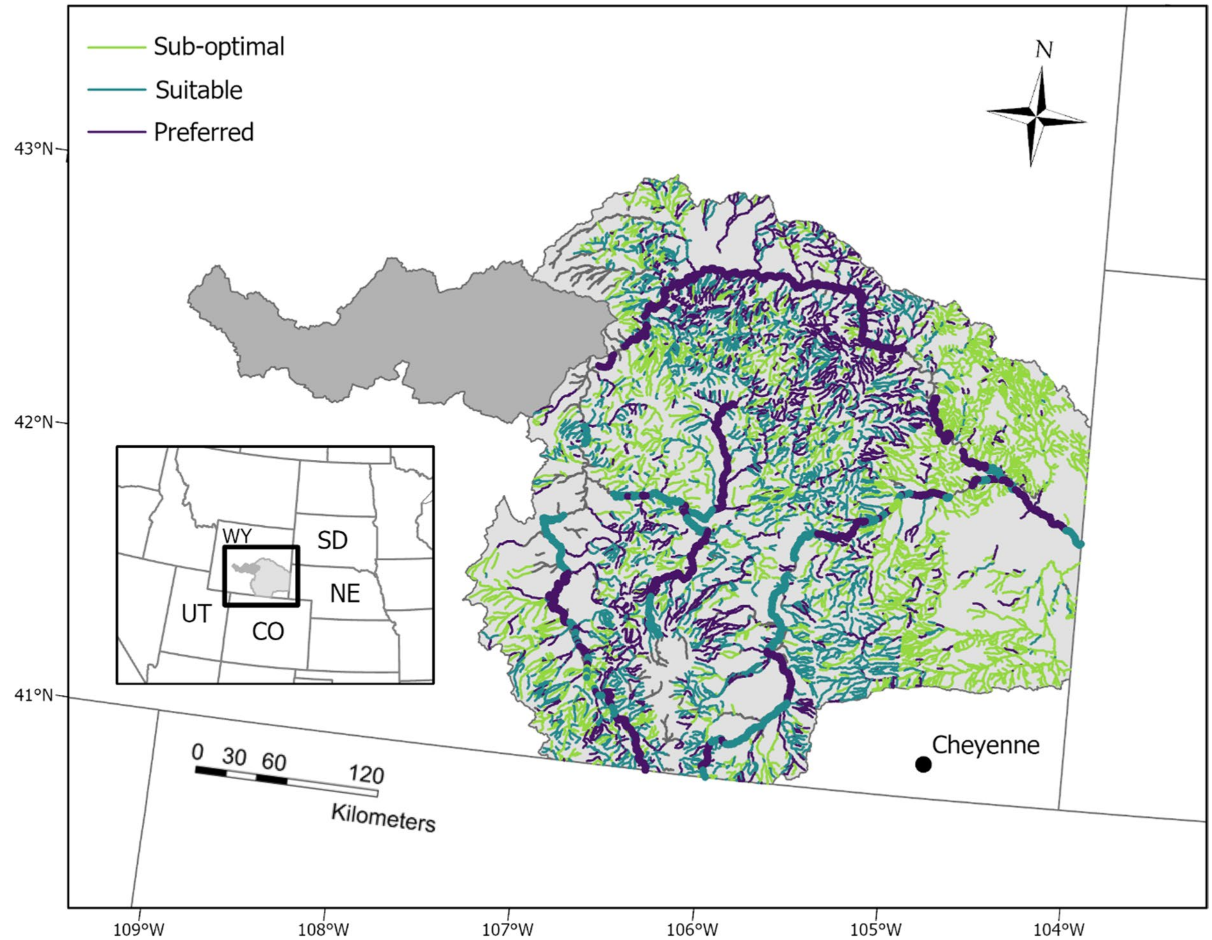

Fig. 4 Predicted habitat suitability of streams in the North Platte River drainage from the random forest model. Primary river systems (North Platte River, Medicine Bow River, Little Medicine Bow River, and Laramie River) are bolded. In total, 61% of streams in the study area are classified as suitable or preferred habitats

management of the species in a previously unstudied region. We found that Brook Stickleback distribution is not currently expanding but rather seems to be in a state of stasis, though this might reflect current drought conditions. Brook Stickleback showed preference for low-gradient streams with moderate disturbance risk, and 61% of streams in the North Platte River drainage likely provide suitable habitat for the species. Finally, Brook Stickleback overlapped spatially with 13 native fishes in our sampling, though spatial overlap among Brook Stickleback, Iowa Darter, and Brassy Minnow was less common than expected given the species' similar habitat preferences. Our results suggest that Brook Stickleback is not currently undergoing a rapid range expansion, though there is the potential for further expansion as suitable habitat exists across the study area. Further, Brook Stickleback presence may affect Iowa Darter and Brassy Minnow.

Establishment and expansion

Brook Stickleback has established and spread in the North Platte River drainage but does not currently appear to be expanding rapidly. An increase in small-bodied fish sampling in Wyoming in the last decade created a perception of expanding Brook Stickleback distribution in our study area. However, despite a further increase in sampling effort during 2020 and 2021, we observed a decrease in the

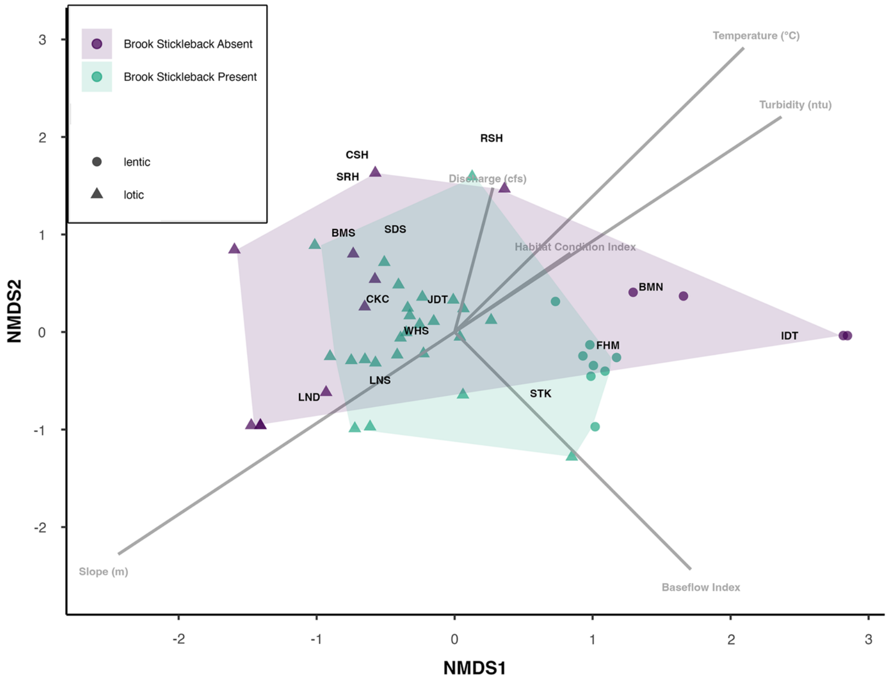

Fig. 5 NMDS (stress = 0.13) ordination of native species associations with Brook Stickleback and habitat indices from data collected during the 2020 and 2021 field seasons. Species codes are as follows: *BMN* Brassy Minnow, *BMS* Bigmouth Shiner *Notropis dorsalis* Agassiz, 1854, *CKC* Creek Chub, *CSH* Common Shiner *Luxilus cornutus* Mitchill, 1817, *FHM* Fathead Minnow, *IDT* Iowa Darter, *JDT* Johnny Darter, *LND* Longnose Dace, *LNS* Longnose Sucker, *RSH* Red Shiner *Cyprinella lutrensis* Baird and Girard, 1853, *SDS* Sand Shiner *Notropis stramineus* Cope, 1865, *SRH* Shorthead Redhorse *Moxostoma macrolepidotum* Lesueur, 1817, *WHS* White Sucker

number of occupied watersheds. Our lack of Brook Stickleback detections at historically occupied sites, and at most of our random and lentic sites, supports our finding that a rapid expansion of their distribution is unlikely to be occurring. It is more likely that rapid expansion occurred soon after initial detection in the early 1990s and that current populations are representative of a state of stasis, in which the species is persisting in ideal habitats. "Boom and bust" dynamics such as this are often used to describe invasive populations and play a key role in informing the distribution of an invader (Elton, 1958; Strayer et al., 2017). Following an initial increase in range, a species may experience a decline before reaching a point of stasis where populations exist at a lower level relative to initial expansion (Strayer et al., 2017). This phenomenon has also been observed in Rusty Crayfish *Faxonius rusticus* (Girard, 1852), whose distribution initially expanded rapidly across the United States but has since started to decline (e.g., Larson et al., 2019).

Drought conditions during 2020 and 2021 could confound the interpretation of our results. Study reaches that did not contain water during our sampling (41 of 47 random lotic sites) may have the potential to support Brook Stickleback during normal water years, so the decrease in the number of occupied watersheds may be an artifact of the high percentage of sites that were dry during our sampling. Indeed, drought conditions could positively affect management of invasive Brook Stickleback as such conditions may further slow Brook Stickleback spread. A re-evaluation of dry sites in normal water years will help further refine our knowledge of Brook Stickleback distribution. Relatedly, the effects of climate change on spread are unknown as while Brook Stickleback is associated with cooler water temperatures, it has a relatively high thermal maximum with previous studies noting mortality and cessation of spawning at water temperatures near 30 °C (Winn, 1960; Reisman & Cade, 1967). This suggests that the species may persist in a wide range of habitats even as temperatures increase with climate change.

Habitat associations and basin-wide occurrence

Landscape-level habitat associations derived from the random forest model align with Brook Stickleback habitat preferences noted in the primary literature. Studies in its native range suggest a preference for low-gradient, spring-fed ponds and streams (Winn, 1960; Reisman & Cade, 1967; Stewart et al., 2007); this is supported by the negative relationship with channel slope and positive relationship with higher baseflow index in the model. Additionally, Brook Stickleback is known to colonize fragmented habitats (Stewart et al., 2007), which is reflected in a higher predicted likelihood of occurrence at sites with moderate disturbance risk than at low-risk sites. However, a limited number of high disturbance risk sites in our study area paints an incomplete picture of the relationship between disturbance risk and Brook Stickleback occurrence. Relatively high probability of occurrence for Brook Stickleback across a wide range of stream temperature values aligns with the idea that stream temperatures across the North Platte River drainage are well below the species' thermal maximum, allowing them to persist in the entire range of stream temperatures found in our model.

While landscape-level modeling provides an initial filter for species occurrence, abiotic and biotic factors interact at multiple scales to inform species distributions and abundances (Labbe & Fausch, 2000). One of the shortcomings of landscape-scale modeling is the inability of covariate values to account for microhabitats due to the coarse resolution of the data; something that is reflected in the generally high probability of Brook Stickleback occurrence across a wide range of streamflow values. For example, though Brook Stickleback may survive in streams with high discharge such as the mainstem of the North Platte River, they are often exploiting slow-moving, heavily vegetated side channels and eddies that provide protection from high flow events and habitat for spawning, as opposed to thalweg habitat (Winn, 1960; Reisman & Cade, 1967; Stewart et al., 2007). In our data, detections of the species in the mainstem of the North Platte River are likely driving the slight increase in predicted occurrence for higher streamflow values (Fig. 3) though, in reality, the microhabitat Brook Stickleback occupies is experiencing low water velocities. Our modeling approach provides a baseline understanding of landscape-level characteristics that serve as an initial filter on Brook Stickleback presence across the landscape, with microhabitat and biotic variables serving as sequential filters that further inform Brook Stickleback's distribution and abundance in the study area. Indeed, the species' abundance varied widely across our sampling of lotic sites. Brook Stickleback abundance was highest (mean = 328 individuals) in low-gradient, low-velocity streams, with high groundwater input (65%) and low turbidity. Observed abundances at sites outside of these landscape-level parameters (e.g., higher flow values) were low, with less than 10 individuals captured at most sites.

Our analysis highlights three different scenarios for Brook Stickleback presence or absence across the study area based on landscape-level environmental conditions. Oftentimes, studies aimed at predicting species distributions use a threshold value to distinguish optimal and sub-optimal habitats (e.g., Da Silva Neto et al., 2020). However, the majority of our predicted occurrence values did not exceed 0.5 despite several sites having known occurrences of Brook Stickleback from 2020 to 2021 sampling. We are unsure why this was, given that our model satisfied various evaluation metrics (OOB error = 0.13, AUC = 0.93, CCI = 0.87); this may be due to the generalist nature of Brook Stickleback which dilutes the species' response to landscape-level environmental gradients. Nonetheless, this necessitated our distinct approach of using predicted values from sites known to have Brook Stickleback to determine habitat suitability across the study area. If Brook Stickleback were to occupy only preferred habitats (i.e., low-gradient, slow-moving streams with high groundwater input and moderate disturbance risk), basin-wide occurrence potential is low (29%). However, our sampling provided evidence of Brook Stickleback occurrence in both preferred and suitable habitats, subjecting a large majority of streams in the study area (61%) to potential occupancy by the species and subsequently creating challenges for managers looking to contain their populations. This may be exacerbated in high elevation regions with cool temperatures, such as Wyoming, as invasive species expansion into such regions may intensify with climate change. Relatedly, basin-wide occurrence potential of Brook Stickleback

Table 1 Total catch for Brassy Minnow and Iowa Darter at sites with and without Brook Stickleback

siteID	Water Type	Year	STK_PA	SpeciesID	Count	Total fish caught	% of catch	Mean % of catch
NPTAR193LE	Lentic	2021	0	BMN	12	1040	1.15	
NPTAR123SC	Lotic	2021	1	BMN	1	249	0.40	
NPTAR191LE	Lentic	2021	0	IDT	3	3763	0.08	50.24
NPTAR192LE	Lentic	2021	0	IDT	25	25	100.00	
NPTAR190LE	Lentic	2021	0	IDT	34	36	94.44	
NPTAR193LE	Lentic	2021	0	IDT	67	1040	6.44	
NPTAR194LE	Lentic	2021	1	IDT	4	20514	0.02	0.88
NPTAR124LE	Lentic	2021	1	IDT	49	2809	1.74	

Note that while relative abundances of both species were generally low, they accounted for a higher percentage of the total catch at sites where Brook Stickleback was absent. SiteIDs are arbitrary and are only presented to show that each row represents a unique site for that species. Column "STK_PA" lists the presence/absence status of Brook Stickleback at each site, where 1 = present and 0 = absent. Species codes (column "SpeciesID") are as follows: *BMN* Brassy Minnow, *IDT* Iowa Darter. Column "Count" shows the number of individuals captured for either BMN or IDT. Column "% of catch" represents the percentage of the total fish caught accounted for by Brassy Minnow or Iowa Darter. Mean values are shown where data from multiple sites are available

may change in normal water years given that sampling was conducted during periods of drought and most of our spatially balanced sites did not contain water. Using habitat suitability rankings in concert with streamflow and/or baseflow index values could help managers pinpoint perennial streams where management actions would have the greatest positive effect.

Spatial overlap with native fishes

A high degree of spatial overlap between Brook Stickleback and native fishes was hypothesized based on findings from previous sampling in the North Platte River drainage (Bear & Barrineau, 2007). Specifically, we expected a high degree of overlap between Iowa Darter, Brassy Minnow, and Brook Stickleback given their shared preference for slow-moving, cool waters with low turbidity and heavy vegetation (Baxter & Stone, 1995). However, we were surprised to find that spatial overlap between these species was not as common as expected (Table 1, Fig. 5). Further, we did not detect Iowa Darter in any of our lotic sites, and only detected a single Brassy Minnow individual in one lotic site, which contradicts the known habitat preferences of the species (Baxter & Stone, 1995; Wyoming Game and Fish Department, 2017a, b). Low abundances of these species across the study area may explain such findings as detection probability is generally lower for species with limited populations. However, non-native species introductions have been hypothesized to contribute to the decline of species such as Iowa Darter (Wyoming Game and Fish Department, 2017a). Though long-term data to show changes in native fish communities in response to Brook Stickleback presence in our study area do not exist, in our sampling Iowa Darter accounted for a mean of 50.24% of the total catch at sites lacking Brook Stickleback, and only 0.88% of the total catch at sites where the species co-occurred (Table 1). This could suggest that competitive exclusion from optimal habitats by Brook Stickleback contributed to declining abundances of Iowa Darter and Brassy Minnow since the species' introduction three decades ago. Our lack of probabilistic sampling of lentic sites confounds these interpretations, as lentic sites were limited to those with known presences of Iowa Darter and Brassy Minnow. Spatially balanced random sampling of lentic sites would likely provide a more accurate estimate of spatial overlap among species.

Conclusions

A thorough understanding of an invasive species in its invaded environments can serve as a valuable tool for managers designing species-specific plans to conserve native fish populations. Our results contribute to knowledge of Brook Stickleback occurrence and environmental drivers in the North Platte River drainage, Wyoming, and provide insight into potential interactions with native fishes. We updated the map of Brook Stickleback distribution in the study area and determined that recent range expansion has been limited, though sites with suitable landscape-level habitat characteristics exist across the drainage. Low-gradient, slow-moving waterbodies with high groundwater input and moderate disturbance risk serve as preferred habitat for Brook Stickleback, similar to what has been documented in their native range. However, the species is known to be a habitat generalist, and our model outputs support this, creating the potential for expansion to suitable and (or) sub-optimal habitats. Our estimate of expansion and occurrence is likely not representative of typical water years as most of our spatially balanced sites were dry during our sampling, introducing some bias to the model. Future expansion may be exacerbated or hindered by a changing climate that could see increased dispersal due to flooding or increased fragmentation due to drought. Human-mediated transport of Brook Stickleback is also likely to contribute to spread, though this may be mitigated by curtailing live bait usage and/or transport. Finally, though Brook Stickleback has high spatial overlap with several native fishes, species with similar habitat preferences such as Iowa Darter and Brassy Minnow may be disproportionately affected by Brook Stickleback presence, highlighting the importance of species-specific management approaches. Given the high abundances of Brook Stickleback in lentic systems, the prevalence of imperiled native fishes, and their ability to serve as source populations for lotic systems, future work on Brook Stickleback in Wyoming may benefit from improved sampling of lentic water bodies. As climate change continues and human-mediated transport of biota becomes increasingly common, establishing a baseline understanding of invasive species in newly invaded regions is crucial for prioritizing management actions. Our work serves as a case study of the factors to consider when assessing a species' invasive potential in a previously unstudied region. Management plans built around an understanding of an invasive species' distribution, habitat preferences, and spatial overlap with native species can more effectively guide efforts to mitigate the risks they pose.

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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