

# Temporal distribution modelling reveals upstream habitat drying and downstream non-native introgression are squeezing out an imperiled headwater fish

Stephanie D. Parker<sup>1</sup> | Joshua S. Perkin<sup>1</sup>  | Megan G. Bean<sup>2</sup> | Dijar Lutz-Carrillo<sup>3</sup> | Matthew R. Acre<sup>1</sup>

<sup>1</sup>Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, USA

<sup>2</sup>Inland Fisheries, Texas Parks and Wildlife Department, Mountain Home, TX, USA

<sup>3</sup>Analytical Services Laboratory, Inland Fisheries, Texas Parks and Wildlife Department, San Marcos, TX, USA

## Correspondence

Joshuah S. Perkin, Department of Ecology and Conservation Biology, Texas A&M University, 534 John Kimbrough Boulevard, College Station, TX 77843, USA.  
Email: jperkin@tamu.edu

## Funding information

Texas Parks and Wildlife Department, Grant/Award Number: TX-T-183-R-1 and SPR-0218-068; USDA National Institute of Food and Agriculture, Grant/Award Number: 1017538; National Park Service, Grant/Award Number: BIBE-2018-SCI-0022; Texas A&M University Animal Care and Use Committee, Grant/Award Number: IACUC 2018-0059

## Abstract

**Aim:** To review the conservation status of Headwater catfish *Ictalurus lupus* (Girard, 1859) in the United States, including quantifying environmental correlates with range contraction and hybridization and introgression with Channel catfish *Ictalurus punctatus* (Rafinesque, 1818) to inform conservation prioritization.

**Location:** Texas and New Mexico, USA.

**Methods:** We used random forest models to construct species distribution models (SDMs) based on historical (1980–1999) and contemporary (2000–2019) data and 13 classes of remotely sensed stream network data. We measured hybridization and introgression with the widely introduced Channel catfish using external morphology, mitochondrial DNA (mtDNA), and a nuclear gene (RAG2).

**Results:** Species distribution models illustrated temporal reduction in suitability for Headwater catfish among the species' namesake headwater streams, including streams with steeper slopes, faster velocities, and higher elevations. Modelling also revealed reduced suitability of larger streams greater distances from groundwater springs, the same streams frequently occupied by non-native Channel catfish. A general pattern of increased use of streams draining watersheds with altered or developed land uses was apparent. Assessment of introgression and hybridization with non-native channel catfish at nine locations showed evidence of ongoing or past hybridization at six locations. Persistence of potentially non-introgressed populations were found at three locations with smaller sample sizes.

**Main conclusions:** Modelling temporal changes in Headwater catfish distribution provided critical insight into the types and locations of streams that should be targeted for habitat preservation or restoration. Conservation and management of Headwater catfish will require priority decisions based on existing levels of introgression and the practicality of preventing further contact with Channel catfish. Maintaining Headwater catfish populations in springs that are also heavily used by humans will be critical for conservation of the species in the United States.

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

© 2020 The Authors. Diversity and Distributions published by John Wiley & Sons Ltd.

## KEYWORDS

conservation planning, habitat loss, Headwater catfish, *Ictalurus lupus*, introgression, species distribution models

## 1 | INTRODUCTION

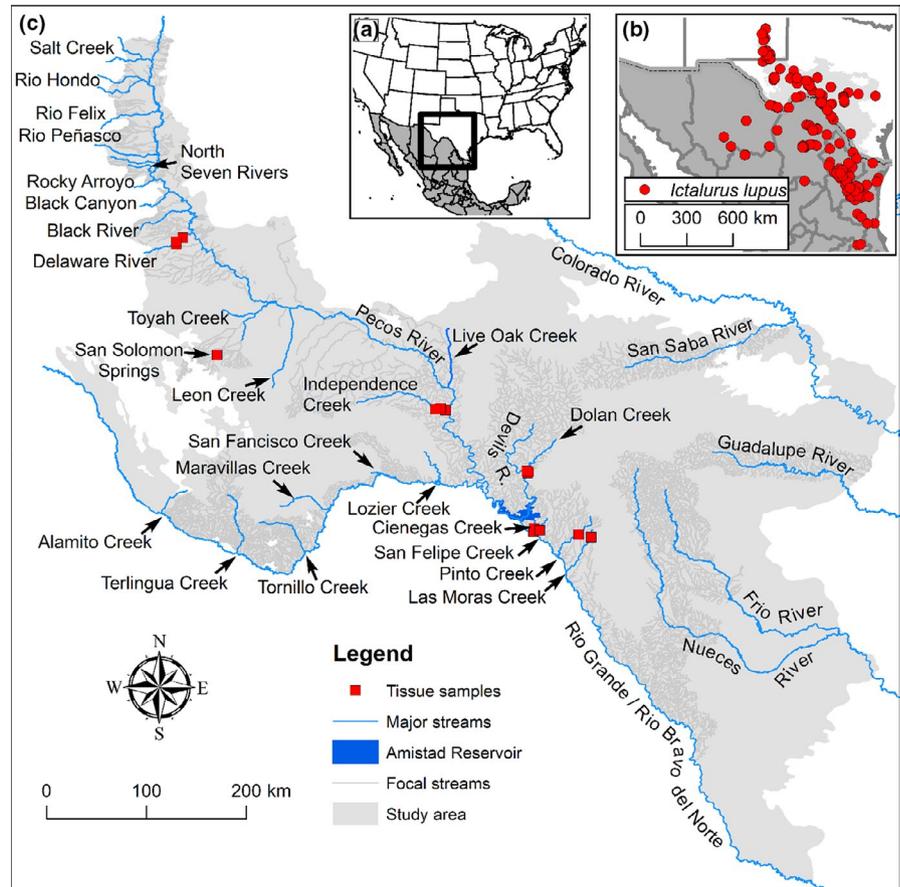
Growing human population densities and human domination of ecosystems are key factors contributing to a global loss of biodiversity (Johnson et al., 2017; McKee et al., 2004; Turak et al., 2017; Tylanakis et al., 2008). The introduction of non-native species, municipal and industrial development, increased agricultural land use, and anthropogenic greenhouse gas emissions are all contributing factors (Sala et al., 2000). Across systems, two threats to biodiversity that commonly occur together are habitat degradation (i.e., destruction of habitat) and non-native species invasions (Arlinghaus et al., 2016; Dudgeon et al., 2006; Vörösmarty et al., 2010). The loss of biodiversity in aquatic ecosystems (i.e., marine and freshwater) is widely documented (Moyle & Leidy, 1992), yet historically received less attention compared with terrestrial systems (Aerts & Honnay, 2011; Sala et al., 2000). Though freshwater covers only 0.8% of the Earth's surface, freshwater fauna represent 9.5% of known species (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Consequently, there is a growing urgency to address threats to biodiversity in freshwater ecosystems through application of systematic conservation planning (Reid et al., 2019).

The aim of systematic conservation planning is to provide conservation managers with decision-support tools that allow for efficient and effective allocation of limited resources (Hermoso et al., 2015; Poiani et al., 2000; Possingham et al., 2015; Williams et al., 2011). Systematic conservation assessments of freshwater systems and their biota are relatively new because of the spatial and temporal challenges posed by rivers and their drainage networks (Barmuta et al., 2011; Erős et al., 2018). Natural riverine landscapes (riverscapes hereafter) maintain connectivity across four dimensions, including longitudinal (upstream to downstream), lateral (main channels to floodplains), vertical (groundwater to surface water), and temporal (flow variability through time; Ward, 1998). Human alterations to riverscapes affect each of these dimensions and result in changes to natural structuring mechanisms for biotic assemblages (Cooper et al., 2017; Dudgeon et al., 2006; Perkin et al., 2015). Consequently, design of freshwater protected areas must integrate information across multiple riverscape dimensions to identify areas where anthropogenic alterations can be mitigated to benefit the greatest number of species (Hermoso et al., 2012). Freshwater stream fishes serve as biological indicators of multi-dimensional riverscape connectivity (e.g., Perkin et al., 2017; Schmutz & Jungwirth, 1999) and are commonly used to identify freshwater protected areas (Araújo & Williams, 2000; Perkin et al., 2019; Williams et al., 2011). This means assessments of fish distributions can inform systematic conservation planning by identifying priority conservation areas where preservation or restoration actions might be targeted (D'amen et al., 2017; Hermoso et al., 2016).

Fishes in arid riverscapes are especially in need of conservation. Drylands, which consist of arid, semi-arid, and desert regions, make up approximately 40% of Earth's terrestrial surface and contain nearly 33% of the human population (James et al., 2013). Streams in drylands rely on vertical connectivity with groundwater to maintain base flow, which usually has limited spatial extent and can vary seasonally (Murray et al., 2003). Human water demand and the frequency and intensity of extreme hydrologic events, such as drought, also affect the availability of water for dryland fishes (Heino et al., 2009; Perkin, Starks, et al., 2019). Thus, the preservation of perennial water sources in dryland regions is a major challenge for conserving aquatic biodiversity (Davis et al., 2017). Furthermore, introductions of non-native fish species are particularly harmful in highly isolated dryland waterbodies where there is increased competition and limited dispersal capacity (Cambray, 2003; Orians, 1995). Non-native introductions can lead to hybridization where individuals with distinguishable, heritable characters from two distinct populations or groups of populations interbreed. Introgression describes the incorporation of alleles from one species into the gene pool of another, typically through hybridization and backcrossing (Harrison & Larson, 2014). Hybridization and introgression are recognized as both potentially destructive as well as important in the evolutionary process, but present many controversial issues in conservation policy (Allendorf et al., 2001), primarily due to conflict with species-centric management practices (Chafin et al., 2019; Cooke et al., 2005; Fitzpatrick et al., 2015). This means successful conservation planning for dryland fishes must address habitat integrity, natural genetic structure, and potential introgression (Echelle, 1991; Hermoso et al., 2015; Meffe & Vrijenhoek, 1988). Simultaneously measuring each of these features across a riverscape requires multidisciplinary frameworks focused on applying modelling tools, genetic techniques, and spatial conservation planning to benefit species persistence in occupied habitats or reintroduction into restored habitats (Malone et al., 2018).

The Headwater catfish *Ictalurus lupus* Girard, 1859 is a member of the family Ictaluridae in the order Suliformes and occurs in riffles, runs, and pools of spring-fed streams and small- to moderate-sized rivers in the American Southwest (Figure 1). The native range of Headwater catfish includes the Rio Grande and Pecos River basins in the United States and Mexico (Hubbs et al., 2008). Although Headwater catfish was among the least studied North American freshwater fishes just a few decades ago (Gilbert & Burgess, 1980), subsequent studies showed its native distribution in the United States was declining as a result of habitat degradation and competition and introgression with Channel catfish *Ictalurus punctatus* Rafinesque, 1818 (Ictaluridae, Suliformes) beginning in the 1980s (Bean et al., 2011; Kelsch & Hendricks, 1990; McClure-Baker et al., 2010). Channel catfish are native to streams east of the Rocky

**FIGURE 1** Study area illustrating (a) the border of the United States and Mexico, (b) range of reported occurrences of Headwater Catfish (*Ictalurus lupus*) from Global Biodiversity Information Facility database, and (c) the range of Headwater catfish in the United States. (c) Study region (light gray), major streams (blue), focal streams where Headwater catfish have been reported (dark gray), and locations of Headwater catfish tissue collections for genetic analysis (red squares)



Mountains in North America but have been widely introduced across the United States. In Texas, Channel catfish have been presumably introduced to the Upper Rio Grande and Pecos Basins despite the species being considered native to the lower Rio Grande (Hubbs et al., 2008). As a result of these pressures, Headwater catfish was listed as a Species of Special Concern by Williams et al. (1989) and Hubbs et al. (2008), Threatened by Jelks et al. (2008), and State Threatened by the Texas Parks and Wildlife Department (M. Bean, *professional communication*). The historical range of Headwater catfish in the United States included the Pecos and Rio Grande basins of Texas and New Mexico and the upper Nueces, Guadalupe and Colorado basins in Texas (Kelsch & Hendricks, 1990). However, Headwater catfish is extirpated from a large portion of this range, with only limited portions of the Pecos, Rio Grande, and Frio River basins currently inhabited (Bean et al., 2011; Kelsch & Hendricks, 1990; McClure-Baker et al., 2010). The systems where Headwater catfish persists in the United States are threatened primarily by land use changes related to irrigated agriculture, declining groundwater tables and spring discharges, and continued introduction of non-native Channel catfish via reservoir stockings (Contreras-Balderas & Escalante, 1984; Souza et al., 2006). Jelks et al. (2008) suggested the minimum time period that a species goes undocumented before it is considered extirpated is 20 years; thus, there is a need to understand where Headwater catfish has been documented since 2000 to inform conservation planning. Furthermore, systematic conservation planning is needed to determine the watershed conditions associated with

historical and contemporary occurrences, where these conditions currently exist, the genetic integrity of existing populations, and how protective measures might be spatially allocated to ensure persistence of the species.

The goal of this study is to provide a comprehensive review of the conservation status of Headwater catfish in the United States. Our first objective was to evaluate change in the geographic distribution of Headwater catfish using machine learning methods to construct species distribution models (SDMs) based on historical (1980–1999) and contemporary (2000–2019) presence–absence data and remotely sensed stream network data. Identifying areas suitable for Headwater catfish will inform decision-making for conservation managers, including locations of suitable habitat across the riverscape and the occurrence of Headwater catfish at these habitats both historically and recently. Our second objective was to measure hybridization and introgression with widely introduced Channel catfish at locations where Headwater catfish persist in Texas, the core range of the species in the United States. The process of hybridization is not a single process leading to a uniform outcome, but rather a set of processes and outcomes shaped by ecological conditions and variations in life history (Epifanio & Nielsen, 2000). The interbreeding of these two closely related species occurs by external fertilization naturally and as a result of human-related activities such as habitat degradation and introductions of Channel catfish. Previous studies by Kelsch and Hendericks (1990) reported introgression between these two species with backcrossing of hybrids

towards Headwater catfish (Argue & Dunham, 1999). Characterizing the genetic integrity of extant populations will help to identify potentially non-introgressed refuge populations that can be included in restoration planning.

## 2 | METHODS

### 2.1 | Study area

We defined the spatial extent of our study based on level IV ecoregions of the conterminous United States (Omernik & Griffith, 2014) and the locations of Headwater catfish occurrences (Figure 1). The Rio Grande, or Rio Bravo del Norte, is located in the south-western United States and northern Mexico (Figure 1a). It is a water supply source for agriculture, industry, municipalities and wildlife (Ward et al., 2006). The Rio Grande flows through multiple biomes, including deserts, wetlands, mountains and subtropical coastal regions. The river forms approximately 2,008 km of international border between Mexico and the United States from El Paso, TX to the Gulf of Mexico (Benke & Cushing, 2011). Other tributaries such as the Pecos River and the smaller Devils River join the Rio Grande at Amistad Reservoir in Val Verde County, Texas. The historical range of the Headwater catfish spreads east to the Edwards Plateau region in Texas, where it was once found in the upper Nueces, Frio, Guadalupe and San Saba rivers (Edwards et al., 2004; Kelsch & Hendricks, 1990). The Pecos River headwaters are in New Mexico and the river flows south for approximately 805 km before it joins with the Rio Grande at Amistad Reservoir. The range of Headwater catfish in New Mexico includes the Pecos River downstream from Sumner Reservoir and the Black River as well as other south-eastern-flowing tributaries to the Pecos River. In Mexico (Figure 1b), the range of Headwater catfish includes various locales in Coahuila, Durango, Nuevo Leon, and Tamaulipas, southward to Rio Soto la Marina (Kelsch & Hendricks, 1986; Miller et al., 2005; Sublette et al., 1990).

### 2.2 | Spatial data collection

We downloaded occurrence data from the Global Biodiversity Information Facility (GBIF) to model the distribution of Headwater catfish. The GBIF is a portal that organizes digitized collection and survey data and is the largest online distributional database (Beck et al., 2014). Within the United States, records for Headwater catfish became increasingly prevalent beginning in the 1980s and 1990s because of work conducted by Kelsch and Hendricks (1986, 1990) and more recent collections by McClure-Baker et al. (2010). Given the temporal nature of occurrences, we used GBIF records (GBIF, 2019a) from across the study area split into historical (1980–1999) and contemporary (2000–2019) time periods. Because these data represent occurrence-only data, we used the target-group absence (TGA) approach described by Mateo et al. (2010) to assign Headwater catfish absences at locations where Channel catfish (GBIF, 2019b), but not

Headwater catfish, was collected. For each time period, georeferenced data were linked to medium-resolution (1:100,000-scale) National Hydrography Dataset (NHD) version 2 Plus inter-confluence stream segments (EPA, 2012) using ArcGIS 10.5.1. Occurrence data were assigned to the nearest segment within 50 m (Frimpong et al., 2005), such that any segment that was linked to a Headwater catfish record was denoted as a presence location (class = 1) and any segment that was linked to only a Channel catfish record was denoted as an absence location (class = 0). Occurrences georeferenced to locations > 50 m away from study area streams were excluded from analysis, and we only retained specimens with physical vouchers or categorized as “research-grade” observations on GBIF. Segments with both Headwater catfish and Channel catfish were denoted as presence locations (class = 1). The TGA method is commonly used in stream fish species distribution modelling implemented with presence-absence model algorithms (Huang & Frimpong, 2015; Malone et al., 2018; Perkin et al., 2019).

We used 23 environmental predictor variables as covariates for Headwater catfish occurrence (Table 1). Covariate choice was based on previous studies linking catchment attributes to the occurrence of stream fishes (Malone et al., 2018). Covariates described anthropogenic land use, as well as hydrologic, climatic and physiographic conditions for each stream segment across the study area. Hydrologic variables included upstream watershed area (km<sup>2</sup>), stream order (Strahler, 1957), stream channel maximum and minimum elevation (cm), stream channel slope (m/m), discharge (m<sup>3</sup>/s), water velocity (m/s) and distance to the nearest known spring outflow (km). Climatic variables included mean annual air temperature (°C) and mean annual precipitation (mm/y) for the period 1961–1990 obtained from EPA (2010). Physiographic variables included the major underlying geologic features and the identity of the 8-digit hydrologic unit code (HUC) in which the stream segment occurred. Land use data were from Falcone et al. (2015) and described the area of upstream watershed covered by 11 land use classes (30-m resolution, Table 1) approximately during the historical (survey year 1974) and contemporary (survey year 2002) periods. Although the survey years for land cover do not exactly match the historical and contemporary periods defined for fish collections, they do represent antecedent conditions for the period from which fish records were compiled (Perkin et al., 2019).

### 2.3 | Species distribution models

We summarized changes in the relationships between watershed covariates and Headwater catfish occurrences during historical, contemporary and combined time periods using SDMs. The SDM process involved five main steps denoted with the acronym ODMAP (Overview, Data, Model, Assessment, Prediction) and reviewed in detail by Zurrell et al. (2020). We provide a general overview of the steps here and additional details based on the ODMAP template developed by Zurrell et al. (2020) are given in Appendix A. Elith et al. (2006) suggested presence-absence models outperform presence-only models;

thus, we used random forest (RF; Breiman, 2001) models fit to historical and contemporary periods separately. Datasets assigned to each time period suffered from class imbalance such that presence records (class = 1) were fewer compared with absence records (class = 0) in the historical (1 = 31, 0 = 154), contemporary (1 = 19, 0 = 114), and combined (1 = 45, 0 = 234) periods. We addressed class imbalance using the synthetic minority over-sampling technique (SMOTE) described by Chawla et al. (2002) and applied the "SMOTE" function from the "DMwR" package in R version 3.6.0 (R Core Team, 2019; Torgo, 2011). This process resulted in balanced numbers of occurrences for historical (1 = 93, 0 = 93), contemporary (1 = 76, 0 = 76), and combined (1 = 180, 0 = 175) periods. Finally, we checked for multicollinearity among predictor variables using the package "corrplot" and removed redundant variables with Pearson correlation absolute values > 0.70. The process resulted in the removal of stream order, maximum elevation, discharge, and air temperature from the model fitting datasets. We then fit RF models to the SMOTE-adjusted datasets using the "randomForest" function from the "randomForest" package (Liaw & Wiener, 2002) in R. The "tuneRF" function from the "rfUtilities" package (Evans & Murphy, 2018) was used to determine the number of variables to try at each split. We used model-specific tree numbers and variables tried at each split, including historical (1,200 trees, 4 variables), contemporary (250 trees, 4 variables), and combined (250 trees, 2 variables) time periods. We assessed model performance using k-fold cross validation ( $k = 5$ ) in which 75% of the data were used to train the model and 25% of the data were used to test the model through the "rf.crossValidation" function and the "confusion.matrix" function from the "dismo" package. The area under the curve (AUC) of the receiver operating characteristic (ROC) is a common measure of predictive accuracy and is threshold independent (Thuiller et al., 2005). The AUC can range from 0 to 1 where values above 0.5 indicate a better than random performance. Cohens Kappa is another metric used to correct the overall accuracy of the model predictions by the accuracy expected to occur by chance. Kappa values range from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Cohen, 1960). We also report alternative performance metrics such as sensitivity, specificity, Jaccard's similarity index, and Sørensen's similarity index (reviewed in Leory et al., 2018). Sensitivity is the proportion of observed presences correctly predicted, and specificity is the proportion of observed absences correctly predicted. Jaccard's similarity index and Sørensen's similarity index are calculated based on the confusion matrix of correctly classified occurrences (i.e., true positives, TP), correctly classified absences (i.e., true negatives, TN), incorrectly classified occurrences (i.e., false positive, FP), and incorrectly classified absences (i.e., false negatives, FN). The formula we used for Jaccard's similarity index was  $TP/(FN + TP+FP)$ , the formula we used for Sørensen's similarity index was  $2TP/(FN + 2TP+FP)$ , and for both metrics values range 0–1 with values nearer to 1 representing stronger agreement between observed versus predicted occurrences. We explored relationships between Headwater catfish suitability and environmental covariates using partial dependence plots generated with the "rf.partial.prob"

function from the "rfUtilities" package in R (Evans & Murphy, 2018). Finally, we assessed differences in sampling locations and environmental conditions between the two periods to determine whether any changes in occurrence detected between periods were related to Headwater catfish distribution or simply the habitats sampled. For this assessment, we used the Kolmogorov–Smirnov test to identify differences in continuous variables between periods and plotted empirical cumulative distribution functions to illustrate patterns. For categorical variables, we used Kolmogorov–Smirnov tests and plotted proportions of categories between the two periods. We conducted these tests for habitat covariates identified by RF models as most important for predicting occurrence and report Cohen's D and P-values. Cohen's D is a common effect size measure for comparing two or more group means (Nakagawa et al., 2015). A Cohen D value of 0.2, 0.5, and 0.8 correspond to small, medium, and large effects, respectively (Cohen, 1988). The effect size indicates the magnitude of the observed effect or relationship between variables, whereas the significance test indicates the likelihood that the effect or relationship is due to chance (Maher et al., 2013). A  $p$ -value will indicate statistical significance (difference from the null distribution) but cannot reveal the size of the effect; therefore, reporting Cohen's  $d$  is complementary to the reporting of results from a test of statistical significance.

## 2.4 | Specimen collections

In 2018, we sampled 36 sites within the historical range of Headwater catfish to collect tissue samples for molecular analysis (Figure 1c). These sites included the Rio Grande and tributaries that directly empty into the Rio Grande, including Cibolo Creek, Alamito Creek, Terlingua Creek, Tornillo Creek, Devils River, Dolan Creek, San Felipe Creek, Pinto Creek, Las Moras Creek, and Elm Creek. We also sampled tributaries to the Pecos River, including the Delaware River, Salt Creek, Independence Creek, and San Solomon Springs in Balmorhea State Park. Specimens were collected using seines, mini gillnets, and backpack electrofishing equipment. Catfishes were euthanized in a lethal solution of Tricaine methanesulfonate (MS-222), and tissue was obtained from the adipose fin and the right maxillary barbel and preserved in 95% non-denatured ethanol. Specimens were tagged using Floy T-bar tags with unique ID numbers and specimens from which tissues were removed were fixed in 10% formaldehyde solution and later transferred to 70% non-denatured ethanol. All specimens were deposited in the Biodiversity Research and Teaching Collections (TCWC) at Texas A&M University, College Station, TX, USA. We also utilized 35 catfish specimens collected from the canal system at Balmorhea State Park by the Texas Parks and Wildlife Department during 2017 (D. Lutz-Carrillo, unpublished data).

Similarities among Headwater catfish and Channel catfish necessitate that detailed morphological analyses be used to identify each species. For each catfish specimen collected in 2018, we recorded anal fin ray count, standard length, pectoral spine length, caudal peduncle depth, and mouth width. Morphometrics were measured with

**TABLE 1** Environmental predictor variables used for species distribution models, including parameter descriptions, sources, and variable importance measured as mean decrease in Gini for historical (1980–1999), contemporary (2000–2019), and combined (1980–2019) time periods. Land use classes of the NAWQA Wall-to-Wall Anthropogenic Land Use Trends dataset (NAWQA, U.S. Geological Survey's National Water-Quality Assessment Program, Falcone, 2015). Variables with no value (–) for mean decrease in Gini were removed prior to analysis because of multicollinearity

| Parameter                        | Description   | Source                      | Historical mean decrease in Gini | Contemporary mean decrease in Gini | Combined mean decrease in Gini |
|----------------------------------|---|-----------------------------|----------------------------------|------------------------------------|--------------------------------|
| Watershed                        | Upstream area of drainage (km <sup>2</sup> ; DivDASqKM) from PlusFlowlineVAA attribute table            | EPA (2012)                  | 5.29                             | 2.65                               | 10.56                          |
| Stream order                     | Stream order (Strahler, 1957; StreamOrde) from PlusFlowlineVAA attribute table                          | EPA (2012)                  | –                                | –                                  | –                              |
| Min. Elevation                   | Minimum elevation of stream segment (cm; MINELEVSMO) from Elevslope attribute table                     | EPA (2012)                  | 5.08                             | 3.27                               | 12.02                          |
| Max Elevation                    | Maximum elevation of stream segment (cm; MAXELEVSMO) from elevslope attribute table                     | EPA (2012)                  | –                                | –                                  | –                              |
| Slope                            | Slope of stream segment (m/m; SLOPE) from elevslope attribute table                                     | EPA (2012)                  | 10.18                            | 2.45                               | 13.82                          |
| Discharge                        | Streamflow from gage adjustment estimate (m <sup>3</sup> /s; Q0001E) from EROMExtension attribute table | EPA (2012)                  | –                                | –                                  | –                              |
| Velocity                         | Water velocity from gage adjustment estimate (m/s; V0001E) from EROMExtension attribute table           | EPA (2012)                  | 5.49                             | 2.46                               | 8.8                            |
| Air temperature                  | Mean annual air temperature (°C*10; Temp) from CatchmentAttributesTempPrecip attribute table            | EPA (2010)                  | –                                | –                                  | –                              |
| Precipitation                    | Mean annual precipitation (mm/y; Precip) from the CatchmentAttributesTempPrecip attribute table         | EPA (2010)                  | 7.43                             | 10.29                              | 18.38                          |
| Major geology                    | Major geology (rock form)   | Schruben et al. (1994)      | 5.74                             | 3.91                               | 13.39                          |
| HUC8                             | 8-digit Hydrologic Unit Code (Subbasin level)   | USDA-NRCS et al. (2015)     | 26.55                            | 25.87                              | 46.7                           |
| Distance to springs              | Distance to springs (Euclidian distance, km)  | Heitmuller and Reece (2003) | 3.43                             | 7.15                               | 11.63                          |
| Land Cover/Land Use (1974; 2002) | water   | Falcone (2015)              | 2.7                              | 4.27                               | 12.26                          |
| Land Cover/Land Use (1974; 2002) | Major transportation  | Falcone (2015)              | 2.01                             | 0.95                               | 3.03                           |
| Land Cover/Land Use (1974; 2002) | Commercial/Services   | Falcone (2015)              | 2.39                             | 0.46                               | 1.99                           |
| Land Cover/Land Use (1974; 2002) | Industrial/Military   | Falcone (2015)              | 1.41                             | 0.54                               | 0.69                           |
| Land Cover/Land Use (1974; 2002) | Residential, low-medium density   | Falcone (2015)              | 1.2                              | 0.41                               | 0.69                           |
| Land Cover/Land Use (1974; 2002) | Developed   | Falcone (2015)              | 3.52                             | 2.44                               | 5.03                           |
| Land Cover/Land Use (1974; 2002) | Urban interface, low-medium   | Falcone (2015)              | 2.13                             | 0.38                               | 0.98                           |
| Land Cover/Land Use (1974; 2002) | Crops   | Falcone (2015)              | 1.17                             | 0.8                                | 2.09                           |
| Land Cover/Land Use (1974; 2002) | Pasture/hay   | Falcone (2015)              | 1.3                              | 0.2                                | 1.16                           |

(Continues)

TABLE 1 (Continued)

| Parameter                        | Description       | Source         | Historical mean decrease in Gini | Contemporary mean decrease in Gini | Combined mean decrease in Gini |
|----------------------------------|-------------------|----------------|----------------------------------|------------------------------------|--------------------------------|
| Land Cover/Land Use (1974; 2002) | Grazing potential | Falcone (2015) | 0.99                             | 3.81                               | 5.03                           |
| Land Cover/Land Use (1974; 2002) | Low use           | Falcone (2015) | 4.38                             | 1.65                               | 8.06                           |

digital callipers to the nearest 0.1 mm, except for large specimens where standard length was measured to the nearest mm with a ruler. A linear canonical discriminant function score (Kelsch, 1995) was calculated from these data with the goal of separating Headwater catfish and Channel catfish based on their morphology. Individual morphology scores ( $S$ ) were calculated using the equations:

$$S = S_1 + S_2 + S_3 + S_4;$$

$$S_1 = \frac{1.244(anl - 25.2)}{1.66};$$

$$S_2 = \frac{0.2 \{ \log_e(psl) - [ - 1.254 + 0.864 + \log_e(stdl) ] + 0.077 \}}{0.144};$$

$$S_3 = \frac{-0.276 \{ \log_e(cpd) - [ - 2.127 + 0.952 * \log_e(stdl) ] - 0.057 \}}{0.087};$$

$$S_4 = \frac{-0.673 \{ \log_e(mw) - [ - 2.996 + 1.129 * \log_e(stdl) + 0.096 ] \}}{0.163}$$

where  $anl$  is anal fin ray count,  $psl$  is pectoral spine length,  $stdl$  is standard length,  $cpd$  is caudal peduncle depth, and  $mw$  is mouth width (Kelsch, 1995). The resulting score for each specimen was later paired with molecular data.

For each specimen-paired tissue sample, DNA was isolated, quantified, and adjusted in concentration for downstream use as described in Lutz-Carrillo et al. (2015). The mitochondrial Cytochrome B gene (mt-CytB) was sequenced and single nucleotide polymorphisms (SNPs) from the nuclear recombination activating 2 gene (nuc-RAG2) were resolved. Cytochrome B typically provides unambiguous species identification (Ketmaier & Bianco, 2015) and was previously used in studies of Headwater catfish (Bean et al., 2011; McClure-Baker et al., 2010). Cytochrome B was amplified and bi-directionally sequenced using primers MT11 and MT29 (Waldbieser et al., 2003). Amplification was performed in 10- $\mu$ L volumes containing 2.5 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 0.2  $\mu$ M each primer, 0.75 U Platinum Taq DNA Polymerase (Thermo Fisher Scientific, Waltham, Massachusetts), 1 $\times$  of supplied buffer, and 50 ng of template DNA. Cycling conditions were 94°C (30 s), 50°C (1 min), and 72°C (1 min) for 35 cycles after an initial denaturation step of 94°C (2 min). Sequencing was performed following the removal of residual dNTPs

and unincorporated primers using ExoSAP-IT (Thermo Fisher Scientific). Sequencing reactions were performed in 10- $\mu$ L volumes containing 0.5X BigDye 3.1 reagent mix (Thermo Fisher Scientific), 0.5 $\times$  BigDye 3.1 buffer, 0.32  $\mu$ M sequencing primer, and 60 ng cleaned amplicons. Sequencing conditions were 94°C (30 s), 55°C (15 s), and 60°C (3 min), for 30 cycles. Completed sequencing reactions were cleaned with EDTA and ethanol before resolution on an ABI 3,500 (Thermo Fisher Scientific). Sequences were trimmed and aligned within Geneious Prime 2019.1 (<http://www.geneious.com/>).

Mitochondrial sequences are limited by their uniparental transmission which can mask potential hybridization or introgression events (Ketmaier & Bianco, 2015). Therefore, primers (Appendix B; RAG2\_f, and RAG2\_r) were designed to amplify a portion of a nuclear locus (RAG2) based on the alignment of GenBank (Benson et al., 2005) sequences for Headwater catfish (AY327075), Channel catfish (AY184245, DQ492398, DQ492511, DQ492595, JT408814), and Blue catfish (*I. furcatus*: KM264171, AY327075). Three primers were designed for a single base extension assay to exploit taxa diagnostic substitutions within this amplicon range (Appendix B; RAG2\_s1, RAG2\_s2, and RAG2\_s3). Multiple SNPs provided redundancy to prevent misclassification of specimens due to in vitro sequencing errors or in vivo mutations. Amplification was performed in 10- $\mu$ L volumes containing 2 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 0.2  $\mu$ M each primer, 0.5 U Platinum Taq DNA Polymerase, 1 $\times$  of supplied buffer, and 50 ng of template DNA. Cycling conditions were 94°C (30 s), 60°C (30 s), and 72°C (1 min) for 40 cycles after an initial denaturation step of 94°C (3 min). The SBE reaction was performed, following ExoSAP-IT treatment of the amplicons, in 10- $\mu$ L volumes containing 1.5- $\mu$ L SNaPshot reaction mix (Thermo Fisher Scientific), 0.1–0.3  $\mu$ M each SBE primer, and 60 ng cleaned amplicons. Reaction conditions were 96°C (10 s), 53°C (5 s), and 60°C (30 s) for 25 cycles after an initial denaturation step of 96°C (30 s). Specimens were classified as having unmixed Headwater catfish genotypes (H), unmixed Channel catfish genotypes (C), or mixed genotypes (H/C). Individuals with mixed genotypes are indicative of past hybridization events.

## 2.5 | Conservation prioritization

We combined information from the contemporary SDM and genetic analyses to prioritize locations where conservation resources might

be allocated. We included locations in the prioritization if they occurred on NHD stream segments (Balmorhea State Park was excluded based on this criteria), and tissue samples were obtained and analysed from the location (all but 8 of the 36 sites sampled during 2018 were removed based on this criteria). We plotted suitability from the contemporary SDM along the x-axis (range 0–1) and the proportion of individuals that were non-introgressed along the y-axis (range 0–1). We weighted the points in the bi-plot by the number of individuals that were collected so that small sample sizes (small points in plot) could be used to direct future sampling efforts if increasing sampling at locations with limited data is a conservation goal. Locations falling in the closest proximity to the upper right of the plot (coordinates 1, 1) are the highest priorities along both habitat conservation and genetic conservation priority ranks. Similar conservation prioritizations along multiple axes of information have been used to prioritize conservation actions (e.g., Malone et al., 2018).

### 3 | RESULTS

#### 3.1 | Species distribution models

Headwater catfish SDMs differed among historical, contemporary, and combined periods. The contemporary and combined models generally had higher performance statistic values than the historical model (Table 2). Cross-validated performance values based on AUC ranged 0.92–0.97, Kappa ranged 0.67–0.87, and accuracy ranged 0.87–0.95 with strong agreement between sensitivity and specificity. Jaccard's similarity index values for historical (i.e., 0.70), contemporary (i.e., 0.87), and combined (i.e., 0.83) models as well as Sørensen's similarity index values for historical (i.e., 0.82), contemporary (i.e., 0.93), and combined (i.e., 0.91) models showed high agreement between observed and predicted occurrences. These values reflect acceptable model performance across all evaluation metrics. The subbasin (HUC 8) from which collections were made was the most important predictor variable of Headwater catfish suitability across all models (Table 1). The five most important variables for the historical model were HUC 8, stream channel slope, annual precipitation, geology, velocity, and watershed area, while the five most important variables for the contemporary model were HUC 8, annual precipitation, distance to the nearest spring, water land cover, and geology (Figure 2a).

Partial dependence plots provided insight into temporal fluctuations in relationships between environmental variables and Headwater catfish suitability. Partial dependence on HUC 8 varied little between the two periods (Appendix C; Appendix D). Suitability declined between periods for stream segments with channel slopes > 0.003 m/m (Figure 2b), annual precipitation < 400 cm/y and > 600 cm/y (Figure 2c), velocities > 3 m/s (Figure 2d), watershed areas > 100,000 km<sup>2</sup> (Figure 2e), and minimum elevations > 500 m above sea level (Figure 2f). Suitability increased between periods among stream segments with watersheds covered by 5%–85% low use land (Figure 2g) and > 2% developed land (Figure 2h). Although

**TABLE 2** Headwater catfish species distribution model performance statistics based on fivefold cross validation for random forest models fit to historical (1980–1999), contemporary (2000–2019), and combined (1980–2019) time periods

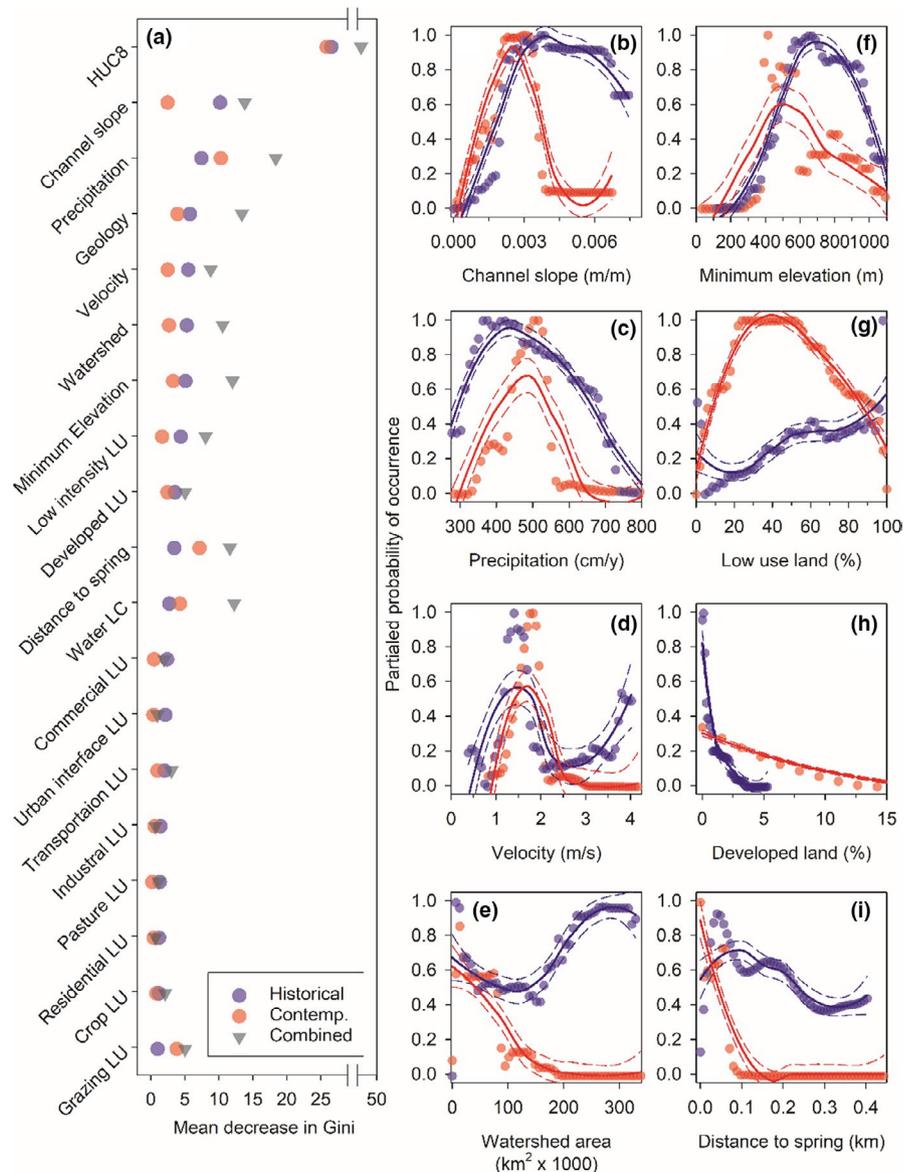
| Performance metric | Historical | Contemporary | Combined |
|--------------------|------------|--------------|----------|
| AUC                | 0.92       | 0.99         | 0.97     |
| Kappa              | 0.67       | 0.87         | 0.84     |
| Accuracy           | 0.87       | 0.95         | 0.93     |
| Sensitivity        | 0.84       | 0.96         | 0.94     |
| Specificity        | 0.89       | 0.95         | 0.93     |
| Jaccard            | 0.70       | 0.87         | 0.83     |
| Sørensen           | 0.82       | 0.93         | 0.91     |

suitability was > 0.50 up to 0.4 km from springs during the historical period, it dropped to 0.00 at distances > 0.1 km during the contemporary period (Figure 2i).

Tests for changes in the environmental gradients at sampled sites revealed consistent habitats were sampled during each period. The geographic area covered by sampling during the historical period (Figure 3a) was consistent with the contemporary period (Figure 3b) with two exceptions. First, a larger number of sites in the Edwards Plateau region of Texas (Guadalupe, Frio, and Nueces river basins) were sampled during the contemporary period. Second, fewer sites along the Rio Grande downstream of Amistad Reservoir were sampled during the contemporary period. Despite these differences, the distributions of observed habitats overlapped between periods for stream slope (Cohen's  $d = 0.09$ ,  $p = 0.54$ ; Figure 3b), precipitation ( $d = 0.09$ ,  $p = 0.59$ ; Figure 3d), discharge ( $d = 0.11$ ,  $p = 0.33$ ; Figure 3e), watershed area ( $d = 0.11$ ,  $p = 0.29$ ; Figure 3f), water velocity ( $d = 0.10$ ,  $p = 0.37$ ; Figure 3g), minimum elevation ( $d = 0.09$ ,  $p = 0.52$ ; Figure 3h), low land use ( $d = 0.09$ ,  $p = 0.48$ ; Figure 3i), developed land ( $d = 0.06$ ,  $p = 0.95$ ; Figure 3j), and major geology types ( $\chi^2 = 0.05$ ,  $df = 4$ ,  $p = 0.99$ ; Figure 3k). Consequently, changes in suitability between periods were most likely related to changes in fish distributions rather than shifts in sampled habitats.

Projections of SDMs to all study area stream segments with complete data (i.e., all model covariates) illustrated temporal changes in Headwater catfish suitability across the riverscape between the historical and contemporary period. Locations with high suitability in the historical model included streams in the upper Pecos River (i.e., Rio Hondo and Rio Felix), Toyah Creek, Independence Creek, Dolan Creek, San Felipe Creek, Tornillo Creek, and Pinto Creek (Figure 4a). The historical model also highlighted streams where Headwater catfish historically occurred outside the Rio Grande basin, including the upper Frio River, upper Nueces River, and upper Guadalupe River. Locations with high suitability in the contemporary model included streams in the Black River, the Devils River, Pinto Creek, and Tornillo Creek (Figure 4b). The combined period model illustrated an increase in suitability among western and headwater streams draining the Pecos River and Rio Grande (Figure 4c). Subtracting historical from contemporary model suitability values underscored a pattern of reduced

**FIGURE 2** (a) Random forest model results for historical (1980–1999; blue), contemporary (2000–2019; red), and combined (1980–2019; gray) time periods illustrating variable importance based on mean decrease in Gini. Partial dependence plots for highly important variables include (b) stream channel slope, (c) annual precipitation, (d) water velocity, (e) watershed area, (f) minimum stream channel elevation, (g) per cent of watershed with low use land, (h) per cent of watershed with developed land, and (i) distance to the nearest spring outflow. See Table 1 for variable definitions and sources



suitability among headwater streams and a general downstream increase in suitability during the contemporary period (Figure 4d).

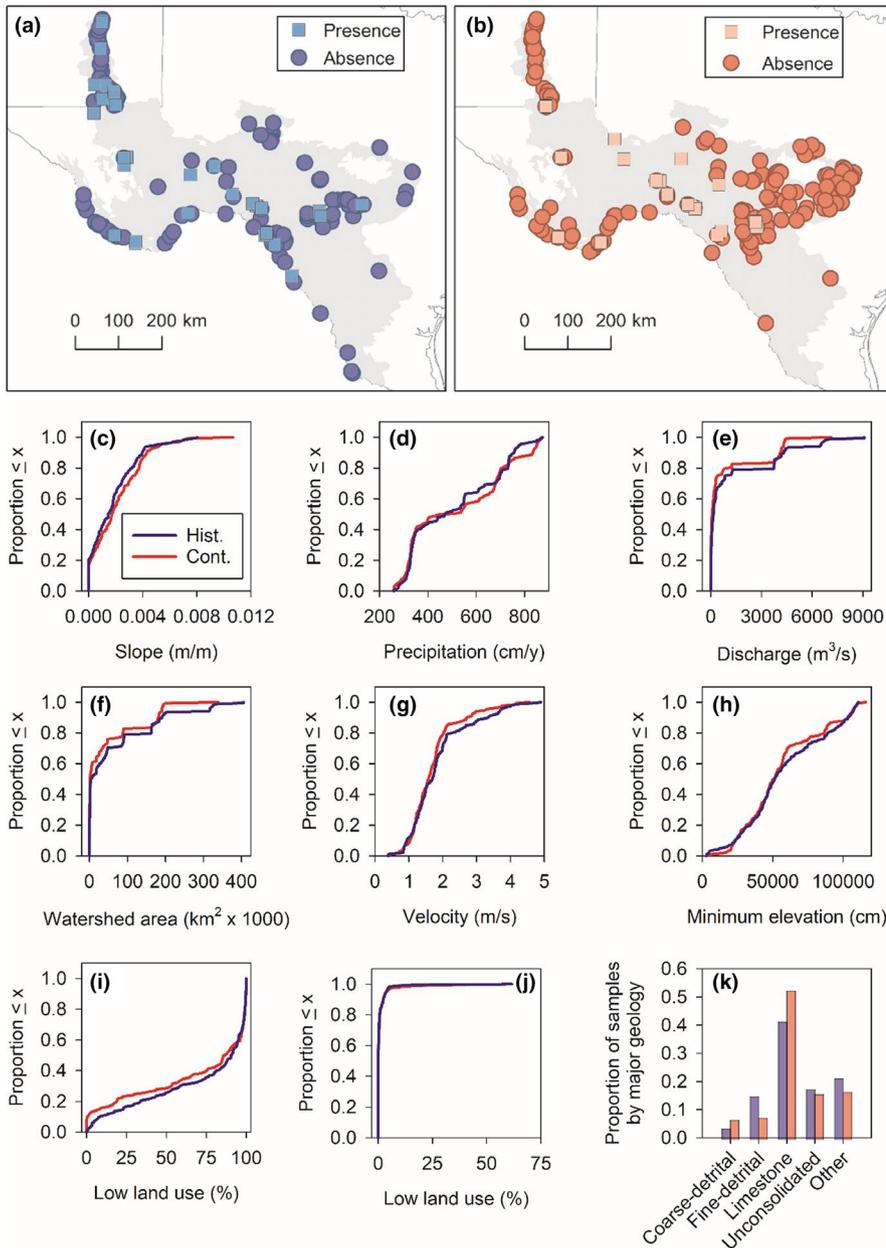
### 3.2 | Molecular markers

Mitochondrial gene sequencing and nuclear SNP analyses facilitated the identification of hybrids, misclassified individuals, and the resolution of genetic structure among populations (Appendix E; Figure 5). Headwater catfish mt-CytB haplotypes were isolated among three regions with no sequence heterogeneity within regions. The three regions included the Pecos River corridor (Delaware River and Independence Creek; Ha1), Balmorhea State Park (Ha2), and the Devils River and Rio Grande tributaries downstream of Amistad Reservoir (Hb; Figure 5a). In contrast, four Channel catfish mt-CytB haplotypes were found with sequence heterogeneity within and among the three regions. Headwater catfish mt-CytB haplotypes were found in isolation (i.e., no Channel catfish present) at Dolan Creek, San Felipe

Creek, Pinto Creek, and Las Moras Creek. Nuclear RAG2 SNPs indicated only Headwater catfish alleles at the Devils River, Dolan Creek, San Felipe Creek, and Las Moras Creek (Figure 5b). The Pecos River corridor, Balmorhea State Park, and two tributaries to the Rio Grande downstream of Amistad (i.e., Cienegas Creek and Pinto Creek) exhibited Channel catfish alleles. Combined mitonuclear genotypes indicated only Headwater catfish at San Felipe Creek, Las Moras Creek, and Dolan Creek (Figure 5c). Non-introgressed Channel catfish samples were only found at Cienegas Creek and the Delaware River, and Channel catfish genotypes out-numbered Headwater catfish genotypes in both locations (including an absence of non-introgressed Headwater Catfish in Cienegas Creek).

### 3.3 | Morphology versus molecular status

Sampling during 2018 yielded 145 catfishes. The canonical discriminant function analysis of phenotype morphology classified 131



**FIGURE 3** Comparison of Headwater catfish sampling locations and environmental gradients for historical (1980–1999; blue) and contemporary (2000–2019; red) periods. Sampling locations for (a) historical and (b) contemporary illustrate presence (squares) and absence (circles) locations within the study area (gray polygon) and geopolitical boundaries (solid lines). Environmental gradients for all sampling locations (presence + absence) during historical (“Hist.”, blue) and contemporary (“Cont.”, red) periods are shown for (c) stream channel slope, (d) annual precipitation, (e) stream discharge, (f) watershed area, (g) velocity, (h) minimum stream channel elevation, (i) per cent of watershed with low use land, (j) per cent of watershed with developed land, and (k) proportion of samples collected over major geology types

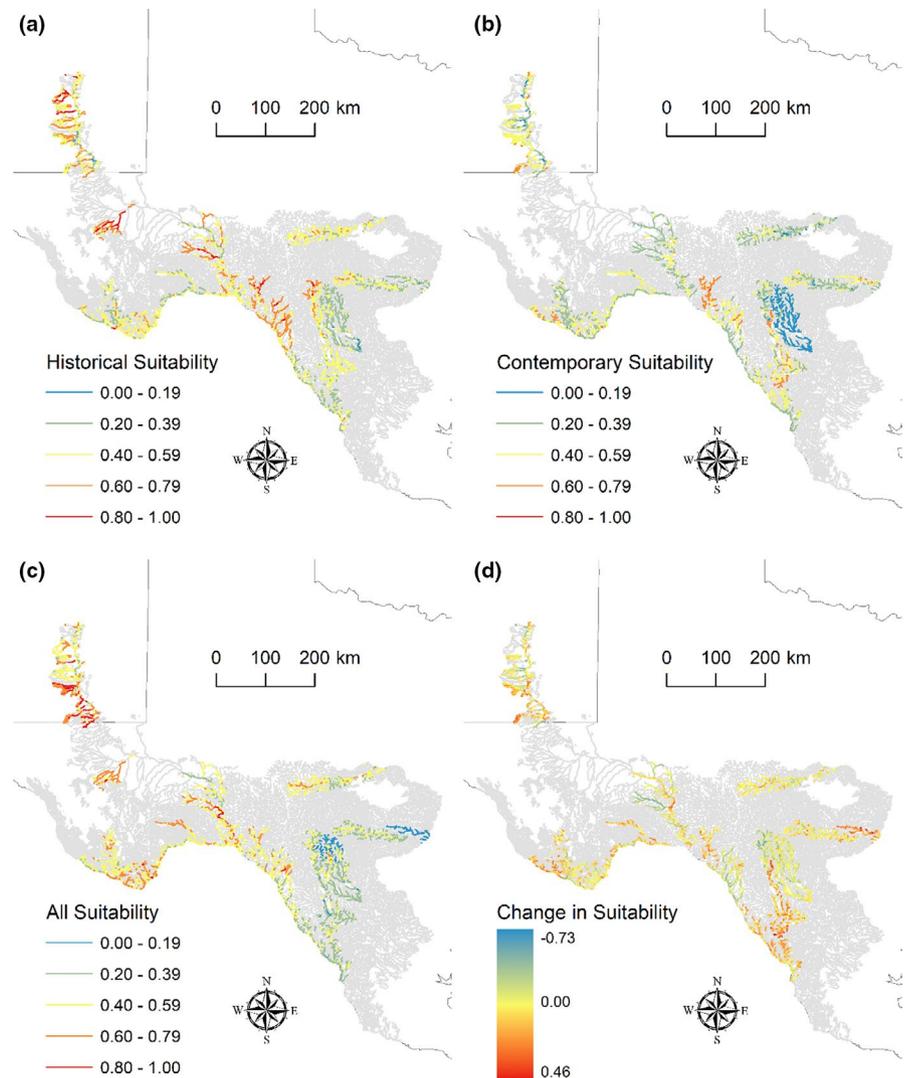
as Headwater catfish and 11 as Channel catfish. Comparison of phenotypic classification with mitonuclear classification indicated congruence in only 43 fish with pure Headwater catfish genotypes. Seventy-six phenotypic Headwater catfish had hybrid genotypes and four phenotypic Headwater catfish had Channel catfish genotypes (Figure 6a). The majority of specimens from Balmorhea State Park had Headwater catfish phenotypes and genotypes; however, seven hybrids (RAG2 heterozygotes) were collected from the canal system during 2017 (Figure 6b). Two Channel catfish and one hybrid were collected from Cienegas Creek (Figure 6c), and a mixture of phenotypes and genotypes were collected from the Delaware River (Figure 6d). Six Headwater catfish with intermediate phenotypes and one hybrid were collected from the Devils River (Figure 6e), six specimens from Dolan Creek had Headwater catfish phenotypes and genotypes (Figure 6f), and Headwater catfish and hybrids, but no Channel catfish, were collected at Independence Creek

(Figure 6g). Two Headwater catfish were collected from Las Moras Creek (Figure 6h), three Headwater catfish and one hybrid were collected from Pinto Creek (Figure 6i) and four Headwater catfish were collected from San Felipe Creek (Figure 6j).

### 3.4 | Conservation prioritization

The conservation prioritization scheme identified priorities based on both habitat suitability and molecular information. The priority ranking for conservation based on combined criteria was (a) Dolan Creek, (b) San Felipe Creek, (c) The Devils River, (d) Pinto Creek, (e) Las Moras Creek, (f) Independence Creek, (g) Delaware River, and (h) Cienegas Creek. The first five locations plotted within the upper right quadrant, indicating high-quality habitat and low levels of introgression (Figure 7). These locations are priorities for preserving

**FIGURE 4** Projections of species distribution models for (a) historical (1980–1999), (b) contemporary (2000–2019), and (c) combined (1980–2019) periods showing predicted suitability for Headwater catfish. (d) Change in suitability (contemporary – historical) illustrates reduced suitability (blue) among headwater streams

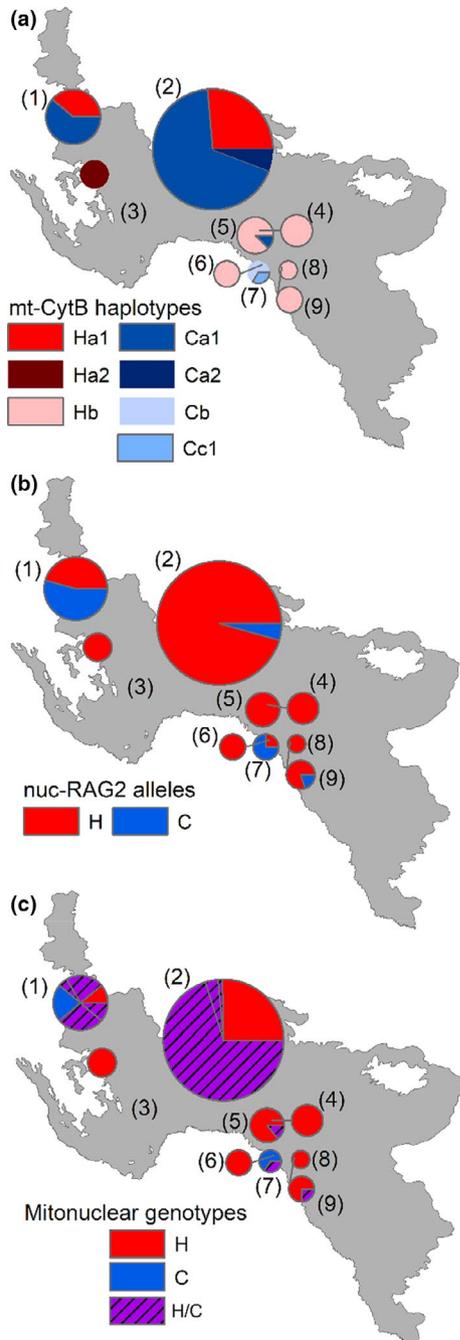


existing conditions; however, each of these sites suffered from low sample sizes for the genetic analysis and should be targeted for future assessments of genetic integrity. Independence Creek and the Delaware River plotted in the lower right quadrant, indicating high-quality habitat but high levels of introgression. Sample sizes at these locations were larger and the habitat in Independence Creek ranked highest among all sites, suggesting this location could be a priority for allocating resources to restoring genetic integrity. Cienegas Creek plotted in the lower left quadrant, indicating low-quality habitat and low genetic integrity (i.e., no Headwater catfish genotypes were recovered).

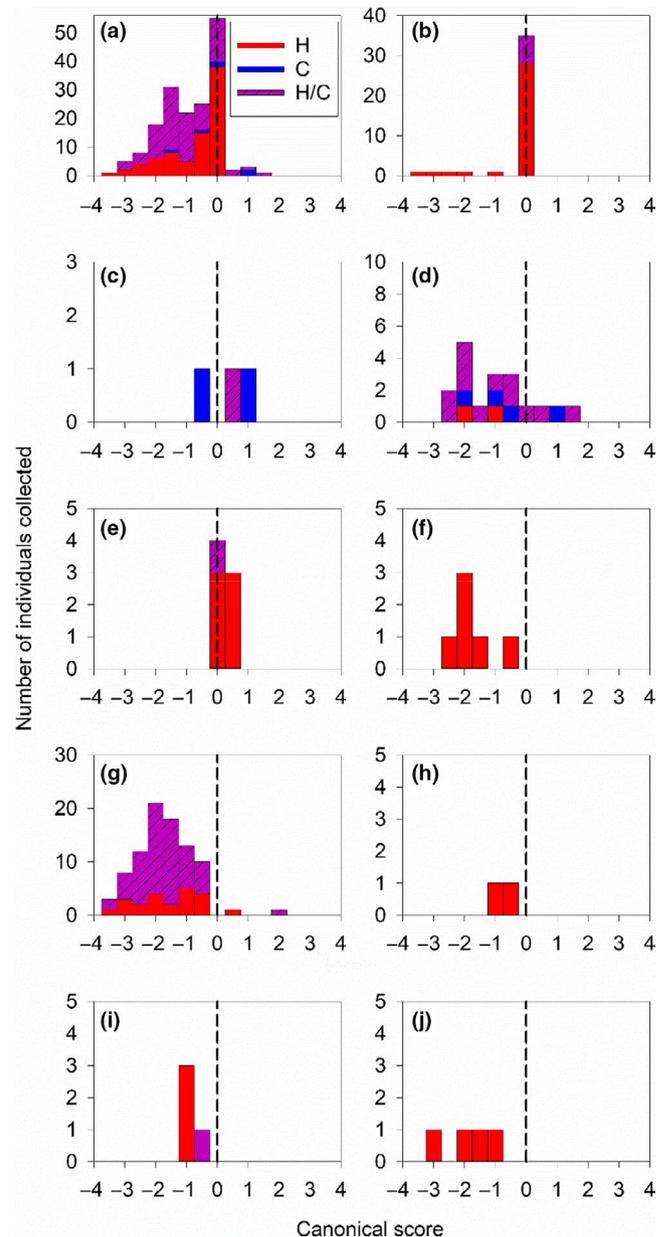
## 4 | DISCUSSION

Our results identified habitats most suitable for Headwater catfish as headwater streams with high elevations, steep slopes, fast current velocities, small watershed areas, low discharges, and with little land development. Our temporal assessment of distribution showed that suitability in these habitats was generally lower in the last 20 years compared with 40 years ago. However, suitability

for Headwater catfish occurrence increased in intermediate sized streams that are the preferred habitat for Channel catfish (Goldstein & Meador, 2004). When and where these species coexist, hybridization and introgression is a consequence. For example, prior to establishment of the Independence Creek preserve, Channel catfish were stocked in nearby ponds (McClure-Baker et al., 2010), and although we found no indication of non-introgressed Channel catfish in our sampling, there was a large number of introgressed Headwater catfish in Independence Creek. We found similar evidence of introgression in the absence of pure Channel catfish genotypes in the Devils River, Pinto Creek, and Balmorhea State Park, and co-occurrence and hybridization with pure Channel catfish genotypes in the Delaware River and Cienegas Creek. Our results thus point to double trouble for Headwater catfish in the United States: declining occurrences in their namesake headwater streams and introgression by Channel catfish among remaining habitats. Fortunately, some high-quality habitats maintain potentially pure populations of Headwater catfish including Dolan Creek, Las Moras Creek, and San Felipe Creek, although larger sample sizes and an increase in the number of loci are needed to confirm the status of those populations.

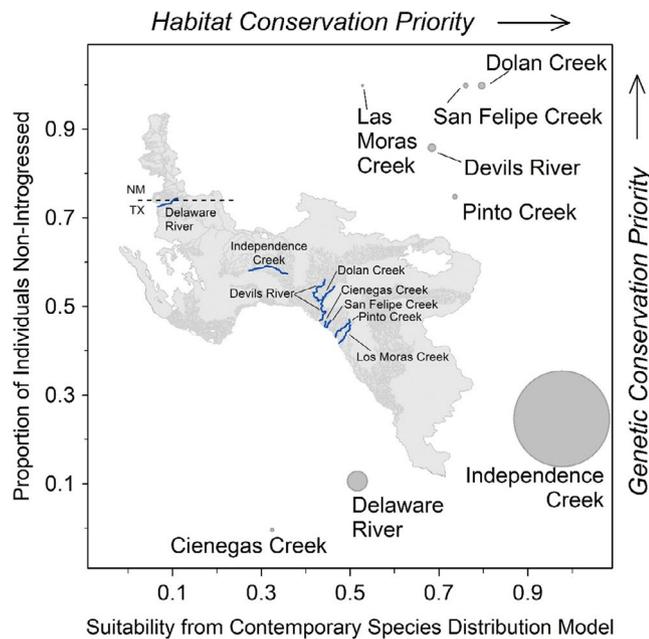


**FIGURE 5** Molecular results from 2018 Headwater catfish surveys showing (a) mitochondrial, (b) nuclear, and (c) mitonuclear results at nine locations. (1) Delaware River, (2) Independence Creek, (3) Balmorhea, (4) Dolan Creek, (5) Devils River, (6) San Felipe Creek, (7) Cienegas Creek, (8) Las Moras Creek, and (9) Pinto Creek. (a) Haplotypes for mt-CytB sequences are shown for Headwater catfish (Ha1, Ha2, Hb; red shades) and Channel catfish (Ca1, Ca2, Cb, Cc1; blue shades) and pie charts (sized according to sample number) show the proportion of individuals with each haplotype. (b) Alleles for nuc-RAG2 gene for Headwater catfish (red) and Channel catfish (blue) with pie charts as in (a). (c) Mitonuclear genotypes are shown for Headwater catfish (H; solid red), Channel catfish (C; solid blue) and mixed genotypes (H/C; hashed purple)



**FIGURE 6** Canonical discriminant function analysis values colour coded by mitonuclear genotypes for specimens from (a) all locations and (b-j) each of nine locations from which tissue samples were collected: (b) Balmorhea State Park, (c) Cienegas Creek, (d) Delaware River, (e) Devils River, (f) Dolan Creek, (g) Independence Creek, (h) Las Moras Creek, (i) Pinto Creek and (j) San Felipe Creek. Canonical scores < 0 represent Headwater catfish and scores > 0 represent Channel catfish. Unmixed Headwater catfish genotypes (H) are shown in red, unmixed Channel catfish genotypes (C) in blue, and mixed genotypes (H/C) in hashed purple. Specimens too small for external morphology analysis or for which only molecular data were available are scored as zero

Habitat degradation and introgression with Channel catfish have caused a decline in the geographic range of Headwater catfish in the United States (Bean et al., 2011; Kelsch & Hendricks, 1990; McClure-Baker et al., 2010). However, identifying the nature of



**FIGURE 7** Conservation prioritization of eight locations based on continuous-scale information from the contemporary species distribution model (x-axis) and molecular results (y-axis). Points are sized according to sample size (larger point = larger sample size) based on sample sizes given in Appendix E. Points are labelled with their associated stream name and the inset map illustrates the locations of each stream

habitat degradation as well as the features that should be conserved is a challenge. Species distribution modelling provides a flexible and comprehensive method to summarize changes in species ranges under predicted or observed environmental change (D'amen et al., 2017), and the results from these models can be used for conservation planning (Malone et al., 2018). Genetic analyses are useful for tracking the locations of introgression, but this approach requires large numbers of specimens and molecular markers. Therefore, we refer to populations where we did not detect introgression with our molecular tools as potentially non-introgressed. When combined, information on habitat and genetic status can be used to prioritize conservation actions, as done here. Our prioritization scheme provides conservation managers with information that can be used in decisions regarding allocation of habitat and/or genetic preservation or restoration resources. Habitat preservation is likely to be critical in the future given locations identified as most suitable for Headwater catfish are threatened by water extractions that could destroy or desiccate existing habitats. Ultimately, successful conservation of Headwater catfish in the United States will require maintenance of both high-quality habitat and ensuring protection from future stockings of Channel catfish.

The range contraction of Headwater catfish previously documented and refined here by ecological modelling illustrates the need to conserve limited perennial water resources in arid riverscapes (Figure 4; Davis et al., 2017). Many tributaries in West Texas have become isolated from larger rivers, and headwater springs that once connected pools and perennial streams have

shrunk to become isolated pools or *ciénegas* (Hoyt, 2002). Habitat loss in the form of declining spring outflows is one of the biggest threats to the species persistence (Bean et al., 2011; Kelsch & Hendricks, 1990). With groundwater declines, flows from headwater springs decrease and, in turn, cause reductions in flow to tributaries that serve as essential habitat for Headwater catfish. For example, Toyah Creek and the surrounding spring-fed system in the vicinity of Balmorhea was once an area of high Headwater catfish occurrence (Kelsch & Hendricks, 1990), but currently the creek is void of surface water due to the overdraft of groundwater and lowering of the water table (Sharp, 2001). Although Toyah Creek is now desiccated, San Solomon Springs in Balmorhea State Park serves as a protected refuge where Headwater catfish persist, among other threatened desert fishes (Comanche Springs pupfish, *Cyprinodon elegans*, and Pecos gambusia, *Gambusia nobilis*). Persistence of Headwater catfish in Balmorhea State Park highlights circumstances in which alteration of habitats for human recreation or domestic water supply result in indirect protection of springs and their biotas (Unmack & Minckley, 2008). Unfortunately, we found evidence of introgression with non-native Channel catfish within Balmorhea State Park. As a second example, Las Moras springs create the headwaters of Las Moras Creek but were converted into a recreational swimming pool in 1971. Just below the dammed pool, we discovered a population of potentially non-introgressed Headwater catfish where no recent records existed (McClure-Baker et al., 2010). Another refuge within highly modified habitats is the San Felipe Country Club golf course where we collected potentially non-introgressed Headwater catfish immediately downstream from the spring outflow. Each of these spring outflows are buffered from land use alterations that influence Headwater catfish distribution because they are close to the location at which water reaches the surface (Saunders et al., 2002). As water flows away from spring outflows, streams become larger, the effects of land use alterations increase, and our work suggests suitability for Headwater catfish declines.

Morphological and molecular information can be used to direct conservation actions targeting preservation of Headwater catfish. There is a high degree of morphological similarity between Headwater catfish, Channel catfish, and their hybrids. Although Kelsch (1995) correctly identified 91% of individuals on the basis of canonical discriminant analyses, only 36% of individuals were correctly identified in this study after we accounted for hybrid individuals. Furthermore, we found some evidence that specimens identified as Channel catfish based on their genotype scored as Headwater catfish based on their phenotype. This suggests that external morphological characters alone are insufficient for species identification in areas where hybrids occur, particularly because hybrids tend to share Headwater catfish phenotypes. Unfortunately, previous records without voucher specimens or voucher specimens that were stored in formalin cannot be accurately assessed for molecular structure; otherwise, these could contribute to unexplained variation in SDMs if species identifications were incorrect (Hermoso et al., 2012; Moritz, 1995).

Identification of Headwater catfish requires the collection and preservation of tissue for molecular analyses to identify hybrid and introgressed individuals (e.g., Ketmaier & Bianco, 2015). These molecular data can also be used to direct repatriation and supplemental stocking locations. We found that mt-CytB haplotypes were not uniformly distributed across the riverscape, namely Ha1 occurred only in tributaries to the Pecos River, Ha2 only at Balmorhea State Park, and Hb in the Devils River, Dolan Creek, and tributaries to the Rio Grande downstream of Amistad Reservoir. Our SDMs suggested high-quality habitats persist in at least one additional tributary to the Pecos River: Live Oak Creek. We were denied access to this stream in our recent sampling, but the species occurred there historically and if future surveys reveal the absence of Headwater catfish and Channel catfish in Live Oak Creek, then this location could represent a candidate repatriation location (e.g., Malone et al., 2018). However, this approach can only proceed after a larger number of diagnostic loci are inspected to assure that only parental individuals are used for recovery (Allendorf et al., 2001). Populations where introgression has taken place should remain areas of conservation priority because they contain unique Headwater catfish phenotypic and even genetic variation within the hybrid genome that should not be disregarded (Demarais et al., 1992; McClure-Baker et al., 2010).

Our use of occurrence records obtained from GBIF paired with remotely sensed environmental predictor variables provided a basis for modelling temporal changes in suitable habitat for Headwater catfish. Although the resulting models provided excellent predictive power, we recognize our projections are subject to some limitations. First, bias in the collection of species occurrence records could result in model predictions that are biased towards environments that have received more intense sampling (Araújo & Guisan, 2006). This issue confounds temporal shifts in species distribution because differences between historical and contemporary time periods could be due to either shifts in species distributions or shifts in the areas sampled. We addressed this issue by considering differences in environmental gradients sampled during each period. Our results suggested similar geographic regions and environmental gradients were sampled during each period, and thus, changes in suitability through time were likely reflective of decline in occurrence of Headwater catfish as opposed to sampling bias. Second, GBIF data represent occurrence-only records and therefore limit the use of presence-absence modelling, a method demonstrated to be more accurate compared with presence-only modelling (Elith et al., 2006). We addressed the issue of no absence data by assigning TGA identified as sites where Channel catfish but not Headwater catfish were collected (Mateo et al., 2010). However, there is potential risk when assigning this method because of the possibility to falsely identify Headwater catfish. Species misidentification may act to contract or expand the predicted distribution of the target species and should not be neglected (Costa et al., 2015). We also point out that the degree to which competition between Channel catfish and Headwater catfish influences the range of Headwater catfish may be worth exploring for future SDMs (Araújo & Guisan, 2006). Third, SDMs

should be interpreted as predictions of potential habitat that are useful as guiding information for conservation planning, but occurrences outside of the predicted areas are still possible. Recent documented occurrence of Headwater catfish in the Frio River where the species was previously believed to be extirpated (Bean et al., 2011) illustrates that the species may persist (though at low densities) in other areas of the riverscape not identified in our SDMs. In addition, low detection among commonly used gears (e.g., seines) could result in potential false negatives among sites with high probability of occurrence (Budy et al., 2015). Finally, our predictions rely on the assumption that current modelled environmental conditions are the primary drivers of Headwater catfish distributions and that these relationships will persist in the future (Araújo et al., 2005; Guisan & Thuiller, 2005). Other environmental variables might be identified and could be included in future research of Headwater catfish distribution. Significant habitat alterations in portions of the study area make Headwater catfish persistence unlikely in some locations (e.g., the now desiccated Toyah Creek), and further repeated surveys are necessary before local extinctions can be confirmed in these locations.

Systematic conservation planning informs decision-makers of the most effective and efficient ways to achieve conservation goals (Hermoso et al., 2015). Our study approach demonstrates the potential for using systematic methods for conservation planning in freshwater ecosystems to identify appropriate habitats and the most likely current distribution of Headwater catfish. The SDMs and molecular assessment provided here will aid in focusing rehabilitation and conservation efforts in priority areas (e.g., Figure 7), as well as other portions of the lower Pecos River and isolated spring habitats. Our work has implications for policies that have already benefited conservation and management of Headwater catfish. Specifically, information from this study, previous studies (Bean et al., 2011; McClure-Baker et al., 2010), and recent status assessments were used to update the Texas Parks and Wildlife Department's State Threatened and Endangered Species list. Headwater catfish was one of 16 fish species that were approved for listing as State Threatened by the TPWD Commission. The Texas Parks and Wildlife Department will continue to work with private landowners on voluntary habitat management practices that will benefit Headwater catfish and work with landowners to voluntarily conserve land through conservation easements (i.e., through the Texas Farm and Ranch Land Conservation Program). The Texas Parks and Wildlife Department has also been partnering with the National Fish and Wildlife Foundation to support habitat conservation and research priorities through the Pecos Watershed Conservation Initiative, including areas identified in this study as important to Headwater catfish persistence. In addition to voluntary conservation actions, the elevated conservation status of Headwater catfish means that The Texas Parks and Wildlife Department can also protect the species by limiting stocking in areas where Headwater catfish persist and setting special considerations during permitting of projects that involve habitat destruction or alteration with a restitution value of \$500 per individual that is destroyed.

This study represents the most recent evaluation of Headwater catfish distribution in the United States, but conservation status in Mexico requires additional research. Alterations to headwater habitats in our study area are consistent with global threats to freshwater biodiversity (Dudgeon et al., 2006), and we expect similar threats exist for Headwater catfish in Mexico and closely related *Ictalurus* spp. elsewhere. For example, Yaqui catfish *Ictalurus pricei* (Rutter, 1896) is on a trajectory towards extinction in the United States because of declining spring flows, reduced surface waters, competition with non-native species, and loss of genetic integrity due to hybridization and introgression with introduced species (Stewart et al., 2017). Similar detrimental effects of human alterations to riverscapes on native freshwater fish species distributions are documented on a global scale using methods similar to our approach, including fishes in the families Salmonidae (McKelvey et al., 2016), Centrarchidae (Alvarez et al., 2015; Koppelman & Garrett, 2002; Taylor et al., 2018), and Cyprinidae (Pyke, 2008; Wilde & Echelle, 1992). For these and other species, maintaining balance between watershed management for natural resources and human usages remains a significant challenge, especially considering the future projections for water availability (Rodell et al., 2018). Even among larger municipalities in the American Southwest where there is a reasonably strong message of water conservation, the surrounding rural areas show signs of increasing agricultural production and water consumption (Edwards et al., 2002, 2004). These conservation circumstances require broad views of the needs of humans and nature, views that come from integrated approaches such as the formation of Native Fish Conservation Areas (NFCAs, James, 2011; Williams et al., 2011). Our research provides context for the geographic overlap between Headwater catfish distribution and recently developed NCFAs in the Chihuahua Desert region of United States (Garrett et al., 2019). Overall, this information can be used by natural resource managers to direct preservation of existing populations and potentially future restoration of populations where they have been lost.

## ACKNOWLEDGEMENTS

We thank P. Bean, K. Conway and X. Wu for comments on earlier versions of this manuscript. C. Corrington, J. Heitiko, R. Loveland and J. Ecker provided valuable assistance with data collection. We thank the Texas Parks and Wildlife Department, The Nature Conservancy, Big Bend National Park, and Devils River State Natural Area, Big Bend Ranch State Park for logistic support and stream access. Financial support for this research was provided by the Texas Parks and Wildlife Department through the State Wildlife Grant Program (Grant # TX-T-183-R-1) and the USDA National Institute of Food and Agriculture (HATCH Project 1017538). All specimens were collected using equipment and procedures approved by the Texas Parks and Wildlife Department (permit SPR-0218-068), the National Park Service (permit BIBE-2018-SCI-0022), and the Texas A&M University Animal Care and Use Committee (protocol IACUC 2018-0059).

## AUTHOR CONTRIBUTIONS

S.D.P and J.S.P conceived the ideas; S.D.P, J.S.P, and M.B collected data in fieldwork, D.L.C conducted molecular analyses, S.D.P, J.S.P, and M.R.A. analysed the data. All co-authors wrote portions of the manuscript.

## DATA AVAILABILITY STATEMENT

Datasets generated during the production of this study are available from the corresponding author upon reasonable request.

## ORCID

Joshuah S. Perkin  <https://orcid.org/0000-0003-4928-9178>

## REFERENCES

- Aerts, R., & Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning. *BMC Ecology*, 11(1), 29. <https://doi.org/10.1186/1472-6785-11-29>
- Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids: Setting conservation guidelines. *Trends in Ecology & Evolution*, 16(11), 613–622. [https://doi.org/10.1016/S0169-5347\(01\)02290-X](https://doi.org/10.1016/S0169-5347(01)02290-X)
- Alvarez, A. C., Peterson, D. O. U. G. L. A. S., Taylor, A. T., Tringali, M. D., & Barthel, B. L. (2015). Distribution and amount of hybridization between Shoal Bass and the invasive Spotted Bass in the lower Flint River, Georgia. In *Black bass diversity: Multidisciplinary science for conservation. American Fisheries Society, Symposium*, 82, 503–521.
- Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33(10), 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, 11(9), 1504–1513. <https://doi.org/10.1111/j.1365-2486.2005.01000.x>
- Araújo, M. B., & Williams, P. H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, 96(3), 331–345. [https://doi.org/10.1016/S0006-3207\(00\)00074-4](https://doi.org/10.1016/S0006-3207(00)00074-4)
- Argue, B. J., & Dunham, R. A. (1999). Hybrid fertility, introgression, and backcrossing in fish. *Reviews in Fisheries Science*, 7(3–4), 137–195. <https://doi.org/10.1080/10641269908951360>
- Arlinghaus, R., Lorenzen, K., Johnson, B. M., Cooke, S. J., & Cowx, I. G. (2016). Management of freshwater fisheries: Addressing habitat, people and fishes. *Freshwater Fisheries Ecology*, 1, 557–579.
- Barmuta, L. A., Linke, S., & Turak, E. (2011). Bridging the gap between ‘planning’ and ‘doing’ for biodiversity conservation in freshwaters. *Freshwater Biology*, 56(1), 180–195. <https://doi.org/10.1111/j.1365-2427.2010.02514.x>
- Bean, P. T., Jackson, J. T., McHenry, D. J., Bonner, T. H., & Forstner, M. R. (2011). Rediscovery of the headwater catfish *Ictalurus lupus* (Ictaluridae) in a western Gulf-Slope drainage. *The Southwestern Naturalist*, 56(2), 285–289. <https://doi.org/10.1894/N10-RJE-08.1>
- Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, 19, 10–15. <https://doi.org/10.1016/j.ecoinf.2013.11.002>
- Benke, A. C., & Cushing, C. E. (Eds.) (2011). *Rivers of North America*. Academic Press.
- Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., & Wheeler, D. L. (2005). Genbank. *Nucleic Acids Research*, 1(33), D34–38.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45(1), 5–32.
- Budy, P., Conner, M. M., Salant, N. L., & Macfarlane, W. W. (2015). An occupancy-based quantification of the highly imperiled status of desert

- fishes of the southwestern United States. *Conservation Biology*, 29(4), 1142–1152. <https://doi.org/10.1111/cobi.12513>
- Cambrey, J. A. (2003). Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. *Hydrobiologia*, 500(1–3), 217–230. <https://doi.org/10.1023/A:1024648719995>
- Chafin, T. K., Douglas, M. R., Martin, B. T., & Douglas, M. E. (2019). Hybridization drives genetic erosion in sympatric desert fishes of western North America. *Heredity*, 123(6), 759–773. <https://doi.org/10.1038/s41437-019-0259-2>
- Chawla, N. V., Bowyer, K. W., Hall, L. O., & Kegelmeyer, W. P. (2002). SMOTE: Synthetic minority over-sampling technique. *Journal of Artificial Intelligence Research*, 16, 321–357. <https://doi.org/10.1613/jair.953>
- Contreras-Balderas, S., & Escalante, M. A. (1984). Distribution and known impacts of exotic fishes in Mexico. In W. R. Courtenay, & J. R. Stauffer (Eds.), *Distribution, biology, and management of exotic fishes* (pp. 102–130). Johns Hopkins University Press.
- Cooke, S. J., Bunt, C. M., Hamilton, S. J., Jennings, C. A., Pearson, M. P., Cooperman, M. S., & Markle, D. F. (2005). Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: Insights from regional case studies of a diverse family of non-game fishes. *Biological Conservation*, 121(3), 317–331. <https://doi.org/10.1016/j.biocon.2004.05.015>
- Cooper, A. R., Infante, D. M., Daniel, W. M., Wehrly, K. E., Wang, L., & Brenden, T. O. (2017). Assessment of dam effects on streams and fish assemblages of the conterminous USA. *Science of the Total Environment*, 586, 879–889. <https://doi.org/10.1016/j.scitotenv.2017.02.067>
- Costa, H., Foody, G. M., Jiménez, S., & Silva, L. (2015). Impacts of species misidentification on species distribution modeling with presence-only data. *ISPRS International Journal of Geo-Information*, 4(4), 2496–2518. <https://doi.org/10.3390/ijgi4042496>
- D'Amen, M., Rahbek, C., Zimmermann, N. E., & Guisan, A. (2017). Spatial predictions at the community level: From current approaches to future frameworks. *Biological Reviews*, 92(1), 169–187. <https://doi.org/10.1111/brv.12222>
- Davis, J. A., Kerezy, A., & Nicol, S. (2017). Springs: Conserving perennial water is critical in arid landscapes. *Biological Conservation*, 211, 30–35. <https://doi.org/10.1016/j.biocon.2016.12.036>
- Demarais, B. D., Dowling, T. E., Douglas, M. E., Minckley, W. L., & Marsh, P. C. (1992). Origin of *Gila seminuda* (Teleostei: Cyprinidae) through introgressive hybridization: Implications for evolution and conservation. *Proceedings of the National Academy of Sciences*, 89(7), 2747–2751. <https://doi.org/10.1073/pnas.89.7.2747>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81(2), 163–182. <https://doi.org/10.1017/S1464793105006950>
- Echelle, A. A. (1991). Conservation genetics and genic diversity in freshwater fishes of western North America. In W. L. Minckley, & J. E. Deacon (Eds.), *Battle against extinction: Native fish management in the American west* (pp. 141–153). University of Arizona Press.
- Edwards, R. J., Garrett, G. P., & Allan, N. L. (2004). *Aquifer-dependent fishes of the Edwards Plateau region. Aquifers of the Edwards Plateau* (pp. 253–268). Texas Water Development Board.
- Edwards, R. J., Garrett, G. P., & Marsh-Matthews, E. (2002). Conservation and status of the fish communities inhabiting the Rio Conchos basin and middle Rio Grande, Mexico and USA. *Reviews in Fish Biology and Fisheries*, 12(2–3), 119–132.
- Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., ... E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Environmental Protection Agency (EPA), United States Geological Survey (USGS), Horizon Systems Corporations (2010). *Database: NHDplusV1 Data*. Retrieved from <http://www.horizon-systems.com/nhdplus/data.php>
- Environmental Protection Agency (EPA), United States Geological Survey (USGS), Horizon Systems Corporations (2012). *Database: NHDplusV2 Data*. Retrieved from [http://www.horizon-systems.com/nhdplus/NHDplusV2\\_data.php](http://www.horizon-systems.com/nhdplus/NHDplusV2_data.php)
- Epifanio, J., & Nielsen, J. (2000). The role of hybridization in the distribution, conservation and management of aquatic species. *Reviews in Fish Biology and Fisheries*, 10(3), 245–251.
- Erős, T., O'Hanley, J. R., & Czeglédi, I. (2018). A unified model for optimizing riverscape conservation. *Journal of Applied Ecology*, 55(4), 1871–1883. <https://doi.org/10.1111/1365-2664.13142>
- Evans, J. S., & Murphy, M. A. (2018). *rUtilities: Random forests model selection and performance evaluation*. R package version 1.0–2, <http://cran.r-project.org/pack-ages=rUtilities>
- Falcone, J. A. (2015). *U.S. conterminous wall-to-wall anthropogenic land use trends (NWALT), 531 1974–2012: U.S. Geological Survey Data Series 948, 33 p.* plus appendixes 3–6 as 532 separate files. Available at: doi: 10.3133/ds948.
- Fitzpatrick, B. M., Ryan, M. E., Johnson, J. R., Corush, J., & Carter, E. T. (2015). Hybridization and the species problem in conservation. *Current Zoology*, 61(1), 206–216. <https://doi.org/10.1093/czoolo/61.1.206>
- Frimpong, E. A., Sutton, T. M., Lim, K. J., Hrodey, P. J., Engel, B. A., Simon, T. P., Lee, J. G., & Le Master, D. C. (2005). Determination of optimal riparian forest buffer dimensions for stream biota landscape association models using multimetric and multivariate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(1), 1–6. <https://doi.org/10.1139/f05-020>
- Garrett, G. P., Birdsong, T. W., Bean, M. G., & Labay, B. J. (2019). Chihuahuan desert native fish conservation areas: A multispecies and watershed approach to preservation of freshwater fish diversity. In D. C. Dauwalter, T. W. Birdsong, & G. P. Garrett (Eds.), *Multispecies and watershed approaches to freshwater fish conservation* (pp. 231–252). American Fisheries Society, Symposium 91.
- Gilbert, C. R., & Burgess, G. H. (1980). *Ictalurus lupus* (Girard), headwater catfish. In D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, & J. R. Stauffer Jr (1980). *Atlas of North American freshwater fishes* (pp. 146). : North Carolina State Museum of Natural History.
- Global Biodiversity Information Facility (GBIF). (2019a). *Ictalurus lupus* (Girard, 1858), GBIF.org (04 June 2019) GBIF Occurrence Download <https://doi.org/10.15468/dl.9atm8k>
- Global Biodiversity Information Facility (GBIF). (2019b). *Ictalurus punctatus* (Rafinesque, 1818), GBIF.org (04 June 2019) GBIF Occurrence Download <https://doi.org/10.15468/dl.ijkiaj>
- Goldstein, R. M., & Meador, M. R. (2004). Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society*, 133(4), 971–983. <https://doi.org/10.1577/T03-080.1>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Harrison, R. G., & Larson, E. L. (2014). Hybridization, introgression, and the nature of species boundaries. *Journal of Heredity*, 105(S1), 795–809. <https://doi.org/10.1093/jhered/esu033>
- Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, 84(1), 39–54. <https://doi.org/10.1111/j.1469-185X.2008.00060.x>

- Heitmuller, F. T., & Reece, B. D. (2003). *Database of historically documented springs and spring flow measurements in Texas: U.S. Geological Survey Open-File Report 03-315*. Available for download through Databasin.org [accessed May 8 2018]
- Hermoso, V., Abell, R., Linke, S., & Boon, P. (2016). The role of protected areas for freshwater biodiversity conservation: Challenges and opportunities in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(S1), 3–11. <https://doi.org/10.1002/aqc.2681>
- Hermoso, V., Kennard, M. J., & Linke, S. (2012). Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. *Diversity and Distributions*, 18(5), 448–458. <https://doi.org/10.1111/j.1472-4642.2011.00879.x>
- Hermoso, V., Linke, S., Januchowki-Hartley, S. R., & Kennard, M. J. (2015). Freshwater conservation planning. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of Freshwater Fishes* (pp. 437–466). Cambridge University Press.
- Hoyt, C. A. (2002). The chihuahuan desert. *Endangered Species Bulletin*, 27, 3–6.
- Huang, J., & Frimpong, E. A. (2015). Using historical atlas data to develop high-resolution distribution models of freshwater fishes. *PLoS One*, 10(6), e0129995. <https://doi.org/10.1371/journal.pone.0129995>
- Hubbs, C., Edwards, R. J., & Garrett, G. P. (2008). *An annotated checklist of the freshwater fishes of Texas, with keys to identification of species*. Second Edition. Texas Journal of Science.
- James, J. J., Sheley, R. L., Erickson, T., Rollins, K. S., Taylor, M. H., & Dixon, K. W. (2013). A systems approach to restoring degraded drylands. *Journal of Applied Ecology*, 50(3), 730–739. <https://doi.org/10.1111/1365-2664.12090>
- James, R. (2011). Native fish conservation areas: A vision for large-scale conservation of native fish communities. *Fisheries*, 36(6), 267–277.
- Jelks, H. L., Walsh, S. J., Burkhead, N. M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., Lyons, J., Mandrak, N. E., McCormick, F., Nelson, J. S., Platania, S. P., Porter, B. A., Renaud, C. B., Schmitter-Soto, J. J., Taylor, E. B., & Warren, M. L. (2008). Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, 33(8), 372–407. <https://doi.org/10.1577/1548-8446-33.8.372>
- Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmschurst, J. M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, 356(6335), 270–275.
- Kelsch, S. W. (1995). Patterns of morphometric variation in the channel and headwater catfishes. *Transactions of the American Fisheries Society*, 124(2), 272–279. [https://doi.org/10.1577/1548-8659\(1995\)124<0272:POMVIT>2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124<0272:POMVIT>2.3.CO;2)
- Kelsch, S. W., & Hendricks, F. S. (1986). An electrophoretic and multivariate morphometric comparison of the American catfishes *Ictalurus lupus* and *I. punctatus*. *Copeia*, 646–652. <https://doi.org/10.2307/1444946>
- Kelsch, S. W., & Hendricks, F. S. (1990). Distribution of the Headwater Catfish *Ictalurus lupus* (Osteichthyes: Ictaluridae). *The Southwestern Naturalist*, 35(3), 292–297. <https://doi.org/10.2307/3671942>
- Ketmaier, V., & Bianco, P. G. (2015). Understanding and conserving genetic diversity in a world dominated by alien introductions and native transfers: The case study of primary and peripheral freshwater fishes in southern Europe. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of Freshwater Fishes* (pp. 506–534). Cambridge University Press.
- Koppelman, J. B., & Garrett, G. P. (2002). Distribution, biology, and conservation of the rare black bass species. *American Fisheries Society Symposium*, 31, 333–341.
- Leroy, B., Delsol, R., Hugué, B., Meynard, C. N., Barhoumi, C., Barbet-Massin, M., & Bellard, C. (2018). Without quality presence-absence data, discrimination metrics such as TSS can be misleading measures of model performance. *Journal of Biogeography*, 45(9), 1994–2002.
- Liaw, A., & Wiener, M. (2002). Classification and Regression by random forest. *R News*, 2(3), 18–22.
- Lutz-Carrillo, D. J., Thibodeaux, C., Elliott, M., Rathjen, N. A., Kittel, C., Fries, L. T., & Garrett, G. P. (2015). Inferred reproductive behavior of captive Guadalupe Bass. M. D. Tringali, J. M. Long, T. M. Birdsong, & M. J. Allen (Eds.), *Black bass diversity: multidisciplinary science for conservation*. (pp. 549–583). : American Fisheries Society, Symposium 82.
- Maher, J. M., Markey, J. C., & Ebert-May, D. (2013). The other half of the story: Effect size analysis in quantitative research. *Cbe—life Sciences Education*, 12(3), 345–351. <https://doi.org/10.1187/cbe.13-04-0082>
- Malone, E. W., Perkin, J. S., Leckie, B. M., Kulp, M. A., Hurt, C. R., & Walker, D. M. (2018). Which species, how many, and from where: Integrating habitat suitability, population genomics, and abundance estimates into species reintroduction planning. *Global Change Biology*, 24(8), 3729–3748. <https://doi.org/10.1111/gcb.14126>
- Mateo, R. G., Croat, T. B., Felicísimo, Á. M., & Muñoz, J. (2010). Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Diversity and Distributions*, 16(1), 84–94. <https://doi.org/10.1111/j.1472-4642.2009.00617.x>
- McClure-Baker, S. A., Echelle, A. A., Van den Bussche, R. A., Echelle, A. F., Hendrickson, D. A., & Garrett, G. P. (2010). Genetic status of headwater catfish in Texas and New Mexico: A perspective from mtDNA and morphology. *Transactions of the American Fisheries Society*, 139(6), 1780–1791. <https://doi.org/10.1577/T10-009.1>
- McKee, J. K., Sciulli, P. W., Foose, C. D., & Waite, T. A. (2004). Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, 115(1), 161–164. [https://doi.org/10.1016/S0006-3207\(03\)00099-5](https://doi.org/10.1016/S0006-3207(03)00099-5)
- McKelvey, K. S., Young, M. K., Wilcox, T. M., Bingham, D. M., Pilgrim, K. L., & Schwartz, M. K. (2016). Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams. *Ecology and Evolution*, 6(3), 688–706. <https://doi.org/10.1002/ece3.1887>
- Meffe, G. K., & Vrijenhoek, R. C. (1988). Conservation genetics in the management of desert fishes. *Conservation Biology*, 2(2), 157–169. <https://doi.org/10.1111/j.1523-1739.1988.tb00167.x>
- Miller, R. R., Minckley, W. L., Norris, S. M., & Gach, M. H. (2005). *Freshwater fishes of Mexico* (No. QL 629. M54 2005). : University of Chicago Press.
- Moritz, C. (1995). Uses of molecular phylogenies for conservation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 349(1327), 113–118.
- Moyle, P. B., & Leidy, R. A. (1992). Loss of biodiversity in aquatic ecosystems: Evidence from fish faunas. In *Conservation biology* (pp. 127–169). : Springer.
- Murray, B. B. R., Zeppel, M. J., Hose, G. C., & Eamus, D. (2003). Groundwater-dependent ecosystems in Australia: It's more than just water for rivers. *Ecological Management & Restoration*, 4(2), 110–113. <https://doi.org/10.1046/j.1442-8903.2003.00144.x>
- Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., & Senior, A. M. (2015). Meta-analysis of variation: Ecological and evolutionary applications and beyond. *Methods in Ecology and Evolution*, 6(2), 143–152. <https://doi.org/10.1111/2041-210X.12309>
- Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. *Environmental Management*, 54(6), 1249–1266. <https://doi.org/10.1007/s00267-014-0364-1>
- Orians, G. H. (1995). Thought for the morrow: Cumulative threats to the environment. *Environment: Science and Policy for Sustainable Development*, 37(7), 6–36.
- Perkin, J. S., Gibbs, K. W., Ridgway, J., & Cook, S. B. (2019). Riverscape correlates for distribution of threatened spotfin chub (*Erimonax monachus*) in the Tennessee River Basin, USA. *Endangered Species Research*, 40, 91–105.

- Perkin, J. S., Gido, K. B., Costigan, K. H., Daniels, M. D., & Johnson, E. R. (2015). Fragmentation and drying ratchet down Great Plains stream fish diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25(5), 639–655. <https://doi.org/10.1002/aqc.2501>
- Perkin, J. S., Gido, K. B., Falke, J. A., Fausch, K. D., Crockett, H., Johnson, E. R., & Sanderson, J. (2017). Groundwater declines are linked to changes in Great Plains stream fish assemblages. *Proceedings of the National Academy of Sciences*, 114(28), 7373–7378. <https://doi.org/10.1073/pnas.1618936114>
- Perkin, J. S., Murphy, S. P., Murray, C. M., Gibbs, W. K., & Gebhard, A. E. (2019). If you build it, they will go: A case study of stream fish diversity loss in an urbanizing riverscape. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(4), 623–638. <https://doi.org/10.1002/aqc.3090>
- Perkin, J. S., Starks, T. A., Pennock, C. A., Gido, K. B., Hopper, G. W., & Hedden, S. C. (2019). Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecology*, 100(6), e2120. <https://doi.org/10.1002/eco.2120>
- Perkin, J. S., Wellemeier, J. C., & Fore, J. D. (2019). *Multiscale fish assemblage distribution models to guide riverscape conservation planning*. In *Advanced in Understanding Landscape Influences on Freshwater Habitats and Biological Assemblages* (pp. 409–440). American Fisheries Society Symposium 90.
- Poiani, K. A., Richter, B. D., Anderson, M. G., & Richter, H. E. (2000). Biodiversity conservation at multiple scales: Functional sites, landscapes, and networks. *BioScience*, 50(2), 133–146. [10.1641/0006-3568\(2000\)050\[0133:BCAMSF\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0133:BCAMSF]2.3.CO;2)
- Possingham, H. P., Bode, M., & Klein, C. J. (2015). Optimal conservation outcomes require both restoration and protection. *PLoS Biology*, 13(1), e1002052.
- Pyke, G. H. (2008). Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. *Annual Review of Ecology, Evolution, and Systematics*, 39, 171–191.
- R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. <https://doi.org/10.1111/brv.12480>
- Rodell, M., Famiglietti, J. S., Wiese, D. N., Reager, J. T., Beaudoin, H. K., Landerer, F. W., & Lo, M. H. (2018). Emerging trends in global freshwater availability. *Nature*, 557(7707), 651–659.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., & Leemans, R. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774.
- Saunders, D. L., Meeuwig, J. J., & Vincent, A. C. J. (2002). Freshwater protected areas: Strategies for conservation. *Conservation Biology*, 16(1), 30–41. <https://doi.org/10.1046/j.1523-1739.2002.99562.x>
- Schmutz, S., & Jungwirth, M. (1999). Fish as indicators of large river connectivity: the Danube and its tributaries. *River Systems*, 115(3), 329–348. <https://doi.org/10.1127/lr/11/1999/329>
- Schruben, P. G., Arndt, R. E., Bawiec, W. J., King, P. B., & Beikman, H. M. (1994). Geology of the Conterminous United States at 1:2,500,000 Scale -- A Digital Representation of the 1974 P.B. King and H.M. Beikman Map: U.S. Geological Survey Digital Data Series DDS-11, U.S. Geological Survey, Reston, VA. Available at: <https://mrdata.usgs.gov/geology/us/>
- Sharp, J. M. Jr (2001). Regional groundwater flow systems in Trans-Pecos Texas. *Texas Water Development Board Report*, 356(356), 41–55.
- Souza, V., Espinosa-Asuar, L., Escalante, A. E., Eguiarte, L. E., Farmer, J., Forney, L., Lloret, L., Rodriguez-Martinez, J. M., Soberon, X., Dirzo, R., & Elser, J. J. (2006). An endangered oasis of aquatic microbial biodiversity in the Chihuahuan desert. *Proceedings of the National Academy of Sciences*, 103(17), 6565–6570. <https://doi.org/10.1073/pnas.0601434103>
- Stewart, D. R., Butler, M. J., Harris, G., & Radke, W. R. (2017). Mark-recapture models identify imminent extinction of Yaqui catfish *Ictalurus pricei* in the United States. *Biological Conservation*, 209, 45–53. <https://doi.org/10.1016/j.biocon.2017.02.010>
- Strahler, A. N. (1957). Quantitative analysis of watershed geomorphology. *Eos, Transactions American Geophysical Union*, 38(6), 913–920. <https://doi.org/10.1029/TR038i006p00913>
- Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), 344–358. <https://doi.org/10.1899/08-171.1>
- Sublette, J. E., Hatch, M. D., & Sublette, M. (1990). *The fishes of New Mexico*. University of New Mexico Press.
- Taylor, A. T., Tringali, M. D., O'Rourke, P. M., & Long, J. M. (2018). Shoal Bass Hybridization in the Chattahoochee River Basin near Atlanta, Georgia. *Journal of Southeastern Association of Fish and Wildlife Agencies*, 5, 1–9.
- Thuiller, W., Lavorel, S., & Araújo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14(4), 347–357. <https://doi.org/10.1111/j.1466-822X.2005.00162.x>
- Torgo, L. (2011). *Data mining with R: Learning with case studies*. (pp. 33487–2742). Boca Raton, FL: Chapman and Hall/CRC Press.
- Turak, E., Harrison, I., Dudgeon, D., Abell, R., Bush, A., Darwall, W., Finlayson, C. M., Ferrier, S., Freyhof, J., Hermoso, V., Juffe-Bignoli, D., Linke, S., Nel, J., Patricio, H. C., Pittock, J., Raghavan, R., Revenga, C., Simaika, J. P., & De Wever, A. (2017). Essential biodiversity variables for measuring change in global freshwater biodiversity. *Biological Conservation*, 213, 272–279. <https://doi.org/10.1016/j.biocon.2016.09.005>
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- United States Department of Agriculture-Natural Resources Conservation Service (USDA-NRCS), the United States Geological Survey (USGS), and the Environmental Protection Agency (EPA). (2015). *Watershed boundary dataset for Texas and New Mexico*. Retrieved from <https://databasin.org/datasets/f57141fecb9849bfa7ccd6ad6634c118>
- Unmack, P. J., & Minckley, W. L. (2008). *The demise of desert springs. Aridland springs in North America: Ecology and conservation* (pp. 11–34). University of Arizona Press.
- Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467(7315), 555. <https://doi.org/10.1038/nature09440>
- Waldbeiser, G. C., Bilodeau, A. L., & Nonneman, D. J. (2003). Complete sequence and characterization of the Channel Catfish mitochondrial genome. *DNA Sequence*, 14(4), 265–277. <https://doi.org/10.1080/1042517031000149057>
- Ward, F. A., Booker, J. F., & Michelsen, A. M. (2006). Integrated economic, hydrologic, and institutional analysis of policy responses to mitigate drought impacts in Rio Grande Basin. *Journal of Water Resources Planning and Management*, 132(6), 488–502. [https://doi.org/10.1061/\(ASCE\)0733-9496\(2006\)132:6\(488\)](https://doi.org/10.1061/(ASCE)0733-9496(2006)132:6(488))
- Ward, J. (1998). Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, 83(3), 269–278. [https://doi.org/10.1016/S0006-3207\(97\)00083-9](https://doi.org/10.1016/S0006-3207(97)00083-9)
- Wilde, G. R., & Echelle, A. A. (1992). Genetic status of Pecos pupfish populations after establishment of a hybrid swarm involving an introduced

congener. *Transactions of the American Fisheries Society*, 121(3), 277–286. [https://doi.org/10.1577/1548-8659\(1992\)121<0277:GSOPP>2.3.CO;2](https://doi.org/10.1577/1548-8659(1992)121<0277:GSOPP>2.3.CO;2)

Williams, J. E., Johnson, J. E., Hendrickson, D. A., Contreras-Balderas, S., Williams, J. D., Navarro-Mendoza, M., McAllister, D. E., & Deacon, J. E. (1989). Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries*, 14(6), 2–20. [https://doi.org/10.1577/1548-8446\(1989\)014<0002:FONAET>2.0.CO;2](https://doi.org/10.1577/1548-8446(1989)014<0002:FONAET>2.0.CO;2)

Williams, J. E., Williams, R. N., Thurow, R. F., Elwell, L., Philipp, D. P., Harris, F. A., Kershner, J. L., Martinez, P. J., Miller, D., Reeves, G. H., Frissell, C. A., & Sedell, J. R. (2011). Native fish conservation areas: A vision for large-scale conservation of native fish communities. *Fisheries*, 36(6), 267–277. <https://doi.org/10.1080/03632415.2011.582398>

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Aroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., ... Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, 43(9), 1261–1277. <https://doi.org/10.1111/ecog.04960>

## SUPPORTING INFORMATION

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

**How to cite this article:** Parker SD, Perkin JS, Bean MG, Lutz-Carrillo D, Acre MR. Temporal distribution modelling reveals upstream habitat drying and downstream non-native introgression are squeezing out an imperiled headwater fish. *Divers Distrib*. 2021;27:533–551. <https://doi.org/10.1111/ddi.13214>

## BIOSKETCH

The authors involved in this publication have an extensive range of knowledge, including fish ecology, applied statistics, genetics, and conservation biology. Our research group is a collaboration between Texas A&M University and the Inland Fisheries Division of the Texas Parks and Wildlife Department. <https://www.river-scapeecology.org/>