

# Native fish abundance and habitat selection changes in the presence of nonnative piscivores

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## Abstract

We compared abundance patterns and developed resource selection models for imperilled native southwestern (USA) fishes in the presence and absence of Black Bass (*Micropterus* spp.) to evaluate how fishes alter their selection for habitats when sympatric with a nonnative piscivore. We collected data using snorkel surveys and in-stream habitat sampling in Fossil Creek (AZ), upstream (native fish only) and downstream (native and nonnative fish) of a fish barrier. The abundance of all Roundtail Chub (*Gila robusta*), small ( $\leq 127$  mm total length [TL]; vulnerable to predation) Sonora Sucker (*Catostomus insignis*) and Speckled Dace (*Rhinichthys osculus*) was significantly reduced, but the abundance of both small and large ( $> 127$  mm TL; invulnerable to predation) Desert Sucker (*Catostomus clarkii*) was similar in sampling reaches with and without Black Bass. When sympatric with Black Bass, small Roundtail Chub increased their selection for riffles by 2.57 times and small Desert Sucker reduce their selection for pools by 6.90 times while also selecting for faster flow velocity and finer substrates in lotic mesohabitats. Large native fishes altered selection least, notwithstanding an increased selection for canopy cover in sampling reaches with Black Bass. Observed shifts in resource selection are consistent with predator avoidance strategies. Our study highlights the behavioural consequences of nonnative piscivores on native fish communities and stresses the importance of maintaining lotic mesohabitats as potential refugia for vulnerable native fishes when nonnative piscivores are present.

## KEYWORDS

desert Southwest, habitat selection, native fish, nonnative species, Roundtail Chub, stream ecology

## 1 | INTRODUCTION

Freshwater ecosystems and the species they support are globally imperilled due to resource overexploitation, water pollution, flow regime modification, climate change, the widespread loss of habitat and the proliferation of nonnative species (Dudgeon et al., 2006; Tickner et al., 2020; Xenopoulos et al., 2005). Freshwater vertebrate populations have declined at more than twice the rate of terrestrial populations and wetlands are being lost at three times the rate

of forest environments (Comte et al., 2013; Dudgeon et al., 2006; Tickner et al., 2020). Endemic freshwater fishes are particularly vulnerable and 28% of species investigated by the IUCN are at significant risk of extinction (IUCN, 2019; Tickner et al., 2020).

Fundamental to the conservation of freshwater fishes is the identification of the physical features of the stream (e.g. depths, substrate, flow, cover and food) that collectively constitute habitat for a target species, and then to maintain that habitat in sufficient quantity to sustain viable populations (Rosenfeld & Hatfield, 2006;

Turner & List, 2007). Assuming that higher quality habitats support a greater density of individuals (Mayor et al., 2009), increasing the spatiotemporal quantity of such habitats can increase the abundance and distribution of a target species (Fretwell & Lucas, 1970; Rosenfeld & Hatfield, 2006). A loss of habitat or reductions in habitat quality may force individuals to occupy suboptimal environments or disperse in search of new environments (McMahon & Tash, 1988; Rosenfeld, 2003), both of which would have negative fitness consequences (Davis & Wagner, 2016; Mannan & Steidl, 2013). The availability of suitable habitats is the major driver of species distribution, abundance and diversity across spatial scales (Bunn & Arthington, 2002) including the spatial distribution of individuals within a stream (Teresa & Casatti, 2013). Under ideal free distribution, individuals arrange themselves in the spatial environment to maximize their fitness by selecting specific environmental features that provide adequate resources for survival, growth and reproduction, while minimizing external sources of mortality (e.g. predation; Fretwell & Lucas, 1970; Rosenfeld & Hatfield, 2006).

Modified flow regimes and other types of aquatic habitat degradation have decreased the quantity and quality of habitat available to native fishes and facilitated the spread and establishment of nonnative fishes (Bunn & Arthington, 2002). Direct impacts of nonnative fishes include predation (Brown & Moyle, 1991), competition (Rinne, 1991), hybridization and disease and parasite transmission (Gozlan et al., 2010; Tyus & Saunders, 2000). Nonnative species can also indirectly affect native fishes. Native fishes avoid nonnative species to minimize predation risk and competition, potentially excluding individuals from previously selected resources (Bowers & Dooley, 1993; Brown & Moyle, 1991; Douglas et al., 1994; Mayor et al., 2009). Many studies have documented shifts in native fishes' habitat selection resulting from the presence of nonnative species across freshwater fish taxa (Bohn et al., 2008; Brown & Moyle, 1991; Rinne, 1991). This illustrates the importance of understanding the habitat associations and requirements of native fishes and how those associations shift in the presence of nonnative fishes.

The native freshwater fish assemblage of the southwestern United States and northern Mexico (hereafter referred to as the Southwest) is one of the most imperilled faunal groups in North America (Minckley & Deacon, 1968; Rahel, 2000; Schade & Bonar, 2005). More than two thirds of the fishes endemic to the Southwest are listed as endangered, threatened or a species of concern by state or federal agencies, one species has gone extinct and multiple others have been locally extirpated (Minckley et al., 2002; Olden & Poff, 2005; Rinne, 1994; Turner & List, 2007). The decline of the native Southwest fishes is primarily attributed to widespread habitat loss and expansion of nonnative fishes. Previous research has found that native Southwest fishes face intense predation (Pilger et al., 2008), competition for resources (Rinne, 1994) and are displaced from their trophic niche towards lower trophic positions by nonnative fishes (Marks et al., 2010; Rogosch & Olden, 2020). The conservation and recovery of native Southwest fishes depend on a comprehensive knowledge of their habitat requirements and the

ecological mechanisms that influence habitat selection (Rosenfeld & Hatfield, 2006). Such efforts also require an understanding of how native species alter their selection for habitat in the presence of nonnative species, which are nearly ubiquitous within the Southwest (Clarkson et al., 2005; Schade & Bonar, 2005).

In this study, we evaluated abundance patterns and modelled habitat selection via resource selection functions (RSFs) for native fishes of Fossil Creek, AZ in the presence and absence of nonnative Black Bass (*Micropterus* spp.) We used data collected upstream and downstream of a fish barrier which divided our study area into two sections, one exclusively occupied by native fish (upstream) and one in which Black Bass were present (downstream). We hypothesised that the abundance of fish occupying the ecological niche most similar to Black Bass would show significant differences in both abundance and habitat selection upstream and downstream of the barrier. Additionally, we hypothesised that species with less niche overlap with the nonnative Black Bass would be less impacted by its presence and would, therefore, have less need to alter their selection for habitat.

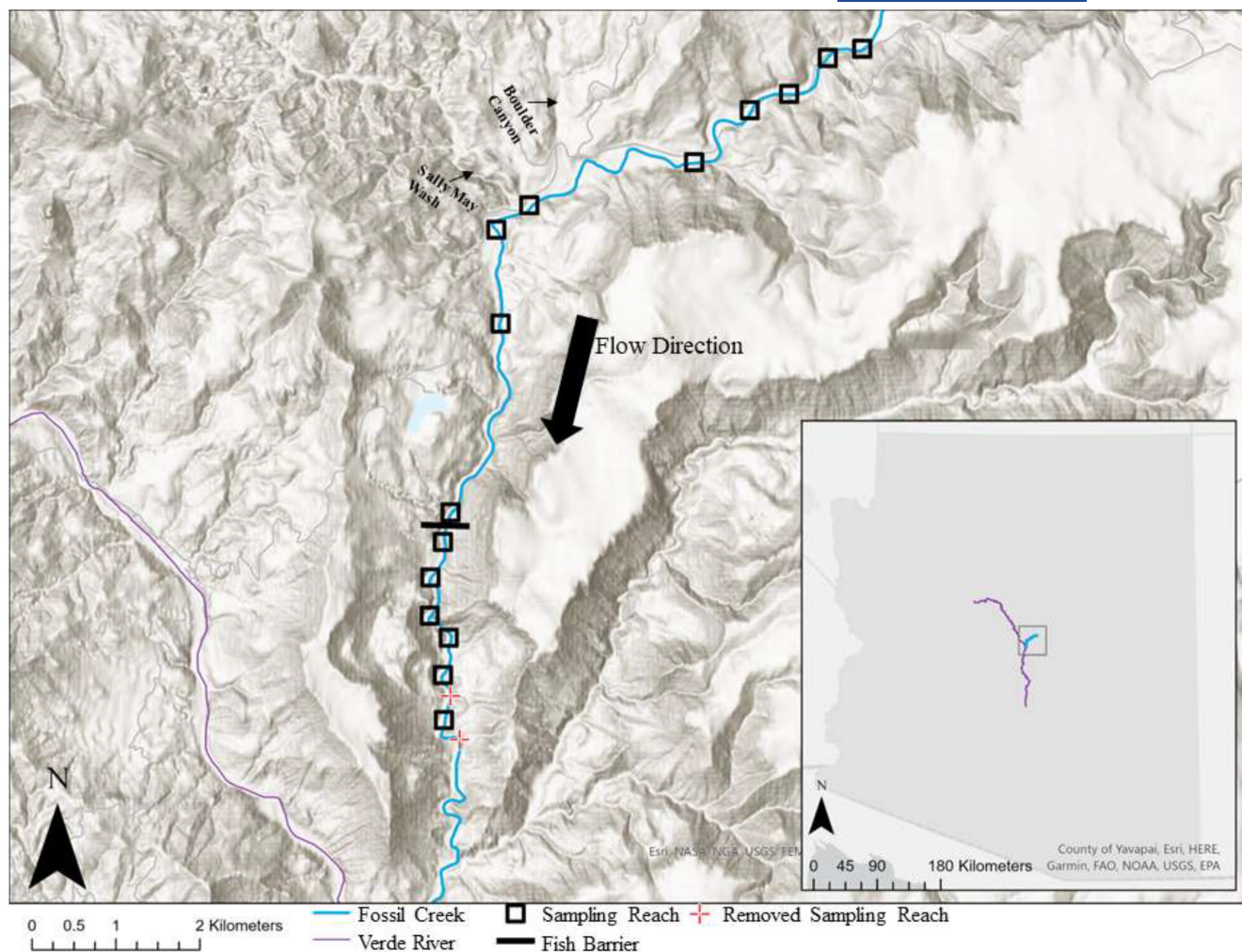
## 2 | METHODS

### 2.1 | Study site

Fossil Creek is a 23-km long spring-fed perennial river in central Arizona originating on the Mogollon Rim of the Colorado Plateau with a terminus at the Verde River (USFS, 2011; Figure 1). The origin of the perennial reach of Fossil Creek, Fossil Springs, discharges 76 m<sup>3</sup>/min, providing a steady year-round baseflow of 1.2–1.6 m<sup>3</sup>/s and a relatively constant temperature of approximately 21.1°C.

From 1909 to 2005, Fossil Creek's flow was diverted to provide hydroelectricity. In 2005, the flow was restored to Fossil Creek and the river was federally designated as Wild and Scenic in 2009 (USFS, 2011). As part of that restoration, a collaboration of management agencies removed nonnative fishes from the river, constructed a fish barrier 7 km upstream from the mouth of Fossil Creek, and repatriated native fishes. Two major washes (Sally May and Boulder Canyon; Figure 1) contribute loose alluvium into Fossil Creek and as a result, there is a transition from large deep pools upstream to shallower pools of finer substrates downstream of these inputs. As such, there are some differences to the physical features of the river upstream and downstream of these washes (Marks et al., 2006, 2010).

Today, the upper 16.5 km of Fossil Creek retains an exclusively native fish community that consists of Roundtail Chub (*Gila robusta*), Desert Sucker (*Catostomus clarkia*), Sonora Sucker (*Catostomus insignis*), Longfin Dace (*Agosia chrysogaster*), Speckled Dace (*Rhinichthys osculus*) and Spikedace (*Meda fulgida*). Since restoration, nonnative fishes have recolonized Fossil Creek from the Verde River, but are not present above the fish barrier. The only nonnative fish observed in our study were Black Bass (likely Smallmouth Bass [*Micropterus dolomieu*] and Redeye Bass



**FIGURE 1** Map of Fossil Creek, Arizona, and the location of the fish barrier and 15 sampling reaches (~100m) snorkelled during summer of 2019 and 2020. Six reaches were located downstream of the fish barrier (nonnative fishes are present) and nine snorkelling reaches were located upstream (native fishes only) of the fish barrier. Two reaches were removed due to poor visibility at the time of snorkelling. Fossil Creek is a tributary of the Verde River, AZ. Two major washes, Sally May and Boulder Canyon, are also pictured.

[*Micropterus coosae*] hybrids [Valente et al., 2021]); however, additional species (e.g. Green Sunfish [*Lepomis cyanellus*], Red Shiner [*Cyprinella lutrensis*] and catfishes [*Ictaluridae* spp.]) are likely present downstream of the barrier.

We conducted snorkel surveys in 17 sampling reaches (mean length=102.53m; range=90–130m) in the summer (June–August) of 2019 and 2020 while Fossil Creek was at baseflow. Nine sampling reaches were upstream of the fish barrier where no nonnative fishes were present and eight were downstream of the fish barrier where native and nonnative fish were present. Four of the ‘upstream’ sampling reaches, and all ‘downstream’ sampling reaches were downstream of the aforementioned Sally May Wash and Boulder Canyon (Figure 1). Because sections of Fossil Creek are extremely remote and difficult to access, we restricted sampling site selection to accessible areas. Within accessible areas, we randomly selected the start of each sampling reach. To avoid beginning a survey in the middle of a mesohabitat unit, which could induce a fright bias, we walked downstream to the start of the nearest mesohabitat unit

(pool, riffle and run) upon arrival at the random point. Each sampling reach extended ~100m upstream from the established starting point. If we snorkelled 100m and were in the middle of a mesohabitat unit, we either shortened or extended the reach to the end of the nearest mesohabitat unit. We removed two sampling reaches located downstream of the fish barrier due to high turbidity at the time of snorkelling.

## 2.2 | Habitat use

The water within Fossil Creek was exceptionally clear and daytime snorkel surveys were effective for estimating fish abundance and habitat use in this river (Marks et al., 2010). Two observers sampled each reach concurrently, beginning 5m below the starting point of the survey, and proceeded upstream to the upstream terminus of the survey. We snorkelled in tandem to split the stream into two equal halves and maintained communication to ensure

full observational coverage as per methods described in Strakosh et al. (2003).

We placed a coloured and numbered washer on the substrate directly below the location of an observed fish. We then recorded washer number and colour, species common name and an estimated fish total length (TL) on a SCUBA slate (Strakosh et al., 2003). We estimated fish size in imperial measurements and converted these measurements to metric, as technicians were more comfortable making estimations on this scale. We limited our analyses to fish with a TL  $\geq 67$  mm (3 in) because smaller individuals, especially cyprinids, are difficult to identify while snorkelling (Li, 1988). We included Speckled Dace in our analysis despite this species falling below the established size threshold as their distinctive coloration and pattern aided their identification. If a group of individuals ( $\geq 1$ ) was located within a 1 m<sup>2</sup> area with homogenous environmental conditions, we recorded the total number of individuals observed and an estimated size for each individual but placed only one washer in the group's central location.

We measured total depth (m), flow velocity (m<sup>3</sup>/s), substrate composition (modified Wentworth scale), canopy cover (proportion) and recorded the GPS coordinates at each washer location immediately after snorkelling. We measured water depth using a U.S. Geological Survey top-setting wading rod and flow velocity at approximately 60% of total depth using a Marsh-McBirney electromagnetic flow meter (Hach Company). We visually assessed the dominant substrate type within 1 m<sup>2</sup> of the washer using a modified Wentworth substrate classification (0 = silt < 0.062 mm; 1 = sand 0.62–2 mm; 2 = gravel 2–4 mm; 3 = pebble 4–64 mm; 4 = cobble 64–256 mm; 5 = boulder > 256 mm) and measured canopy cover with a spherical densiometer following methods in Lemmon (1956), in which four canopy measurements are taken (upstream, downstream, left bank and right bank) and the mean canopy cover value recorded. Finally, we assigned each washer to a mesohabitat type (pool, riffle or run).

## 2.3 | Available habitat

We measured the same five habitat measurements along transects set perpendicular to the stream thalweg within each sampling reach to characterize habitat availability. We placed the first transect one mean-stream-width upstream from the start of the sampling reach, with additional transects placed every 10 m upstream until the end of the sampling reach. We then acquired measurements at five equidistance points along each transect. If the width of the transect was > 10 m, we took the first measurement 1 m off the streambank and if the width of the transect was < 10 m, we took the first measurement at 0.5 m from the stream bank. We alternated each transect's starting point between stream banks. To measure substrate, we placed a 1 m chain with demarcations every 10 cm on the streambed, perpendicular to the transect. We categorized the dominant substrate type (modified Wentworth Scale) by estimating substrate class at each 10 cm demarcation and calculating the mode of the 10 substrate classes.

## 2.4 | Data analysis

We classified all fish  $\leq 127$  mm (5 inches) TL as small fish and all fish > 127 mm TL as large fish. This classification was based on Gaeta et al. (2018), which found that cyprinids > 127 mm TL exceed the maximum prey size of most Black Bass  $\geq 300$  mm TL, which was the upper range of Black Bass TL observed within Fossil Creek. We assumed large fish to be invulnerable to predation by Black Bass.

## 2.5 | Fish abundance

We calculated relative abundance as the number of fish per 100 m of sampled stream ( $n = 15$ ). We calculated relative abundance for both small and large fish individually. We used a Wilcoxon signed-rank test to test differences in the relative abundance of each native species in the presence and absence of nonnative Black Bass. Our null hypothesis was that there was no difference in the mean abundance of species or size-classes between sampling reaches with and without nonnative fishes present. Additionally, we modelled fish abundance relative to mesohabitat (pool, riffle and run) for small and large fish, both in the presence and absence of Black Bass. We standardized observations to a single mesohabitat unit and calculated the number of fish present per mesohabitat unit in pools, riffles and runs separately. We then compared the mean abundance of each species/size class among mesohabitats using a nonparametric Kruskal-Wallis test. Our null hypothesis was that there is no difference in the mean abundance of fish among mesohabitats: pool, riffle and run. We conducted all analyses in Program R (v. 4.2.2; R Core Team, 2021) and used  $\alpha = 0.05$ .

## 2.6 | Habitat selection (resource selection functions)

We modelled habitat selection using resource selection functions (RSFs) which are proportional to the probability of selection and quantify the relative selection strength for habitat features (e.g. sampling points or raster pixels; Avgar et al., 2017; Lele et al., 2013; Manly et al., 2002). We estimated RSF's using a used versus available study design, where habitat covariates are measured at units used by the study species and also at random units representing the range of habitat conditions available to the study species (Johnson et al., 2006; Manly et al., 2002). In our study, used units represented sampling units where fish were observed, and available units represented measurements from our transects. We used the exponential form of the RSF (generalized linear mixed model (GLMM); for example, logistic regression; Johnson et al., 2006; Manly et al., 2002; Warton & Shepherd, 2010). Under this form, the coefficients from the binomial GLM ( $\beta$ ) are selection coefficients describing the relative strength of selection for habitat covariate

$X$  (Avgar et al., 2017; Fieberg et al., 2021) and  $W(x)$  describes the relative probability or intensity of use of a particular location within the stream:

$$W(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n) \quad (1)$$

Prior to analysis, we z-score standardized continuous covariates to facilitate comparing the selection strength of each covariate. We weighted used points based on the count of individuals present at each sampling unit (e.g. washer location). We also assigned large weights (5000) to each available point because previous studies have demonstrated the equivalence between a binomial GLM with highly weighted available points and an inhomogeneous Poisson point process model which facilitates the interpretation of RSF coefficients as relative selection strength and provides better estimates of relative intensity of use (Fieberg et al., 2021; Fithian & Hastie, 2013; Warton & Shepherd, 2010). We used a mixed-modelling framework and specified random intercepts by sampling reach ( $n=15$ ) to account for differences among sampling reaches and pseudo-replication (Gillies et al., 2006). We fit our RSFs using a GLMM with a binomial error distribution and logit link using the glmmTMB package (Brooks et al., 2017) in R.

We used a hierarchical approach to modelling habitat selection. We first modelled mesohabitat selection, and then modelled selection of microhabitat resources within each mesohabitat. We modelled mesohabitat selection with a RSF model which included the categorical covariate (i.e.  $X$ ) mesohabitat (pool, riffle, run with 'run' acting as the reference level in all models) and the random intercept for sampling reach. We then subset our used and available data by mesohabitat and modelled microhabitat (depth, flow velocity, substrate composition and canopy cover) selection within pools, riffles and runs separately. For each of these two analyses, we fit two models, one using data above the barrier (Black Bass absent) and one using data below the barrier (Black Bass present). We identified significant differences to resource selection between sampling reaches with and without Black Bass with non-overlapping 95% confidence intervals for a given coefficient. We were unable to evaluate changes in habitat selection for Sonora Sucker and Speckled Dace due to insufficient sample sizes.

We evaluated RSF models for mesohabitat selection using  $k$ -fold cross-validation following Johnson et al. (2006), where we divided our data into  $k$ -folds with each sampling reach serving as a fold. We then refit our RSF using  $k-1$  randomly selected folds (training data) and predicted relative intensity of use for both used and available points in the withheld fold (testing data) using Equation (1) and calculated the observed proportion of used observations within each suitability bin and the expected proportion of available observations within each bin. A well-calibrated RSF will show a 1:1 relationship between the observed and expected proportions. We repeated this process  $k$  times and used Lin's (1989) concordance correlation coefficient (CCC) to quantify the deviation of observed and expected proportions from a line with intercept = 0 and slope = 1. We considered models with a CCC value <0.50 to be a poor fit.

### 3 | RESULTS

#### 3.1 | Fish abundance

We observed and recorded the location of 1999 fish of five species: 1793 native fishes (63.4% small fish/36.5% large fish) and 206 non-native Black Bass (75.2% small fish/24.8% large fish). We observed no nonnative fishes upstream of the fish barrier and Black Bass was the only nonnative fish observed downstream of the fish barrier. Black Bass accounted for 32.2% of total fish abundance downstream of the fish barrier (Table 1).

#### 3.2 | Roundtail Chub *Gila robusta*

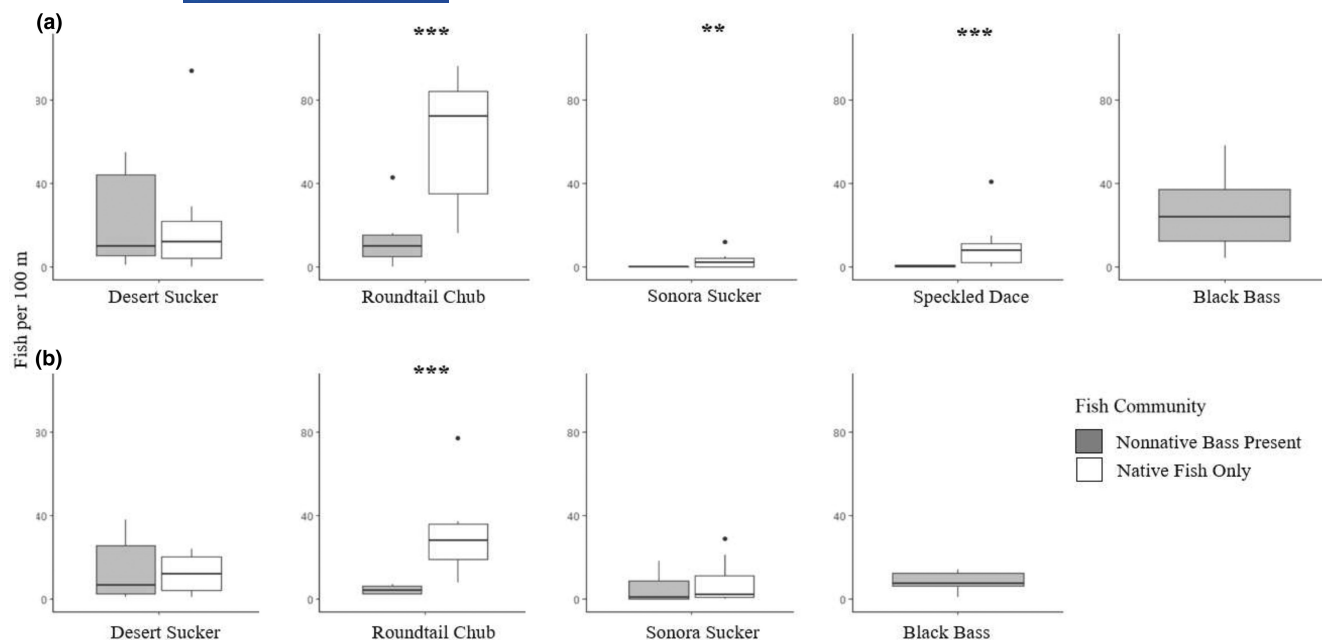
Small Roundtail Chub were significantly more abundant in sampling reaches without Black Bass ( $p < .01$ ; Figure 2). In sampling reaches without Black Bass, small Roundtail Chub abundance was not different among mesohabitat units, and marginal evidence ( $p = .09$ ) suggests that small Roundtail Chub abundance was greater in riffles with Black Bass present (Table 2). Small Roundtail Chub selected for pools and riffles more than runs and significantly increased their selection for riffles by 2.57 times when Black Bass were present (Figure 3). Selection for microhabitat remained similar in locations with and without Black Bass, although small Roundtail Chub increased their selection for canopy cover in runs with Black Bass (Figure 4). We were unable model small Roundtail Chub microhabitat selection in pools due to low abundance when Black Bass were present.

Large Roundtail Chub were significantly less abundant in sampling reaches with Black Bass ( $p < .01$ ; Figure 2). The abundance of large Roundtail Chub was not different among mesohabitats,

**TABLE 1** Number of fish (standard deviation in parentheses) observed per 100m snorkelling reach ( $n=15$ ) in Fossil Creek, Arizona where a fish barrier divides the river into two sections, one with only native fishes, and one where nonnative Black Bass are present.

Species/size	Native fish only	Black Bass present	Wilcoxon p-value
Roundtail Chub (S)	60.68 (30.20)	13.83 (15.43)	<b>.01</b>
Roundtail Chub (L)	31.33 (19.76)	4.33 (2.25)	<b>&lt;.01</b>
Desert Sucker (S)	20.89 (29.03)	33.50 (47.23)	1.00
Desert Sucker (L)	11.58 (9.30)	14.17 (16.44)	.95
Sonora Sucker (S)	2.89 (3.86)	0.17 (0.10)	<b>.02</b>
Sonora Sucker (L)	7.67 (10.58)	5.16 (7.60)	.51
Speckled Dace (S)	10.44 (12.46)	0.33 (0.52)	<b>.01</b>
Black Bass (S)	Not present	20.67 (20.18)	–
Black Bass (L)	Not present	8.33 (5.01)	–

Note: Fish  $\leq 127$  mm TL were classified as small (S, vulnerable to predation) and fish  $>127$  mm TL were classified as large (L, invulnerable to predation). Significant p-values ( $\alpha = .05$ ) are bolded.



**FIGURE 2** Relative abundance of small  $\leq 127$  mm TL (panel a) and large  $> 127$  mm TL (panel b) fish per 100m sampling reach. Grey boxes show abundance in sampling reaches with Black Bass present and white boxes show abundance in sampling reaches with native fishes only. Significance of the Wilcoxon signed-rank test is symbolized as follows:  $p < .01^{***}$  |  $0.01 < p < .05^{**}$  |  $0.05 < p < .10^{*}$ .

**TABLE 2** Relative abundance (standard deviation in parentheses) of fish per mesohabitat type: Pool, riffle or run in sampling reaches with exclusively native fishes and in sampling reaches with nonnative Black Bass present.

Species	Sz	Native fish only				Nonnative black bass present			
		Pool	Riffle	Run	p-Value	Pool	Riffle	Run	p-Value
Desert Sucker	S	0.39 (0.87)	0.39 (0.54)	0.52 (0.59)	.48	0.02 (0.04)	0.57 (0.73)	0.77 (1.22)	.06
	L	0.13 (0.27)	0.33 (0.32)	0.23 (0.30)	.12	0.12 (0.20)	0.42 (0.51)	0.15 (0.32)	.26
Roundtail Chub	S	2.14 (2.64)	1.38 (1.20)	0.94 (0.37)	.95	0.04 (0.10)	0.45 (0.52)	0.09 (0.10)	.09
	L	0.55 (0.89)	0.71 (0.45)	0.68 (0.41)	.38	0.12 (0.21)	0.14 (0.17)	0.04 (0.06)	.40
Sonora Sucker	S	0.05 (0.11)	0.02 (0.04)	0.08 (0.08)	.14	Not present			
	L	0.11 (0.13)	0.09 (0.13)	0.18 (0.31)	.61	0.25 (0.61)	0.12 (0.19)	0.06 (0.13)	.61
Speckled Dace	S	0.02 (0.03)	<b>0.41 (0.47)</b>	0.12 (0.17)	<b>.01</b>	Not present			
Black Bass	S	Not present				0.12 (0.20)	0.29 (0.38)	0.16 (0.16)	.58
	L	Not present				0.92 (1.77)	0.11 (0.08)	0.10 (0.11)	.87

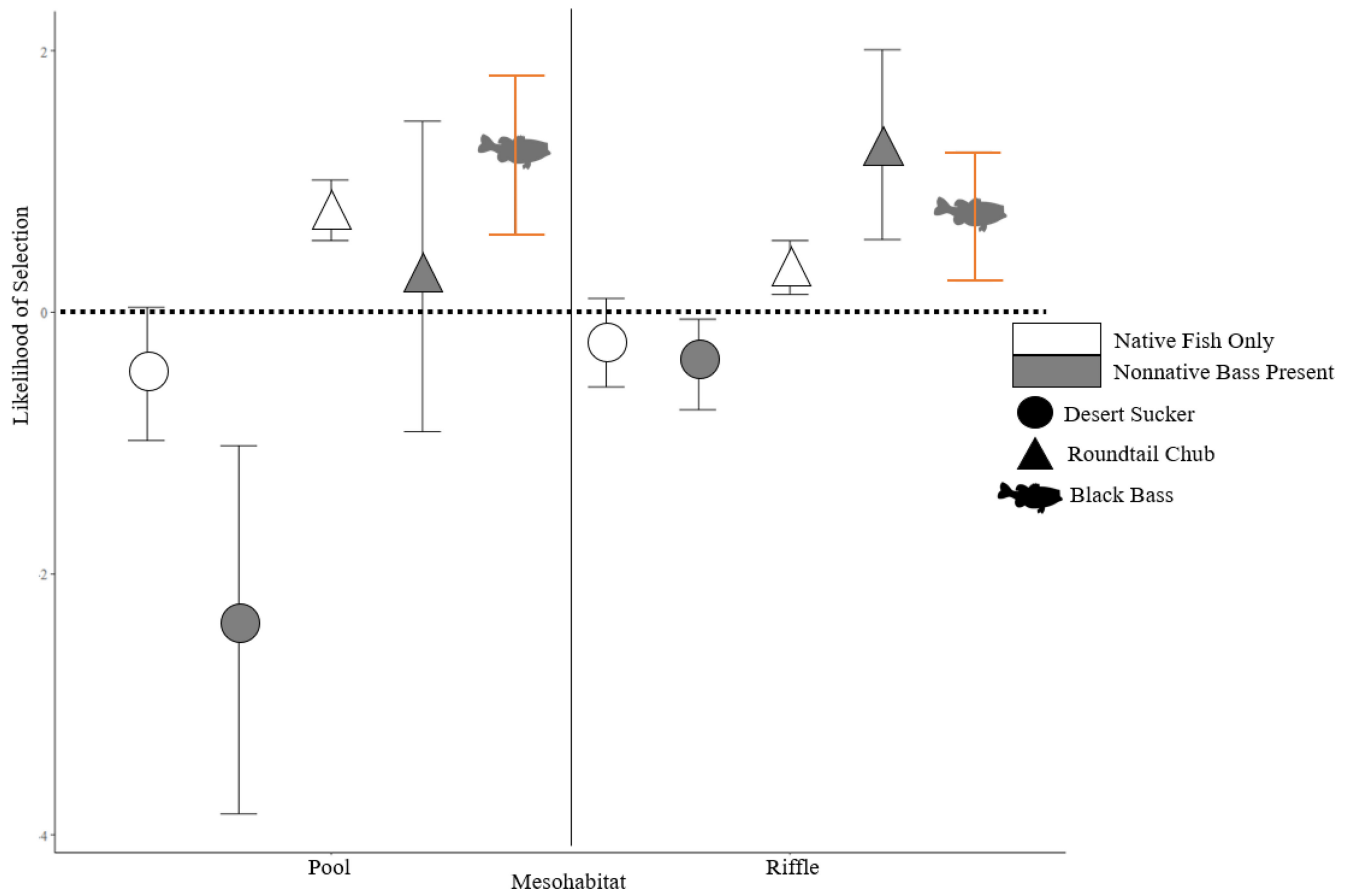
Note: We analysed data from areas without Black Bass and areas with Black Bass separately. Small fish are those under  $\leq 127$  mm TL (vulnerable to predation) and large fish are those  $> 127$  mm TL (invulnerable to predation). Speckled Dace and Sonora Sucker were not present in sufficient abundance in sampling reaches with Black Bass, and Black Bass were only present downstream of the fish barrier. Bolded numbers show  $p$ -values  $\leq .05$  from the Kruskal–Wallis tests.

and this distribution remained consistent regardless of Black Bass presence ( $p = .38$ ; Table 2). In sampling reaches without Black Bass, we found no selection for mesohabitat; but marginal evidence suggests large Roundtail Chub increased their selection for pools by 4.10 times when sympatric with Black Bass (Figure 5). In general, large Roundtail Chub used microhabitats within pools in proportion to their availability, but selected deep water, avoided fast flow velocities and used a range of substrates and canopy cover in riffles and runs. We only modelled change to microhabitat selection in riffles due to insufficient observations and poor model convergence in other mesohabitats. Microhabitat selection

in riffles remained consistent regardless of Black Bass presence (Figure 6).

### 3.3 | Desert Sucker *Catostomus clarkii*

The abundance of small Desert Sucker was similar between sampling reaches with and without Black Bass ( $p \geq .95$ ; Figure 2). Small Desert Sucker abundance was not related to mesohabitat in sampling reaches without Black Bass, however; some evidence suggests ( $p = .06$ ) that the abundance of small Desert Sucker was less



**FIGURE 3** Small fish ( $\leq 127$ -mm TL; vulnerable to predation) mesohabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions for mesohabitat selection of small fish in the presence and absence of Black Bass. 'Run' was the reference level for the explanatory categorical variable mesohabitat (levels: pool, riffle and run). Coefficients estimate relative selection strength of pools and riffles relative to runs. White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Significant change to selection is represented by non-overlapping 95% confidence intervals. Table of coefficient estimates, confidence intervals, and CCC values can be found in [Table S1](#).

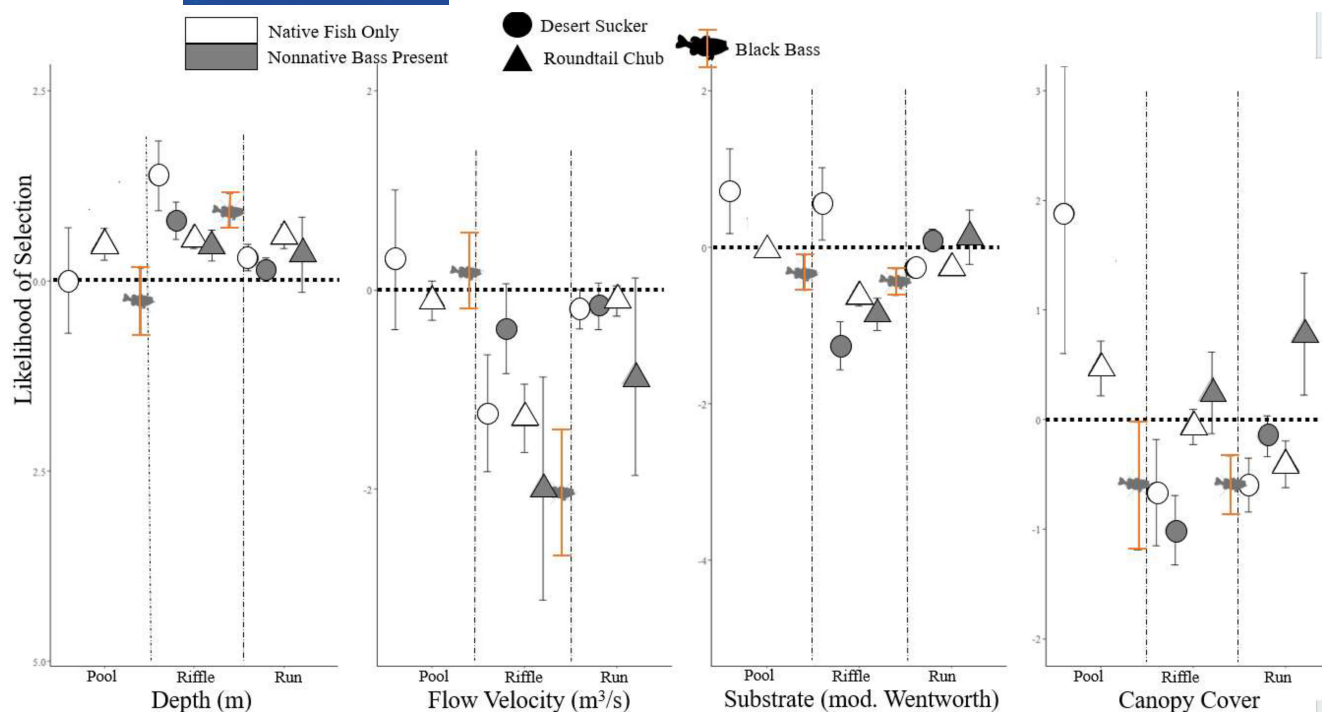
in pools with Black Bass ([Table 2](#)). When Black Bass were absent, small Desert Sucker did not select for mesohabitat, but when sympatric with Black Bass, small Desert Sucker were 6.90 times more likely to avoid pools ([Figure 3](#)). In general, small Desert Sucker selected for deep water of slower flow velocity in riffles and runs, selection that remained consistent regardless of Black Bass presence. Small Desert Sucker selected for smaller substrates in riffles, and larger substrates and increased levels of overhead cover in runs when sympatric with Black Bass ([Figure 4](#)). Desert Sucker were generally not found in pools with Black Bass and microhabitat selection was not modelled in these environments due to insufficient sample sizes.

The abundance of large Desert Sucker was not significantly different between sampling locations with and without Black Bass ( $p = .95$ ; [Figure 2](#)) and we found no significant differences to the abundance of large Desert Sucker among mesohabitats ( $p = .61$ ; [Table 2](#)). Large Desert Sucker selected for riffles, and some evidence suggests this selection for riffles increased by 3.40 times in sampling reaches with Black Bass ([Figure 5](#)). We were only able to model change to microhabitat selection in riffles due to insufficient

observations in runs and pools with Black Bass present. In riffles, large Desert Sucker selected for deep water of slow flow velocity and large substrates, selection that remained consistent in sampling reaches with and without Black Bass ([Figure 6](#)). Large Desert Sucker did, however, significantly increase their selection for canopy cover in riffles with Black Bass.

### 3.4 | Sonora Sucker *Catostomus insignis* and Speckled Dace *Rhinichthys osculus*

The abundance of small Sonora Sucker was significantly reduced in sampling reaches with Black Bass ( $p = .02$ ); however, the abundance of large Sonora Sucker was not different ( $p = .51$ ; [Figure 2](#)). The abundance of Sonora Sucker of either size-class was not different among mesohabitats with or without nonnative Black Bass ( $p \geq .14$ ; [Table 2](#)). The abundance of Speckled Dace was significantly reduced in sampling reaches with Black Bass present ( $p = .01$ ). In sampling reaches with exclusively native fishes, the abundance of Speckled Dace was greatest in riffles than other mesohabitats ( $p = .01$ ; [Table 2](#)).



**FIGURE 4** Small fish ( $\leq 127$ -mm TL; vulnerable to predation) microhabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions for microhabitat features (depth [m], flow velocity [ $\text{m}^3/\text{s}$ ], substrate composition [modified Wentworth Scale, and canopy cover (proportion)]) for small fish within each mesohabitat (pool, riffle and run). White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Insufficient observations of small native fishes in pools and small Black Bass in runs prevented the modelling of microhabitat selection in those areas. Significant change to selection is represented by non-overlapping 95% confidence intervals. Table of coefficient estimates, confidence intervals, and CCC values for microhabitat selection in riffles, pools, and runs can be found in [Tables S2–S4](#), respectively.

### 3.5 | Black Bass *Micropterus* spp.

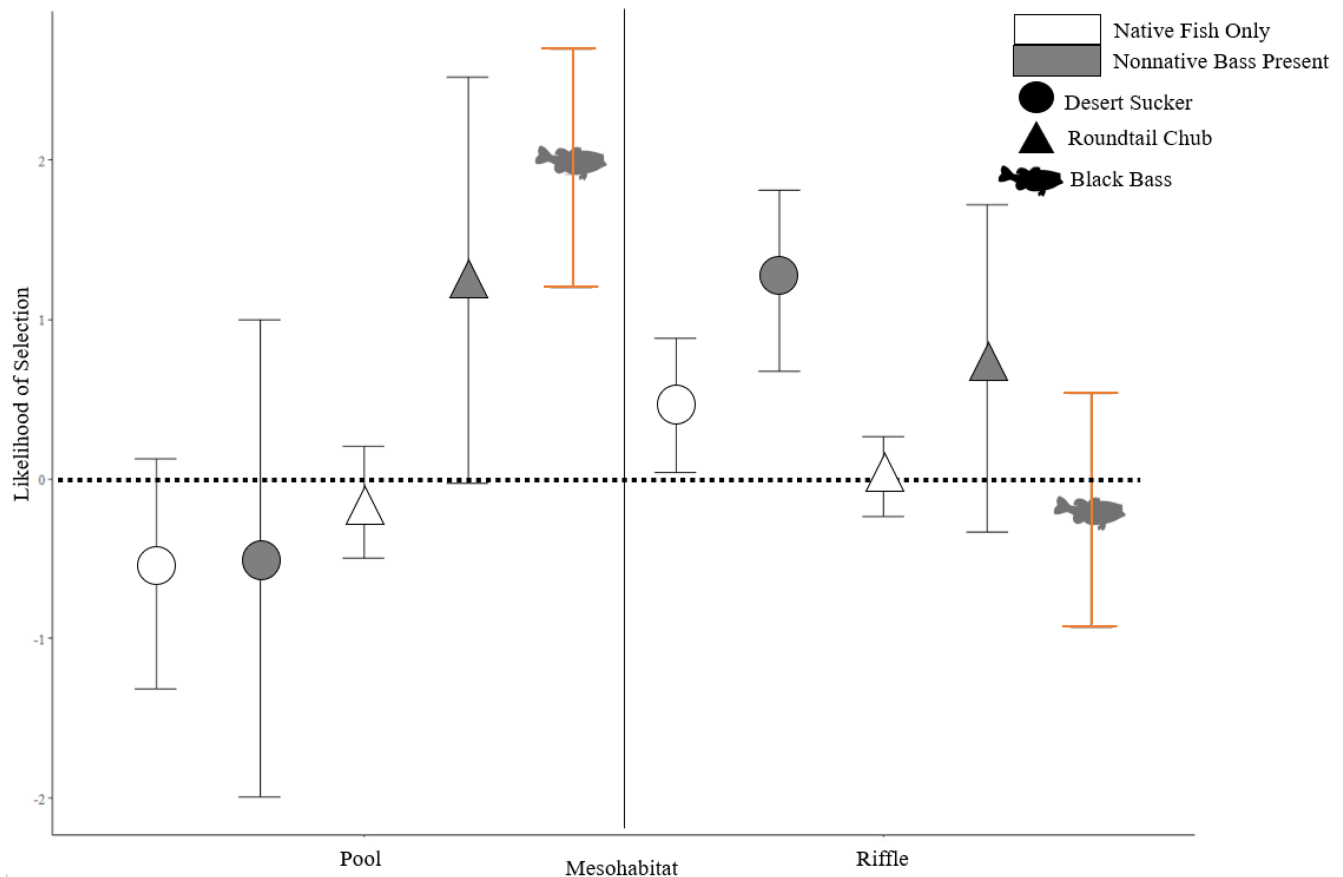
Black Bass were restricted to sampling reaches downstream of the fish barrier. Small Black Bass abundance did not differ among mesohabitats ( $p = .58$ ; [Table 2](#)); however, small Black Bass selected pools 3.33 times and riffles 2.08 times more than runs (CCC = 0.56; [Figure 3](#)). Small Black Bass did not selectively use microhabitats in pools but selected deep and slow environments with smaller substrates and less canopy cover in riffles ([Figure 4](#)). We could not model microhabitat selection in runs due to insufficient observations.

Large Black Bass abundance was unrelated to mesohabitat ( $p = .87$ ; [Table 2](#)), but large Black Bass selected pools 7.01 times more than they selected runs ([Figure 5](#)). Large Black Bass did not selectively use microhabitats, notwithstanding a strong selection for canopy cover in pools and riffles ([Figure 6](#)). We were unable to model large Black Bass microhabitat selection in runs due to poor model convergence and small sample sizes.

## 4 | DISCUSSION

Our results support the hypothesis that native fishes alter their habitat selection in the presence of a nonnative predator (i.e. Black

Bass) in a manner consistent with predator avoidance. Additionally, the abundance of many species (e.g. Roundtail Chub, Sonora Sucker, Speckled Dace) was lower in the presence of Black Bass, presumably because of their susceptibility to Black Bass predation (Pilger et al., 2008). Black Bass are one of the most problematic nonnative species for native fishes of the Colorado River Basin (Johnson et al., 2008). Roundtail Chub, Sonora Sucker and Speckled Dace lack behavioural and morphological adaptations to avoid predation and are increasingly vulnerable to predation (Arena et al., 2012; Marsh & Brooks, 1989; Pilger et al., 2010; Rees et al., 2005; Schlosser, 1987; Ward & Figiel, 2013). Additionally, predation risk is a strong determinant in habitat selection decisions because predation has more immediate and stronger fitness consequences than a temporary resource deficit (Hugie & Dill, 1994; Mayor et al., 2009; Power, 1987). Large Black Bass selected for pools over other mesohabitats, and as such, small (i.e. vulnerable) Desert Sucker reduced their selection for pools by 6.9 times (avoidance) and small Roundtail Chub increased their selection for riffles by 2.5 times in the presence of Black Bass. Predator-induced shifts in habitat selection can reduce the availability of suitable habitats by forcing individuals to occupy suboptimal environments (Barrett & Maughan, 1995; Brown & Moyle, 1991; Douglas et al., 1994), which affects individual fitness and population viability (Werner et al., 1983; Werner & Hall, 1988).

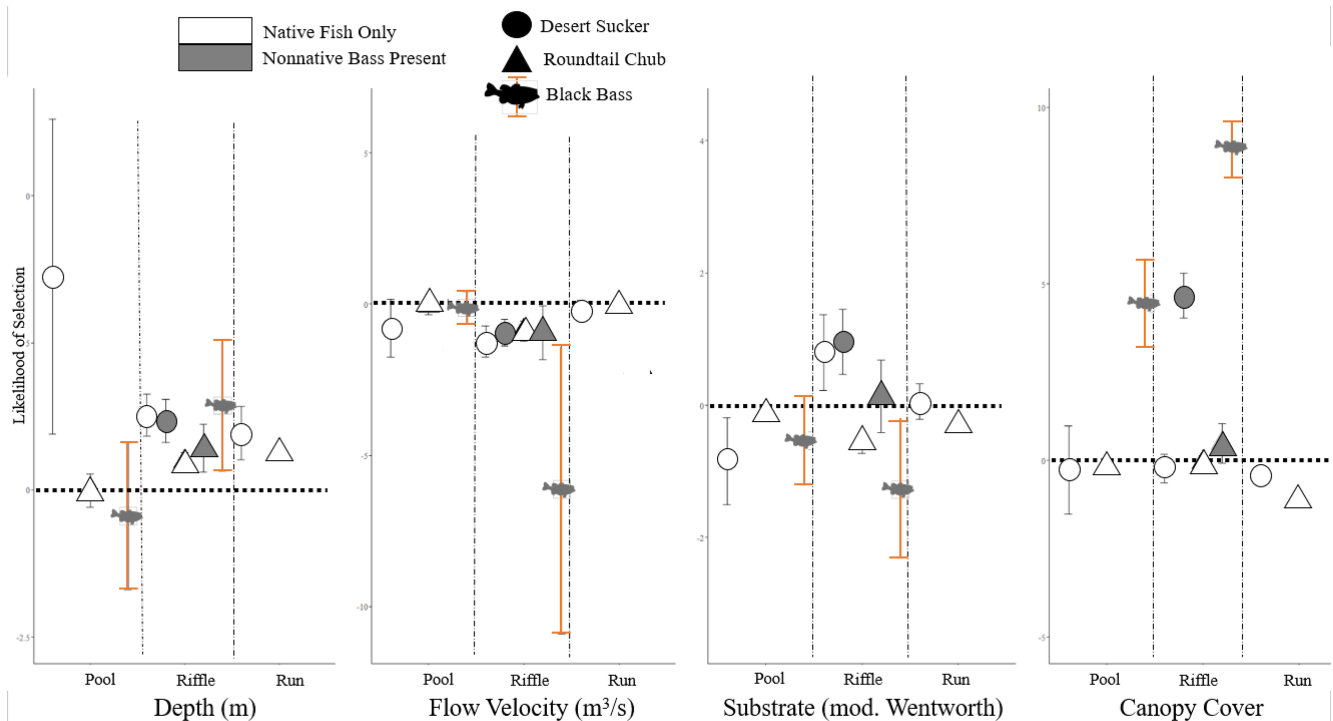


**FIGURE 5** Large fish (>127 mm TL; invulnerable to predation) mesohabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions (RSF) for large fish in the presence and absence of Black Bass. Run was the reference level for the RSF, so coefficients estimate relative selection strength of pools and riffles relative to runs. White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Significant change to selection is represented by non-overlapping 95% confidence intervals. Table of coefficient estimates, confidence intervals, and CCC values can be found in [Table S1](#).

The abundance of both small and large Roundtail Chub was significantly reduced when Black Bass were present, which supports our initial hypothesis that species that were ecologically similar to Black Bass would be most impacted. Roundtail Chub and Black Bass often occupy the highest trophic level within their resident stream environment (Arena et al., 2012); however, Roundtail Chub have been shown to reduce their trophic position when sympatric with nonnative fishes indicating a competitive inferiority (Marks et al., 2010; Rogosch & Olden, 2020). Additionally, Black Bass become piscivorous within their first-year post-hatch. Small Roundtail Chub likely experience high levels of predation from, and competition with, Black Bass. The reduced abundance of Roundtail Chub suggests that predator-induced shifts to habitat selection insufficiently offset negative interactions with Black Bass (Brown & Moyle, 1991; Schlosser, 1987, 1988). Roundtail Chub might not have the capacity to alter their selection of resources or behaviour to adequately segregate from Black Bass because of the species' ecological similarity. Vulnerable Roundtail Chub did, however, increase their selection for riffles when Black Bass were present. Bestgen and Propst (1989) similarly found that small Roundtail Chub were restricted to nearshore shallow environments when nonnative fishes were present but used

midchannel environments when nonnative fishes were removed by a natural flow event. This highlights the importance of riffle habitat as potential refuge habitat when Black Bass are present. The low abundance of large Roundtail Chub likely reflects reductions in Roundtail Chub recruitment. Predation by nonnative fishes on young native fishes can result in recruitment failure and is a primary cause for the decline of native Southwest fishes (Clarkson et al., 2005; Tyus & Saunders, 2000).

We were unable to compare Sonora Sucker and Speckled Dace meso- and microhabitat selection between sampling locations due to the significant reduction in abundance of both species in sampling reaches with Black Bass. Sonora Sucker were observed in a relatively low abundance regardless of sampling reach. The overall low abundance of Sonora Sucker might reflect their preference for slow and deep waters (Minckley, 1973) which are characteristic of larger mainstem rivers. Sonora Sucker abundance was similarly low in neighbouring tributaries (Wet Beaver Creek, West Clear Creek and Sycamore Creek; Gahl 2022, unpublished data). Nevertheless, the reduced abundance of small Sonora Sucker in sampling reaches with Black Bass is indicative of predation and/or competitive exclusion. The abundance of large Sonora Sucker was not different between



**FIGURE 6** Large fish (>127 mm TL; invulnerable to predation) microhabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions for microhabitat features (depth [m], flow velocity [ $\text{m}^3/\text{s}$ ], substrate composition [modified Wentworth Scale and canopy cover (proportion)]) large fish within each mesohabitat (pool, riffle and run). White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Insufficient observations of large native fishes in pools and runs and poor model convergence for Black Bass in runs prevented the modelling of microhabitat selection in those areas. Significant change to selection is represented by non-overlapping 95% confidence intervals. Table of coefficient estimates, confidence intervals, and CCC values for microhabitat selection in riffles, pools, and runs can be found in [Tables S2–S4](#), respectively.

sampling reaches with and without Black Bass, suggesting that some Sonora Suckers are recruiting into larger size-classes or emigrating from locations upstream of the fish barrier where Black Bass are not present. Source-sink population dynamics of an artificially fragmented river (Rahel, 2013) would warrant further investigation. Speckled Dace larvae are smaller than larvae of other native species with poorer swimming abilities (Robinson et al., 1998), contributing to this species' vulnerability to predation. Even as adults, Speckled Dace never achieve a size that exceeds the gape limitation of most Black Bass, exposing this species to predation at all life stages.

Small and large Desert Sucker abundance was unrelated to Black Bass presence, supporting our hypothesis that fish with less ecological overlap with the nonnative Black Bass would be least impacted. Less ecological niche overlap between these species is likely to reduce opportunities for negative interspecific interactions. Desert Sucker further reduced the opportunity for negative interspecific interactions via shifts to habitat selection. Small Desert Sucker strongly avoided pools in sampling reaches with Black Bass, while also altering microhabitat selection in riffles and runs, behaviours assumed to reduce spatial overlap with the largest and most piscivorous Black Bass (Gaeta et al., 2018; Schlosser, 1988). Desert Sucker are known riffle and run inhabitants (Minckley & Marsh, 2009; Ward et al., 2003). Their increased selection for lotic environments likely resulted in fewer fitness consequences than would be experienced

by species less adapted to these environments. We did, however, observe a Black Bass consuming a small Desert Sucker, confirming some predation on this native fish.

Habitat selection is behavioural and inherently hierarchical (Johnson, 1980; Mayor et al., 2009). Microhabitat selection is conditional upon the available habitat features within a given mesohabitat, yet mesohabitat use is a product of selection at a higher hierarchical level (Bowers & Dooley, 1993). Modelling habitat selection at a single spatial scale is likely to result in misleading inferences by ignoring selection at larger spatial scales (Mayor et al., 2009). For example, when we pooled microhabitat data across all mesohabitats, as is often done in fisheries studies, we found that small Desert Sucker selected deep waters with slow flow velocity, implying a selection for pools. However, our multi-scale, hierarchical approach found that small Desert Sucker avoided pools and instead selected deep areas with slow flow velocity in riffles and runs; conditions that are consistent with 'pocket-water' and previously described habitat selection for this species (Booth & Shipley, 2012). Ignoring the hierarchical nature of habitat selection in native stream fishes, particularly in the presence of nonnative piscivores, may underestimate the value of these important environments for conserving native fishes.

Our study was observational, and we cannot derive causal relationships between the presence of Black Bass, observed shifts to native fish abundance, and habitat selection from this study, alone.

However, our results combined with evidence from previous research (Barrett & Maughan, 1995; Brown & Moyle, 1991; Gilliam & Fraser, 1987), strongly suggest that native fishes shift habitat to avoid Black Bass, specifically by shifting their selection from pools towards more lotic mesohabitat types. Alternatively, observed shifts in habitat selection might represent the selective removal of individuals from riskier environments rather than individual behavioural shifts. Finally, habitat selection was not modelled for Sonora Sucker and Speckled Dace due to limited observations and we were unable to model the impact of other native species as they were not present in Fossil Creek at the time of sampling. Possibly due to periodic flooding (Minckley & Meffe, 1987), other nonnative species have been slow to recolonize the lower reaches of Fossil Creek.

Our study underscores the importance of protecting riffles and runs as within-stream refuges for native fishes when Black Bass are present (Rahel, 2000; Schade & Bonar, 2005). The desert Southwest is currently amid a  $\geq 21$ -year megadrought (Williams et al., 2022) and lotic mesohabitats are being lost via lentification (i.e. the transformation of lotic river environments into a series of disconnected lentic environments via surface water reductions; Sabater, 2008; Sabo et al., 2010). As surface waters recede, fishes will become increasingly concentrated into pools, mesohabitats dominated by nonnative fishes, exposing native fishes to greater predation risk (Bestgen & Platania, 1991; Gibson et al., 2015). A reduction to surface water has not been observed in Fossil Creek, however, streamflow throughout the Verde River Basin has declined considerably since the mid-twentieth century (Jaeger et al., 2013; Schenk et al., 2022; Serrat-Capdevilla et al., 2013), with concurrent declines to native fish populations (Neary & Rinne, 1998; Rinne, 2005; Rinne et al., 1998; Rinne & Miller, 2006). While studies have found that the enhancement of instream habitat is likely to benefit native fishes, most have concluded that habitat enhancements alone are insufficient to restore native fish populations if nonnative fishes remain (Marks et al., 2010; Walsworth & Budy, 2015). Our study provides more evidence of this as habitat and flow conditions are similar throughout Fossil Creek (Marks et al., 2010); however, the abundance of native fishes was reduced and their selection for habitats altered when Black Bass were present. The removal of nonnative species combined with the intentional fragmentation of the stream preventing natural recolonization by nonnative fishes (Rahel, 2013), as done in Fossil Creek, appears to be a viable solution to preserve native fish populations. When segregation from, or suppression of nonnative fish populations is not tenable, maintaining flows at a level that preserves or enhances the spatial availability and extent of lotic mesohabitats would provide some refuge to an imperilled native fish community.

## AUTHOR CONTRIBUTIONS

CJ and SB conceived and designed the investigation and performed all laboratory and field work. CJ and JB analysed the data. CJ, JB and SB wrote the article.

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## CONFLICT OF INTEREST STATEMENT

No potential conflict of interest was reported by the authors of this study.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Open Science Framework at <https://osf.io/>, reference number DOI:10.17605/OSF.IO/3J2KP.

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## REFERENCES

- Arena, A., Ferry, L. A., & Gibb, A. C. (2012). Prey capture behavior of native vs. nonnative fishes: A case study from the Colorado River drainage basin (USA). *Journal of Integrative Biology*, 317, 103–116.
- Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative selection strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution*, 7, 5322–5330.
- Barrett, P. J., & Maughan, O. E. (1995). Spatial habitat selection of Roundtail Chub *Gila robusta* in two central Arizona streams. *The Southwestern Naturalist*, 40(3), 301–307.
- Bestgen, K. R., & Platania, S. P. (1991). Status and conservation of the Rio Grande silvery minnow, *Hybognathus amarus*. *The Southwestern Naturalist*, 36(2), 225–232.
- Bestgen, K. R., & Propst, D. L. (1989). Distribution, status, and notes on the ecology of *Gila robusta* (cyprinidae) in the Gila River drainage, New Mexico. *The Southwestern Naturalist*, 34(3), 402–412.
- Bohn, T., Amundesen, P. A., & Sparrow, A. (2008). Competitive exclusion after invasion? *Biological Invasions*, 10(3), 359–368.
- Booth, M. T., & Shipley, A. J. (2012). Spatial dynamics and growth of two native species of catostomids: are movements restricted? *The Southwestern Naturalist*, 57(3), 248–256.
- Bowers, M. A., & Dooley, J. L. (1993). Predation hazard and seed removal by small mammals: Microhabitat versus patch scale effects. *Oecologia*, 94(2), 247–254.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017).

- GlmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.
- Brown, L. R., & Moyle, P. B. (1991). Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish *Ptychocheilus grandis*. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 849–856.
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30(4), 492–507.
- Clarkson, R. W., Marsh, P. C., Stefferud, S. E., & Stefferud, J. A. (2005). Conflicts between native fish and nonnative sport fish management in the southwestern United States. *Fisheries*, 30, 20–27.
- Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58, 625–639.
- Davis, A. D., & Wagner, T. (2016). Scale-dependent seasonal pool habitat use by sympatric wild Brook Trout and Brown Trout populations. *Transactions of the American Fisheries Society*, 145, 888–902.
- Douglas, M. E., Marsh, P. C., & Minckley, W. L. (1994). Indigenous fishes of western North America and the hypothesis of competitive displacement: *Meda fulgida* (Cyprinidae) as a case study. *Copeia*, 1, 9–19.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Leveque, C., Naiman, R. J., Prieur-Rechard, A., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status, and conservation challenges. *Biological Reviews*, 81, 163–182.
- Fieberg, J., Singer, J., Smith, B., & Avgar, T. (2021). A 'how to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, 00, 1–17.
- Fithian, W., & Hastie, T. (2013). Finite-sample equivalence in statistical models for presence-only data. *The Annals of Applied Statistics*, 7, 1917–1939.
- Fretwell, S. D., & Lucas, H. J., Jr. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19, 16–36.
- Gaeta, J. W., Ahrenstorff, T. D., Diana, J. S., Fetzer, W. W., Jones, T. S., Lawson, Z. J., McInerney, M. C., Santucci, V. J., Jr., & Vander Zanden, M. J. (2018). Go big or... don't? A field-based diet evaluation of freshwater piscivore and prey fish size relationships. *PLoS One*, 13(3), e0194092.
- Gibson, P. P., Olden, J. D., & O'Neill, M. W. (2015). Beaver dams shift desert fish assemblages toward dominance by non-native species (Verde River, Arizona, USA). *Ecology of Freshwater Fish*, 24, 355–372.
- Gilliam, J. F., & Fraser, D. F. (1987). Habitat selection under predation hazard: Test of a model with foraging minnows. *Ecology*, 68(6), 1856–1862.
- Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E., & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, 75, 887–898.
- Gozlan, R. E., Britton, J. R., Cowx, I., & Copp, G. H. (2010). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, 76, 751–786.
- Hugie, D. M., & Dill, L. M. (1994). Fish and game: A game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology*, 45, 151–169.
- International Union for Conservation of Nature (IUCN). (2019). *The IUCN red list of threatened species, version 2019-1*. IUCN. [www.iucnredlist.org](http://www.iucnredlist.org)
- Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2013). Climate change poised to threaten hydrological connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, 111(38), 13894–13899.
- Johnson, B. M., Martinez, P. J., Hawkins, J. A., & Bestgen, K. R. (2008). Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management*, 28, 1941–1953.
- Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDonald, T. L., & Boyce, M. S. (2006). Resource selection functions based on use-available data: Theoretical motivation and evaluation methods. *The Journal of Wildlife Management*, 70(2), 347–357.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.
- Lele, S. R., Merrill, E. H., Keim, J., & Boyce, M. S. (2013). Selection, use, choice, and occupancy: Clarifying concepts in resource selection studies. *Journal of Animal Ecology*, 82, 1183–1191.
- Lemmon, P. E. (1956). A spherical densiometer for estimating forest over-story density. *Forest Science*, 2(4), 314–320.
- Li, S. K. (1988). Measuring microhabitat in swift water. In K. D. Bovee & J. R. Zuboy (Eds.), *Proceedings of a workshop on the development and evaluation of habitat suitability criteria*. US Fish Wild Serv. Biol. Rep. 88. 11 (pp. 392–407). US Fish and Wildlife Service.
- Lin, L. I. (1989). A concordance correlation coefficient to evaluate reproducibility. *Biometrics*, 1, 255–268.
- Manly, B. F. J., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical design and analysis for field studies*. Kluwer Academic Publishers.
- Mannan, R. W., & Steidl, R. J. (2013). Habitat. In P. R. Krausman & J. W. Cain III (Eds.), *Wildlife management and conservation* (pp. 229–245). John Hopkins University Press.
- Marks, J. C., Haden, G. A., O'Neill, M., & Pace, C. (2010). Effects of flow restoration and exotic species removal on recovery of native fish: Lessons from a dam decommissioning. *Restoration Ecology*, 18(6), 1–10.
- Marks, J. C., Parnell, R. A., Carter, C., Dinger, E. C., & Haden, G. A. (2006). Interactions between geomorphology and ecosystem processes in travertine streams: Implications for decommissioning a dam on Fossil Creek, Arizona. *Geomorphology*, 77, 299–307.
- Marsh, P. C., & Brooks, J. E. (1989). Predation by ictalurid catfishes as a deterrent to re-establishment of hatchery-reared razorback suckers. *The Southwestern Naturalist*, 34(2), 188–195.
- Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, 16(2), 238–247.
- McMahon, T. E., & Tash, J. C. (1988). Experimental analysis of the role of emigration in population regulation of desert pupfish. *Ecology*, 69(6), 1871–1883.
- Minckley, W. L. (1973). *Fishes of Arizona*. Sims Printing Co.
- Minckley, W. L., & Deacon, J. E. (1968). Southwestern fishes and enigma of endangered species. *Science*, 159, 1424–1432.
- Minckley, W. L., & Marsh, P. C. (2009). *Inland fishes of the greater southwest: Chronicle of a vanishing biota*. University of Arizona Press.
- Minckley, W. L., & Meffe, G. K. (1987). Differential selection by flooding in stream-fish communities of the arid American Southwest. In W. J. Matthews & D. C. Heins (Eds.), *Community and evolutionary ecology of North American stream fishes* (pp. 93–104). University of Oklahoma Press.
- Minckley, W. L., Miller, R. R., & Norris, S. M. (2002). Three new pupfish species, *Cyprinodon* (Teleostei, Cyprinodontidae), from Chihuahua, Mexico, and Arizona, USA. *Copeia*, 2002, 687–705.
- Neary, D. G., & Rinne, J. N. (1998). Baseflow trends in the upper Verde River relative to fish habitat requirements. *Hydrological Water Resource Arizona Southwest*, 27, 57–64.
- Olden, J. D., & Poff, N. L. (2005). Long-term trends of native and non-native fish faunas in the American southwest. *Animal Biodiversity and Conservation*, 28, 75–89.

- Pilger, T. J., Franssen, N. R., & Gido, K. B. (2008). Consumption of native and nonnative fishes by introduced largemouth bass (*Micropterus salmoides*) in the San Juan River, New Mexico. *The Southwestern Naturalist*, 53(1), 105–108.
- Pilger, T. J., Gido, K. B., & Propst, D. L. (2010). Diet and trophic niche overlap of native and nonnative fishes in the Gila River, USA: Implications for native fish conservation. *Ecology of Freshwater Fish*, 19, 300–321.
- Power, M. E. (1987). Predator avoidance by grazing fishes in temperate and tropical streams: Importance of stream depth and prey size. In W. C. Kerfoot & A. Sih (Eds.), *Predation: Direct and indirect impacts on aquatic communities* (pp. 333–351). University of New England Press.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rahel, F. J. (2000). Homogenization of fish faunas across the United States. *Science*, 288, 854–856.
- Rahel, F. J. (2013). Intentional fragmentation as a management strategy in aquatic systems. *Bioscience*, 63(5), 362–372.
- Rees, D. E., Ptacek, J. A., & Miller, W. J. (2005). *Roundtail Chub (Gila robusta)*: A technical conservation assessment. USFS Forest Service, Species Conservation Project.
- Rinne, J. N. (1991). Habitat use by Spikedace, *Meda fulgida* (Pisces: Cyprinidae) in southwestern streams with reference to probable habitat competition by red shiner, *Notropis lutrensis* (Pisces: Cyprinidae). *The Southwestern Naturalist*, 36(1), 7–13.
- Rinne, J. N. (1994). Declining southwestern aquatic habitats and fishes: Are they sustainable? *US Forest Service, Rocky Mountain Forest Range Experiment Station, General Technical Report*, 247, 256–265.
- Rinne, J. N. (2005). Changes in fish assemblages, Verde River, Arizona, 1974–2003. In J. N. Rinne, R. M. Hughes, & B. Calamusso (Eds.), *Historical changes in fish assemblages of large rivers in the Americas* (pp. 115–126). American Fisheries Society.
- Rinne, J. N., & Miller, D. (2006). Hydrology, geomorphology, and management: Implications for sustainability of native southwestern fishes. *Reviews in Fisheries Science*, 14(2), 91–110.
- Rinne, J. N., Stefferud, J. A., Clark, A., & Sponholtz, P. (1998). Fish community structure in the Verde River, Arizona, 1974–1997. *Hydrology and Water Resources in Arizona and the Southwest*, 28, 75–80.
- Robinson, A. T., Clarkson, R. W., & Forrest, R. E. (1998). Dispersal of larval fishes in a regulated river tributary. *Transactions of the American Fisheries Society*, 127(5), 772–786.
- Rogosch, J. C., & Olden, J. D. (2020). Invaders induce coordinated isotopic shifts in native fish species. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 1348–1358.
- Rosenfeld, J. (2003). Assessing the habitat requirements of stream fishes: An overview and evaluation of different approaches. *Transactions of the American Fisheries Society*, 132, 953–968.
- Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fish and Aquatic Sciences*, 63, 83–698.
- Sabater, S. (2008). Alterations of the global water cycle and their effects on river structure, function, and services. *Freshwater Reviews*, 1, 75–88.
- Sabo, J. L., Sinha, T., Bowling, L. C., Schoups, G. H. W., Wallender, W. W., Campana, M. E., Cherkauer, K. A., Fuller, P. L., Graf, W. L., Hopmans, J. W., Kominski, J. S., Taylor, C., Trimble, S. W., Webb, R. H., & Wohl, E. E. (2010). Reclaiming freshwater sustainability in the Cadillac Desert. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 21263–21270.
- Schade, C. B., & Bonar, S. A. (2005). Distribution and abundance of nonnative fishes in streams of the western United States. *North American Journal of Fisheries Management*, 25, 1386–1394.
- Schenk, E. R., Jenness, J. S., & Stevens, L. E. (2022). Declines in an arid land river's baseflow due to increasing air temperature: Implications for springs ecosystems. *Journal of the Arizona-Nevada Academy of Science*, 49(2), 92–98.
- Schlosser, I. J. (1987). The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, 68(3), 651–659.
- Schlosser, I. J. (1988). Predation risk and habitat selection by two size classes of a stream cyprinid: Experimental test of a hypothesis. *Oikos*, 52, 36–40.
- Serrat-Capdevilla, A., Valdes, J. B., Dominguez, F., & Rajagopal, S. (2013). Characterizing the water extremes of the new century in the US southwest: A comprehensive assessment from state-of-the-art climate model projections. *International Journal of Water Resources Development*, 29(2), 152–171.
- Strakosh, T. R., Neumann, R. M., & Jacobson, R. A. (2003). Development and assessment of habitat suitability criteria for adult brown trout in southern New England rivers. *Ecology of Freshwater Fish*, 12, 265–274.
- Teresa, F. B., & Casatti, L. (2013). Development of habitat suitability criteria for neotropical stream fishes and an assessment of their transferability to streams with different conservation status. *Neotropical Ichthyology*, 11(2), 395–402.
- Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclerc, D., Lynch, A. J., Leonard, P., McClain, M. E., Muraven, D., Olden, J. D., ... Young, L. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *Bioscience*, 70(4), 330–342.
- Turner, D. S., & List, M. D. (2007). Habitat mapping and conservation analysis to identify critical streams for Arizona's native fish. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 17, 737–748.
- Tyus, H. M., & Saunders, J. F. (2000). Nonnative fish control and endangered fish recovery: Lessons from the Colorado River. *Fisheries*, 29(9), 17–24.
- U.S. Forest Service (USFS). (2011). *Fossil creek wild and scenic river resource assessment*. March 28, 2011. version: 1-40.
- Valente, M. J., Benson, C. E., Chmiel, M. R., Lewis, M. R., Peatman, E., & Eaton, H. L. (2021). A case of mistaken identity: Genetic and morphological evidence for the presence of Redeye Black Bass in the Verde River, Arizona. *Journal of Fish and Wildlife Management*, 12(2), 554–564.
- Walsworth, T. E., & Budy, P. (2015). Integrating nonnative species in niche models to prioritize native fish restoration activity sampling units along a desert river corridor. *Transactions of the American Fisheries Society*, 144(4), 667–681.
- Ward, D. L., & Figiel, C. R., Jr. (2013). Behaviors of southwestern native fishes in response to introduced catfish predators. *Journal of Fish and Wildlife Management*, 4(2), 307–315.
- Ward, D. L., Schultz, A. A., & Matson, P. G. (2003). Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. *Environmental Biology of Fishes*, 68, 87–92.
- Warton, D. I., & Shepherd, L. C. (2010). Poisson point process models solve the “pseudo-absence problem” for presence-only data in ecology. *The Annals of Applied Statistics*, 4(3), 1381–1402.
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64(6), 1540–1548.
- Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology*, 69(5), 1352–1366.
- Williams, A. P., Cook, B. I., & Smerdon, J. E. (2022). Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. *Nature Climate Change*, 12, 232–234.

Xenopoulos, M. A., Lodge, D. M., Alcamo, J., Marker, M., Schulze, K., & Van Vuuren, D. P. (2005). Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, 11, 1557–1564.

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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