

LANDCAPE-SCALE FACTORS AFFECTING
DETECTION AND OCCURRENCE OF THREATENED
YAQUI CATFISH IN THE YAQUI RIVER BASIN,
MEXICO

By

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Abstract: Desert fishes are some of the most threatened species in the world because of anthropogenic alterations and competition for limited freshwater. Among threatened desert fishes is the Yaqui Catfish, *Ictalurus pricei*, which is native to southwest United States and northwestern Mexico. Yaqui Catfish populations are declining due to anthropogenic alterations, habitat degradation, fragmentation, and species introductions. Non-native Channel Catfish *I. punctatus*, pose a significant threat because they can hybridize with native Yaqui Catfish endangering its genetic integrity in the Yaqui River basin. Little else is known about Yaqui Catfish, so we sought to determine what factors were affecting its distribution in the Yaqui River basin. Understanding a species' distribution is critical in taking conservation action, as well defining its habitat and environmental associations. I used MaxEnt to create a species distribution model to estimate the potential distribution of Yaqui Catfish. My findings showed the most important variables in determining distribution were size of stream. The MaxEnt model was based off of historical data collected no later than 2005, to understand current distribution, I collected current data and further examined how interactions of Channel Catfish were affecting occupancy, I sampled environmental DNA (eDNA) and habitat covariates in the Yaqui River basin. I used those results in a hierarchical Bayesian occupancy model, that allowed me to determine important variables associated with Yaqui Catfish occupancy and detection probability. I found that interactions with Channel Catfish had a substantial effect on both Yaqui Catfish occupancy and detection.

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CHAPTER I

INTRODUCTION

Freshwater ecosystems are some of the most diverse ecosystems in the world, with 45% of all fish species found in freshwater (Lévêque et al. 2007). However, aquatic ecosystems are also some of the most threatened ecosystems in the world, largely due to competition with humans for freshwater (Malmqvist and Rundle 2002; Dudgeon et al. 2006). Anthropogenic activities have caused a myriad of consequences for native aquatic flora and fauna, including water overallocation, extensive habitat loss, habitat degradation, fragmentation, and altered natural flows (Dudgeon et al. 2006). These activities are largely why aquatic species are some of the most imperiled on earth (Jelks et al. 2008).

The southwestern United States (US) is one of two locations in the world where extinction rates are more than twice the rate of major geological extinction events (Minckley and Douglas 1991). Desert fishes are highly adapted to their environments, where extreme temperature variations, variable flows, and desiccation of streams during dry seasons, occur regularly. However, the high endemism desert fishes have to unique ecosystems has made them vulnerable, as systems change due to anthropogenic alterations. Introduced species can disturb the characteristics desert fishes have adapted to, negatively impacting their survival (Minckley and Douglas 1991). The combined effects of species introductions, habitat loss, and climate change have caused increased threats to desert fishes (Jaeger et al. 2014).

Yaqui Catfish, *Ictalurus pricei*, native to the Sonoran Desert, was once dispersed throughout Northwestern Mexico and Southwestern US, occurring in five major river basins (Sonora, Yaqui, Casas Grandes, Mayo, and Fuerte; Miller et al. 2005). First observed in 1892 near the border of Mexico and US (Rutter 1896), the Yaqui Catfish has remained understudied, with little information known about life cycles or habitat requirements (Varela-Romero et al. 2011). Water use, land change, and dam construction has likely reduced Yaqui Catfish populations across their native range. In fact, Yaqui Catfish are now considered extirpated from the US, where it is believed excessive groundwater pumping led to springs and creeks likely once occupied by Yaqui Catfish to go dry (Stewart et al. 2017).

In an attempt to restore Yaqui Catfish in the US, more than 100 individuals were collected

from Mexico and sent to Uvalde National Fish Hatchery where attempts to artificially propagate the species began (Varela-Romero et al. 2011). A few successful attempts occurred in the late 1990s and the resulting progeny have remained in multiple ponds at San Bernardino National Wildlife Refuge. However, this captive population has failed to reproduce at a sustainable rate and the populations are considered functionally extinct (Stewart et al. 2017). Yaqui Catfish has thus been listed as threatened in the United States (Contreras-Balderas et al. 2002; USFWS 2019). In Mexico, the population is presumed to be declining and Yaqui Catfish is now limited to only three river basins (Yaqui, Fuerte, and Mayo) and is listed as special concern (de La Federación 2010).

Yaqui Catfish has been encountered in a variety of environmental conditions, from large rivers to small, mountain streams, in slow to medium flow, and over gravel and sand substrates (Hendrickson et al. 1980). Habitat destruction, fragmentation from dams, and water diversions are current threats to Yaqui Catfish (Hendrickson et al. 1980). Perhaps the biggest threat to Yaqui Catfish is impacts from introduced species, specifically Channel Catfish *I. punctatus*, which readily hybridizes with Yaqui Catfish (Varela-Romero et al. 2011; Contreras-Balderas et al. 2002; NatureServe and Lyons 2019). Introgression between Channel Catfish and Yaqui Catfish could threaten the genetic integrity of already vulnerable remnant Yaqui Catfish populations in its remaining distribution (Contreras-Balderas et al. 2002; Varela-Romero 2007).

The main goal of my thesis was to increase understanding of the distribution of Yaqui Catfish. The first objective of my thesis was to determine the potential distribution of Yaqui Catfish by creating a species distribution model based on historical Yaqui Catfish occurrences. The second objective was to estimate occupancy and detection probability of Yaqui Catfish in relation to non-native Channel Catfish in the Yaqui River basin using environmental DNA (eDNA).

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CHAPTER II

DEVELOPMENT OF A STREAM-SEGMENT NICHE MODEL TO SUPPORT
CONSERVATION OF THREATENED YAQUI CATFISH *ICTALURUS PRICEI*

ABSTRACT

Yaqui Catfish, *Ictalurus pricei*, is an understudied species with limited data on its ecology, distribution, and local habitat use. Native to southwestern United States and northwestern Mexico, Yaqui Catfish populations are declining, causing the species to be listed as threatened in the United States and specially protected in Mexico. Water over-allocation, habitat degradation, invasive species introductions, and hybridization with non-native Channel Catfish, *I. punctatus*, have caused the populations in Mexico to decline. To help better focus conservation efforts, as well as define important habitat for Yaqui Catfish, I modeled its potential distribution in the Yaqui River Basin of Mexico using occurrence data and MaxEnt, a machine-learning program. I sought to determine how Yaqui Catfish occurrence related to landscape-level covariates. To account for potential influences of spatial sampling bias, I built one model with spatially filtered background locations (“reduced”) and another with all background locations (“full”). Area-under-the-curve (AUC) values indicated little better than random predictions (0.57) for the reduced model but good predictions (0.89) for the full model. Under the full model, environmental covariate response curves indicated relationships with stream order (positive), percent of riparian cropland (negative), and percent of riparian shrubland (negative), resulting in 39% of total stream segments predicted as suitable. With the species facing declines in the region, this work will help inform future conservation efforts aimed at securing this species, protecting suitable habitat and better defining its current status in Mexico.

Introduction

Yaqui Catfish, *Ictalurus pricei*, is a federally threatened species in the US, and listed as a species of special concern in Mexico (de la Federación 2010). Yaqui Catfish have been recorded from a multitude of environmental conditions from large rivers to small streams, in slow to medium flow, and over gravel and sand substrates (Hendrickson et al. 1980). Threats to Yaqui Catfish include habitat destruction via construction of dams and water diversions (Hendrickson et al. 1980), as well as impacts from introduction of non-native species, particularly Channel Catfish *I. punctatus*, which can hybridize with Yaqui Catfish (Varela-Romero et al. 2011). A refuge population in the US was established in the late 1980s, but multiple attempts to get the species to reproduce failed, leading the species to be considered functionally extinct in the US (Stewart et al. 2017). In the remainder of its range in Mexico, Yaqui Catfish persist in the Yaqui, Mayo, and Fuerte river basins. Among these three river basins, the Rio Yaqui is the largest and the only one shared between Mexico and the US (Hendrickson et al. 1980; Varela-Romero et al. 2011). Failure to arrest declines of the species in Mexico could ultimately result in the loss of this species globally.

Understanding the distribution and habitat requirements of the species will be required for developing management plans and remediation of threats to the species' sustainability (Pellet and Schmidt 2005; Peterson et al. 2007). Principal among the threats to Yaqui Catfish persistence is the extensive and long-standing water management infrastructure developed to support large-scale, intensive, and economically-important agriculture in the lower Yaqui basin (as reviewed by Matson and Jewett 2012).

Habitat suitability mapping can be used to identify habitats in need of preservation, as well as areas for restoration (Rodriguez et al. 2007). Models estimating species distribution can also identify vital environmental covariates to explore functional responses to components of the environment (Wenger et al. 2011; Stewart et al. 2018). Species distribution models can help focus future inventory

and management activities on areas where Yaqui Catfish are considered likely to occur and may allow biologists to anticipate consequences of large-scale habitat change.

Maximum entropy models like MaxEnt are commonly used in conservation planning and can help estimate relationships between species and habitat (Phillips 2005; Phillips et al. 2006). MaxEnt can produce estimates of habitat suitability from geo-referenced occurrence data linked to habitat variables (Elith et al. 2011; Dyer et al. 2013). MaxEnt modeling has been used to identify areas with high species richness (Stewart et al. 2018), describe the distribution of rare and threatened species (Taylor et al. 2018; Hegel et al. 2010), estimate effects of changes in river discharge and stream morphology on species' distributions (e.g., Worthington et al. 2014), and ranks as one of the best performing presence-background methods for these purposes (Phillips et al. 2006).

Understanding how Yaqui Catfish distribution is influenced by environmental factors is one of the first pieces of information needed to conserve the species in its native range. However, little information exists to guide development of models as river basins in Mexico have relatively poor coverage of geospatial datasets compared to the US. With these considerations in mind, my objectives were to 1) use MaxEnt to identify habitat associations that correspond to Yaqui Catfish presence and 2) identify areas of potentially suitable habitat for Yaqui Catfish throughout the Yaqui River basin.

Study Area

Yaqui Catfish is native to northwestern Mexico and southern Arizona (Varela-Romero et al. 2011), and have historically occurred in the Yaqui, Mayo, Casas Grandes, Sonora and Fuerte basins in Mexico, though it currently occupies only the Yaqui, Mayo, and Fuerte basins (Varela-Romero et al. 2011). I focused my modeling in the Yaqui River basin. (Figure 1). The Yaqui River basin encompasses 74,640 km² (Comision Nacional Del Agua 2018) in two states in México, Chihuahua and Sonora, and a small area in Southwestern New Mexico and Southeastern Arizona in the US (Hendrickson et al. 1980). I did not model the portion in the US because the species is functionally

extinct there. Rios Yaqui, Bavispe, Moctezuma, and Aros are the largest tributaries in the Yaqui basin. Río de Bavispe is in the northern portion of the basin and joins with the Río Aros, which comes from the southeast. These two rivers continue south to join the Río Moctezuma to form the Río Yaqui, which drains into the Gulf of California. Discharge is regulated by three large dams, El Novillo, El Oviachic and La Angostura. Uplands of the basin remain largely undisturbed while irrigation for agriculture in the delta and developed areas of the entire basin oftentimes leaves the streambed dry (Hudson et al. 2005). The vegetation varies from coniferous evergreen at higher elevations of the Sierra Madre Occidental, to a mix of Sonoran Desert vegetation and thorn scrub at lower elevations (Gentry 1942).

Methods

Yaqui Catfish Presence Data.— I obtained Yaqui Catfish records from three sources: Arizona State University (<http://sharedresources.asu.edu>, downloaded 28 August 2018), the Global Biodiversity Information Facility (GBIF) (GBIF Occurrence Download [hash://sha256/5749de6b8c62206af66cdaab9793f72af340fde277ae5d6a6616866959bd4254](https://doi.org/10.15468/dl.cp6swe) accessed at <https://doi.org/10.15468/dl.cp6swe> downloaded 17 September 2018), and peer-reviewed literature (i.e., Varela-Romero et al. 2011). The records in these sources represent opportunistic collections, with no set sampling strategy apart from broad-based, inclusive ichthyofaunal surveys (e.g., Hendrickson et al. 1980; Varela-Romero et al. 2011). I deleted duplicate records and records that lacked coordinates or locality information. For records that contained only locality descriptions, I used the website geo-locate (<http://www.geo-locate.org>) to estimate geographic coordinates and spatial uncertainty. Locality descriptions not specific enough to narrow to a specific stream segment (appx. 5 km) were not used. This process resulted in 88 occurrences (from 1901-2011). To account for spatial bias of the model (Elith et al. 2011; Boria et al. 2014), I used spatial filtering on the 88 points by creating a 1 km buffer around each point and selecting the most recent occurrence to retain where there was overlap. Thirty-eight points were thus left for MaxEnt modeling, representing Yaqui

Catfish presence locations from 1901-2008, although most ($N= 33$) represented dates from 1977-2008 (Figure 1). These points represented a diversity of stream types; most ($N = 27$) were labeled as intermittent and ranged in size from stream order one to eight with most ($N = 21$) in first and second order systems.

Environmental Data. —Landscape level environmental data were limited for the Yaqui River basin (Table 1). A hydrology layer of sub-basins and stream segments was available from the Instituto Nacional de Estadística y Geografía website (http://antares.inegi.org.mx/analisis/red_hidro/siatl/, accessed 8 December 2019), which included measures of stream size and permanence (Table 1). A 30-m digital elevation model (DEM) was available from the US Geological Survey (<https://viewer.nationalmap.gov/basic/>, downloaded 22 September 2018), which I used to calculate slope (stream gradient) for each stream segment. Landcover at 30-m resolution was obtained from the North American Land Change Monitoring System (NALCMS <http://www.cec.org/north-american-environmental-atlas/land-cover-2010-landsat-30m/>, 28 September 2018), which I summarized for each stream segment at the sub-basin scale, meaning each stream segment in its respective sub-basin had the same value of landcover types in the sub-basin . Finally, precipitation and temperature (i.e., annual average precipitation, average precipitation for the month of the driest year, annual average air temperature, average air temperature of the hottest month of the year) were available from <https://www.worldclim.org/>, downloaded 21 August 2018), at a 1-km resolution scale, which I summarized for each stream segment in the GIS. I summarized these variables at the sub-basin scale, by calculating the mean of all values located in a sub-basin, then applied the values to each stream segment in the sub-basin.

I used Geospatial Modelling Environment (GME) (<http://www.spatalecolology.com/gme>) in ArcGIS to summarize climate and landcover raster data, summarized at the sub-basin scale, then applied values to each stream segment. Proportions of landcover types were calculated for each stream segment at the sub-basin scale and for the riparian corridor at each stream segment by using a

30-m buffer and summarizing within the buffer zone. For the sub-basins, I reclassified the vegetation types into six categories (trees, shrubland, grassland, agriculture land, urban and barren land), then determined the proportion of each type for each sub-basin and assigned that value to each stream segment contained within. For riparian landcover, I reclassified the landcover raster into seven categories (deciduous trees, coniferous trees, shrubland, grassland, agriculture, urban, and barren land) and summarized within the buffer zones. Because vegetation type has been shown to be locally important for fishes, by providing shade and cover, whereas trees in general at a watershed scale can affect runoff and nutrient loads (Gregory et al. 1991; Stewart et al. 2001).

To address the assumption that background locations are sampled at equal probability across the landscape, I created a reduced-background model by identifying stream segments where fishes had previously been sampled in the basin. For this model, I downloaded all records of Class “Actinopterygii” from GBIF (<https://doi.org/10.15468/dl.r5babe>, downloaded 16 July 2020) for the entire Yaqui basin and summarized them by location. I then removed all instances that were not georeferenced to a stream segment with a 5 km measure of precision. This filtering resulted in 500 unique stream segments to be used as background for a reduced model run.

MaxEnt modeling.— I related Yaqui Catfish occurrences to individual stream segments within the river network (Elith et al. 2011; Domisch et al. 2015) using ArcGIS to create a samples-with-data (SWD) format for use in MaxEnt version 3.4.1 software (Elith et al. 2011). To avoid collinearity, I used a Pearson correlation test to identify highly correlated ($\geq |0.70|$) variables, and then withdrew the intercorrelated variables of least importance based on preliminary models to determine which variables were most influential (Dormann et al. 2013).

Model evaluation. —I evaluated two different models: one with a full background of stream segments and another with a reduced background of stream segments that represented only areas that had documented historic fish occurrences. Because MaxEnt’s presence-background approach can be

sensitive to spatial sampling bias (Merow et al. 2013; Townsend Peterson et al. 2007), and because I had limited species occurrence data available, I constructed a model with each background dataset and compared the results. For the full model, I used the complete stream layer (351,796 segments) as a background.

For both models, I analyzed contributions of each environmental variable, and used marginal response curves as well as percent contribution of each variable to model gain. After removing highly correlated variables ($N = 7$), I ran models with all remaining variables. To decrease model overfitting, I removed those variables that contributed less than 10% in the reduced model leaving six variables for the final models. I used a five-fold cross-validation to estimate error around fitted functions and to evaluate the importance of variables with jackknife tests (Elith et al. 2011). Because of the low number of Yaqui Catfish presence locations upon which to build the model, I used only hinge, quadratic and linear features to avoid model over-fitting (Merow et al. 2013; Phillips and Dudik 2008); otherwise, I used default model settings. To assess model performance (Fielding and Bell 1997), I used the receiver operator characteristic (ROC) area under the curve (AUC), where the ROC curve is a measure of the sensitivity and specificity of the model and AUC is a measure of cumulative performance over all potential thresholds of occurrence. I also used threshold-dependent metrics to evaluate model performance (Jiménez-Valverde 2013). I used two different threshold values to convert the continuous MaxEnt clog-log estimates into binary (presence/absence) responses to produce maps of Yaqui Catfish habitat suitability (Radosavljevic and Anderson 2014; Jiménez-Valverde 2013). One threshold was the value at which no omission of training locations occurred (i.e., the minimum training presence in MaxEnt), which provided an inclusive estimate of projected presence within the river basin. A second threshold value allowed for 10% omission of training presence locations, which provided a more conservative estimate of distribution. For both threshold values, I calculated mean omission rates of the testing data set across the five-fold cross validations.

Results

Both full and reduced models contained the same six variables: stream order, upstream length, proportion of trees in the sub-basin, proportion of cropland in the riparian area, proportion of shrubland in the riparian area, and annual mean precipitation (Table 2). The AUC performance for the full model was 0.89 (± 0.19), suggesting adequate discriminative capabilities (Figure 2). The minimum training presence logistic threshold average was 0.08 (± 0.03 SD) resulting in 139,668 of 351,796 (39.7%) stream segments designated as suitable for Yaqui Catfish (Figure 3). In this model, four large contiguous regions were identified as suitable: a small area in the northeast near the U.S. border (Cajon Bonito), the headwaters of a large tributary to Rio Moctezuma above Lake Novillo, the headwaters of the Rio Aros and Rio Sirupa watersheds in the southeast portion of the basin, and the lower southwest portion of the basin, including headwater tributaries of the Rio Yaqui above Lake Oviachic. Allowing for 10% omission, the presence threshold average was 0.20 (± 0.03 SD), which resulted in 69,597 of 351,796 (19.8 %) stream segments designated as suitable. In this model, areas of suitability were generally similar to the previous model, but more fragmented, and more restricted to larger streams within those major areas of suitability previously identified. Mean omission rates of testing data indicated slight overfitting, with an omission rate at 0.08 (± 0.10 SD) based on the minimum training presence threshold, and an omission rate of 0.23 (± 0.21 SD) at the 10% omission threshold.

Results for the reduced background model with 500 background stream segments had an AUC performance of 0.57 (± 0.18 SD) which indicated a low discriminative capability (Figure 2). Projected onto the entire background of 351,796 stream segments, the minimum training presence logistic threshold average was 0.34 (± 0.05 SD), which resulted in 246,847 stream segments as suitable (63.13%) (Figure 3). In this model, suitable rivers were identified throughout the entire basin, although mostly concentrated in the southern portion. The model based on 10% omission in training presence threshold was 0.49 (± 0.05 SD), resulting in 117,101 suitable stream segments (33.3%). This

model resulted in suitable streams situated similarly to the model based on full background model at the minimum training presence threshold, except that more mainstem river segments were considered suitable. Mean omission of testing data at the minimum presence threshold was 0.18 (± 0.15 SD), and 0.35 (± 0.12 SD) at the 10% omission threshold. Omission rates of the testing data were slightly higher in this model, perhaps indicating decreased predictive ability or model overfitting.

Because the performance of the reduced background model was demonstrably poorer than the model constructed with the full background, I did not further parse the response curves for the reduced background model. For the full model, the sum of upstream segment length contributed the most (58.9%) to model predictions, followed by stream order (20.7%), both of which are measures of stream size and positively related to probability of presence. Tree landcover in the sub-basin (15.4%), annual precipitation (2.9%), cropland in riparian landcover (1.5%), and shrubland in riparian landcover (0.5%) further contributed to the model (Table 2) (Figure 4). Sum of upstream length, the highest contributing variable, was positively associated with Yaqui Catfish distribution, as was stream order. Annual mean precipitation was positively associated with Yaqui Catfish distribution until reaching an inflection point at approximately 300 mm and then decreasing thereafter. Occurrence of Yaqui Catfish remained stationary in relation to tree proportion in the landcover until about 90% coverage and then decreased. Probability of presence decreased as both cropland and shrubland in riparian landcover proportion increased.

Discussion

Based on my modeling, Yaqui Catfish appears to have four major regions with contiguous potential distribution in the river basin. Furthermore, even though response curves of probability of occurrence were positively associated with stream size, the smallest streams still had high (>50%) probability of occurrence. Moreover, a large proportion of occurrences used in my model were associated with small streams (stream order ≤ 2) and classified as “intermittent”. These results suggest

that Yaqui Catfish may not occupy all sites throughout a year and would suggest some ability for long-distance dispersal to recolonize dried segments as water returns. Little information exists regarding the role that hydrology plays in Yaqui Catfish biology (Stewart et al. 2017), such as for spawning or feeding. However, in the closely-related Channel Catfish, individuals migrate up to 400 km for feeding and spawning in association with precipitation, temperature, and hydrology regimes (Hubert 1999). Additionally, closely related Blue Catfish (*I. furcatus*) are considered one of the most migratory species of the genus (Graham 1999) and have been observed moving as much as 689 river km (Tripp et al. 2011). My results suggest that research on Yaqui Catfish movement and how this relates to changing environmental conditions (i.e., Monsoon seasonal rains, barriers, anthropogenically altered flow regimes) would help fill in critical gaps in knowledge about their habitat use and reproductive requirements that is needed for conservation of this species.

The negative relationships with riparian cropland and shrubland suggest an important driver for Yaqui Catfish distribution. Riparian vegetation in arid freshwater systems has been shown to be important in species distributions, and shifts from native vegetation to cropland or non-native vegetation have negative effects on native species by decreasing shade, which increases water temperature (Richardson et al. 2007). The temporal range of Yaqui Catfish occurrence records (107 years) used was intended to estimate the natural distribution of Yaqui Catfish, although I acknowledge that some variables, specifically landcover, may better represent current, rather than historic, conditions in the study area. To address these issues, I omitted urban landcover in the analyses as an obvious influence of human activity, as this would be the most likely to change in the time of occurrences. However, most occurrences (87%) were within 31 years of each other, providing a shorter time period among samples, potentially reducing discrepancies among other landcover variables among time periods

A lack of available data hampered this effort to estimate the potential distribution of Yaqui Catfish in its native environment at a stream-segment scale. For example, to avoid over-fitting and

account for spatial sampling bias, my model was constructed with only 38 presence locations. In addition, none of the presence data were obtained systematically, potentially over-representing easily-accessible areas. I attempted to address the lack of data, and its' potential for spatial bias, by constructing models with a full background of stream segments and one where only fish sampling events had occurred. However, the small sample size of the reduced background model likely contributed to its poor discriminative capability. Therefore, conclusions on the effects of spatial sampling bias are difficult to determine. Variation in sub-basin size may have also been a limiting factor in modeling. Because I summarized landcover and other climate data to the sub-basin scale, the low-resolution scale modeled may not represent actual state of the stream segments. Despite these limitations, however, the full background model provides some useful results to aid conservation planning.

I identified major contiguous tracks of suitable habitats for Yaqui Catfish. For example, my results indicate that suitable habitats exist in a small area near the U.S. border (Cajon Bonito), the headwaters of a large tributary to Rio Moctezuma above Lake Novillo, the headwaters of the Rio Aros and Rio Sirupa watersheds in the southeast part of the basin and the lower southwest part of the basin, including headwater tributaries of the Rio Yaqui above Lake Oviachic. Cajon Bonito has long been known as a population stronghold in the Yaqui basin and was once used as an important source for the captive stock in the US (Varela-Romero et al. 2011; Stewart et al. 2017). Collectively, these areas may represent areas of high conservation priority in the Yaqui basin, although more research is needed to assess threats (i.e., landscape and nonnative species) and the status of Yaqui Catfish there.

While my modeling effort was able to examine the role of abiotic factors potentially affecting Yaqui Catfish distribution, it is also generally acknowledged that non-native Ictalurids stocked in the basin are further affecting this species. For example, during the most recent basin-wide survey, non-native Channel Catfish or Blue Catfish were found everywhere Yaqui Catfish were found (Varela-Romero et al. 2011). In general, the primary mode of interference is recognized as hybridization

(Cobble 1995; Ruiz-Campos et al. 2003; Varela-Romero et al. 2011), although the effect of interspecific competition has not been investigated and cannot be ruled out. I did not attempt to collect presence data on non-native species for my modeling, although attempts could be made if data are available (e.g., Taylor et al. 2018).

Because multiple attempts at rearing Yaqui Catfish in captivity to create captive self-sustaining refuge populations have been largely ineffective (see Stewart et al. 2017), identifying natural habitats where Yaqui Catfish can be protected in the wild would be beneficial for conservation. Blue Catfish and Channel Catfish have been widely stocked in Mexico, especially in larger rivers and reservoirs. Thus, negative biotic interaction effects would likely be strongest in these areas (Johnson et al. 2008). If the strength of those interactions favor non-native species or hybrids, then refugia for Yaqui Catfish are more likely to be restricted to smaller streams higher in the basin where my model estimates most of the suitable habitat exists. Maintaining these areas free from non-natives catfishes, especially where native vegetation, along the riparian corridor is abundant, could benefit Yaqui Catfish.

Further research to assess suitability of the entire Yaqui basin with more and finer scale environmental covariates and information about the other nonnative Ictalurids in a single analysis would better identify potential refuge sites in the wild (e.g., Stewart et al. 2018). Advances in sampling methods, such as with eDNA (Janosik and Johnston 2015; McKelvey et al. 2019; Piggot 2016; Strickland and Roberts 2019), could make this process easier, especially in this inhospitable and difficult-to-access region.

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Table 2.1. Variables considered in a presence-only model to determine the potential distribution of Yaqui Catfish in the Yaqui River basin, Mexico.

Variable	Units	Resolution downloaded	Source	Modeled resolution	Max	Min
Drainage area	km ²	Sub-basin	Inegi.org.mx	basin	7,051	26
Stream order*		Stream segment	Inegi.org.mx	Stream segment	8	1
Land cover*	Proportion of landcover classifications	30 meter	Cec.org	Sub-basin		
Elevation	Meters	30 meter	ArcGIS	Stream segment	3,043	0
Slope	Percent grade	30 meter	ArcGIS	Stream segment	16	0
Mean annual precipitation*	Millimeters	1 km	Worldclim.org	Stream segment	258	0
Mean precipitation of month of driest year	Millimeters	1 km	Worldclim.org	Stream segment	16	0
Mean annual temperature	Celsius	1 km	Worldclim.org	Stream segment	25	0
Mean temperature of month of hottest month of the year	Celsius	1 km	Worldclim.org	Stream segment	32	12.2
Sum of upstream stream length*	Meters	Stream segment	Inegi.org.mx	Stream segment	30,361,019	0
Riparian land cover*	Proportion of land cover classifications	30 m	Cec.org	30 m buffer around stream segment		

*Variables used in MaxEnt models.

Table 2.2. Variable contributions of MaxEnt results. Permutation importance (on a scale of 1 - 100) only depends on the final model, unlike percent contribution, which is ranked by path and results.

Variable	Full background		Reduced background	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Sum of upstream stream length	58.9	19.0	12.2	23.1
Stream order	20.7	13.9	20.9	13.9
Sub-basin tree landcover	15.4	11.2	10.7	5.8
Annual mean precipitation	2.9	27.1	13.3	27.1
Riparian cropland	1.5	23.1	26.4	19.0
Riparian shrubland	0.5	5.8	16.5	11.2

Figure 2.1. Map of Yaqui River basin and sub-basins in northern Mexico including locations of Yaqui Catfish presence points used in Maxent modeling.

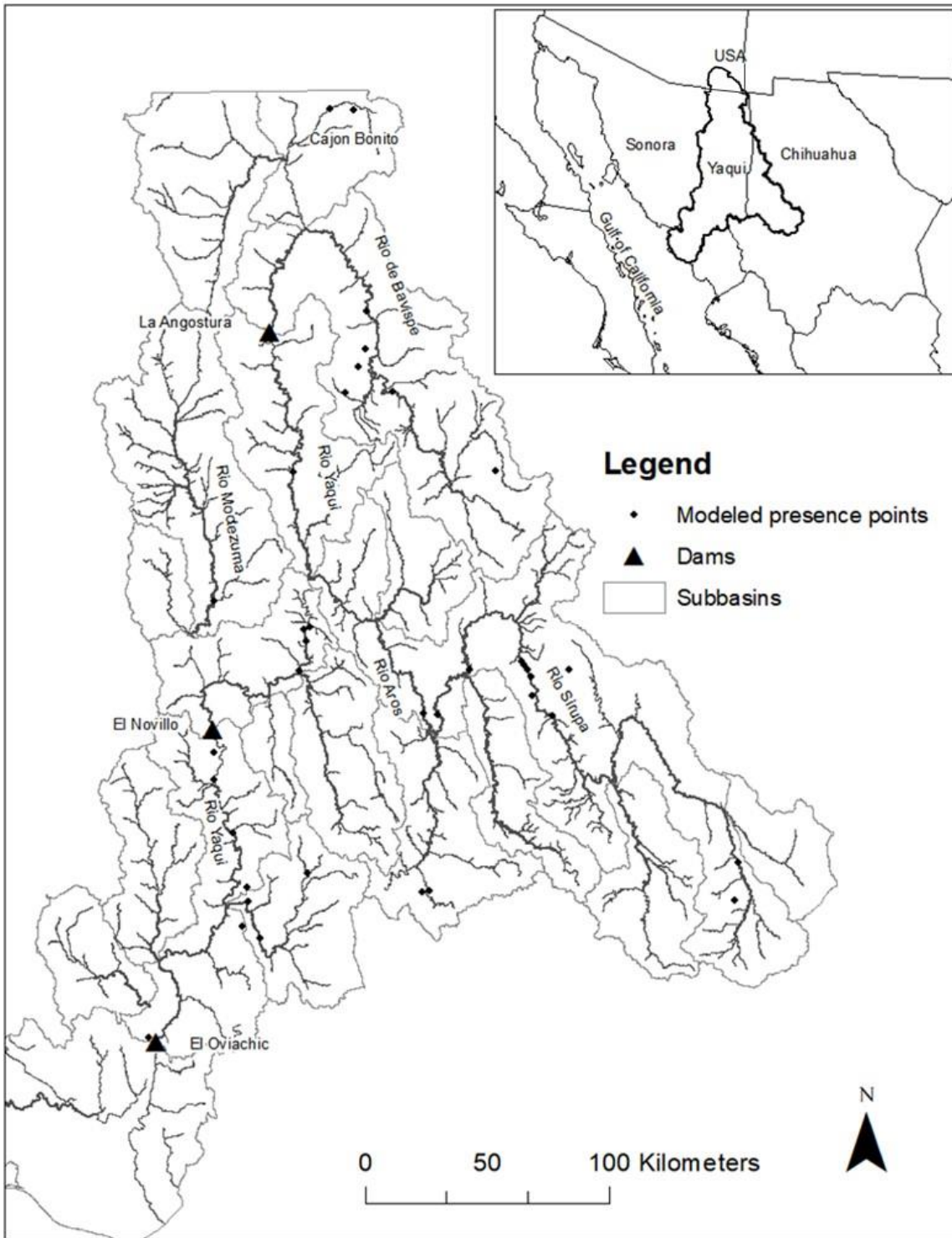


Figure 2.2. ROC (receiver operator characteristic) curves of MaxEnt model results (blue line), dashed black line represents a value of 0.5. Top figure is the ROC curve from the model based on the full background (AUC [area under the curve] = 0.887) and the bottom figure is from the model based on a reduced background of other fish sampling locations in the basin (AUC = 0.566).

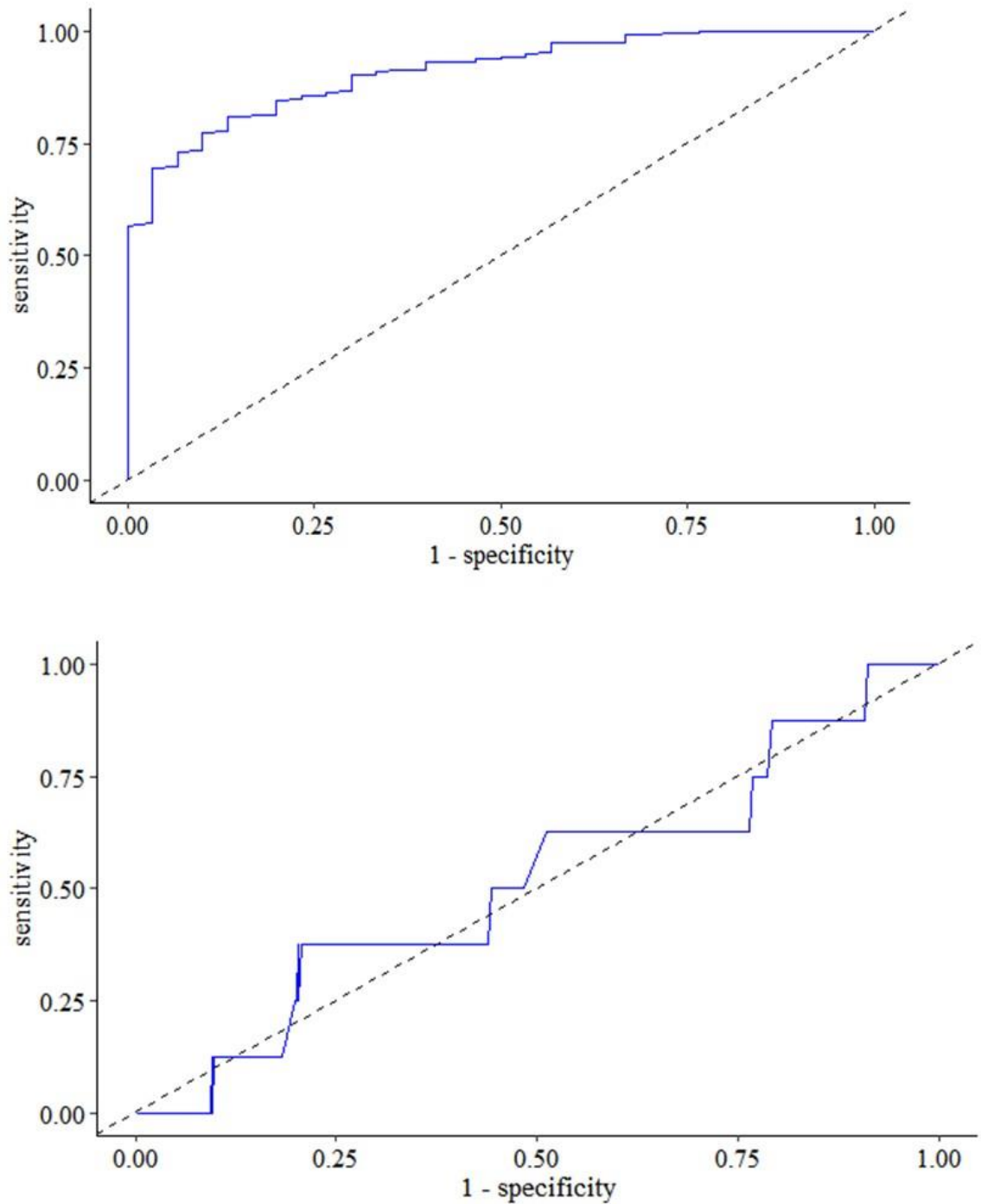


Figure 2.3. Predicted probability of habitat suitability of Yaqui Catfish in the Yaqui River basin as determined through MaxEnt modeling based on two levels of background data (full, reduced) and two different threshold levels (0% and 10% omission).

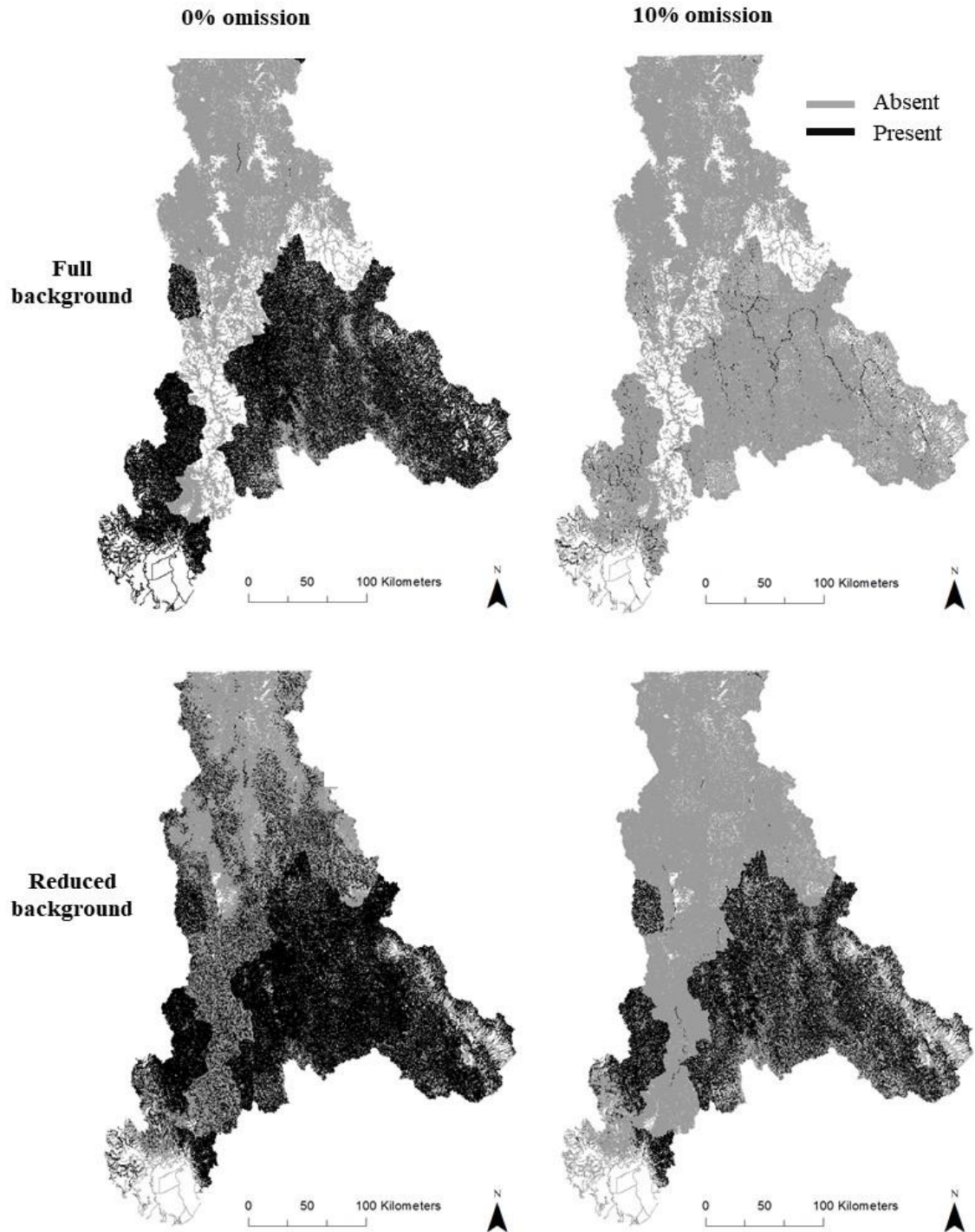
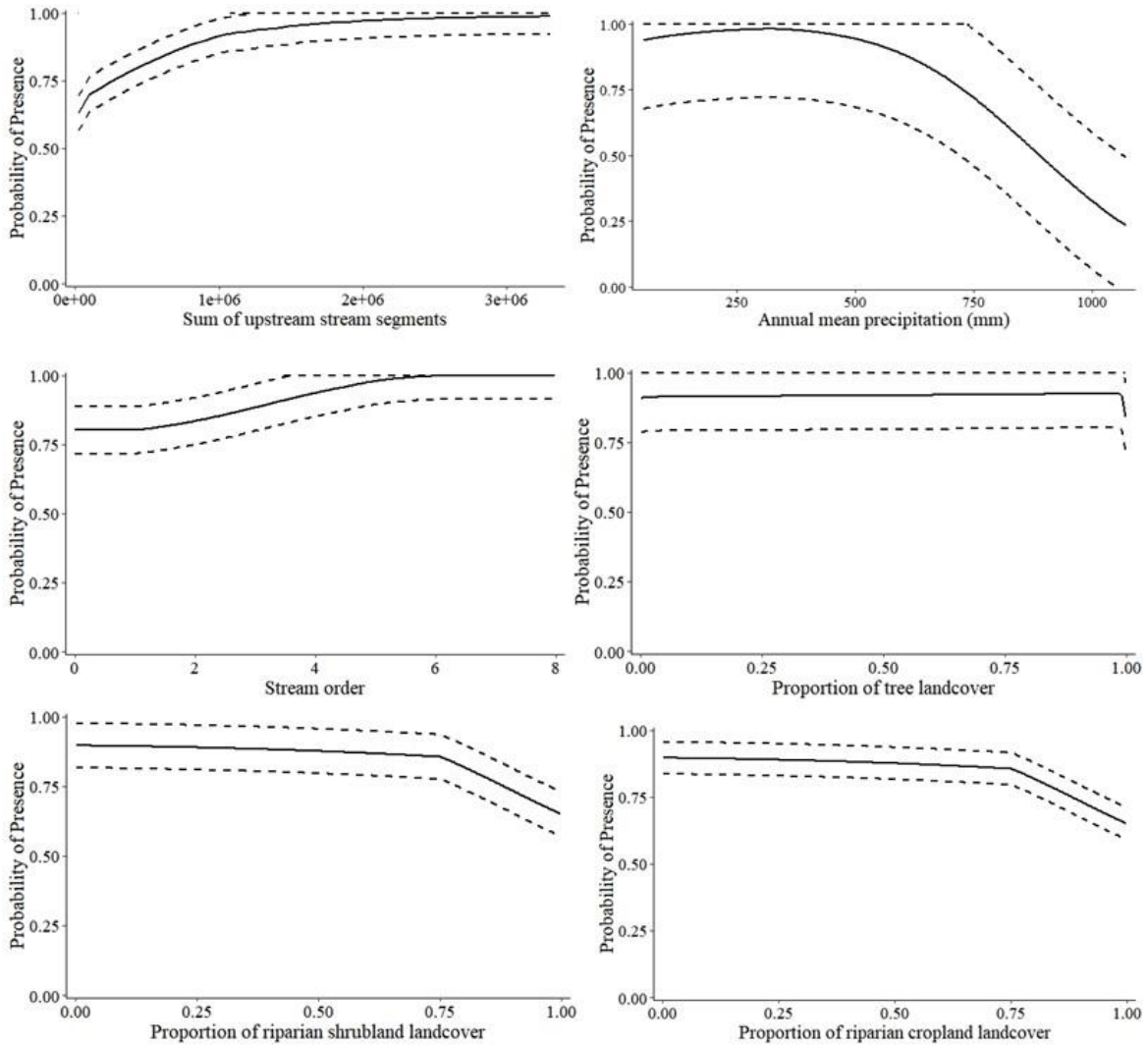


Figure 2.4. Response curves from MaxEnt results based on the full background relating Yaqui Catfish presence to several environmental covariates. Dashed lines represent +/- one standard deviation.



CHAPTER III

ENVIRONMENTAL DNA (eDNA) TO ASSESS OCCUPANCY OF YAQUI CATFISH

ICTALURUS PRICEI IN THE YAQUI RIVER BASIN, MEXICO

ABSTRACT

Environmental DNA (eDNA) surveys can be effective for detecting rare species and typically require less effort than more traditional fish sampling methods. I used eDNA surveys targeting threatened Yaqui Catfish (*Ictalurus pricei*) and non-native Channel Catfish (*Ictalurus punctatus*) in the Yaqui River Basin, Sonora, Mexico. I used a stratified random sampling method to collect water for eDNA from 35 locations. I used an occupancy model to account for imperfect detection, and factors that may have influenced detection, as well as to determine the effects that habitat and other environmental factors may have on occupancy and detection. I separated models into two categories: one wherein Channel Catfish occupancy was allowed to affect Yaqui Catfish occupancy, and another wherein I assumed species interactions did not affect occupancy. Occupancy estimates were 64% for the best ranked model for Yaqui Catfish and detection probability was 64%. Non-native Channel Catfish were detected in all except five locations where Yaqui Catfish were detected, suggesting a high likelihood interaction, including possible hybridization. Other variables affecting Yaqui Catfish occupancy were downstream link and longitude. I detected Yaqui Catfish where they had not been found for over 30 years, but the co-occurrence of non-native Channel Catfish demonstrates that the threat of introgression is widespread.

Introduction

Desert rivers are unique ecosystems with defining characteristics such as highly variable flows, fluctuating temperatures, and dynamic streambeds (Miller et al. 1991; Kingsford 2006; Minckley 1991). To survive these conditions, native fishes have adapted to their specific surroundings, which has resulted in a large number of endemic species with restricted distributions across desert landscapes (Miller et al. 1991; Pister 1974). However, this high endemism makes species vulnerable to habitat disturbances, water development for human use, and introduction of invasive species (Fagan 2002; Thomaz et al. 2016). As a result, a large proportion of desert fishes in North America are currently threatened, endangered, or extinct (Sheldon 1988; Jelks et al. 2008; Johnson and Rinne 1982; Meffe and Vrijenhoek 1988). In fact, the desert southwest United States (US) is one of two locations in North America where extinction rates are more than twice the rate of major historical extinction events (Miller et al. 1991). In the adjacent state of Sonora, Mexico where this study focused, 19 fish species are listed as threatened or endangered (Contreras-Balderas et al. 2002).

The Yaqui Catfish *Ictalurus pricei* is one of these threatened species native to the deserts of southwestern United States and northwestern Mexico. First described from San Bernardino Creek, near the US-Mexico border (Rutter 1896), Yaqui Catfish is very similar to Channel Catfish with slight morphometric differences of the caudal fork, anal fin rays, fusion of the supraoccipital process, and dorsal supraneurals and anal fin base (Minckley 1971; Minckley and Marsh 2009).

In Mexico, the Yaqui Catfish is considered of special concern (de la Federación 2010; Jelks et al. 2008) and the latest recommendation from the 2019 five-year review by the US Fish and Wildlife Service was to uplist their status to endangered (USFWS 2019). Yaqui Catfish were historically encountered in the Casas Grandes, Fuerte, Mayo, Sonora, and Yaqui River basins of Mexico, however, from the most recent range-wide survey, Yaqui Catfish are now only found in the Yaqui, Mayo, and Fuerte river basins (Varela-Romero et al. 2011). Varela-Romero et al. (2011) further reported that non-native Channel Catfish (*I. punctatus*) were found at every site where Yaqui Catfish were found, indicating that the presence of this invasive species is one of the primary threats to Yaqui Catfish persistence because of introgression between the two species and interspecific competition.

Lack of environmental data on the landscape impedes robust, on-the-ground, conservation efforts for Yaqui Catfish and any effort to conserve this species in the wild will require landscape-scale data to identify potential refuge areas. From historical data, a Maximum entropy (MaxEnt) model showed that stream size and tree landcover were positively associated with Yaqui Catfish occurrence (Hafen et al. *In Review*). In addition, this model identified three large areas (and one small area) that provided contiguous suitable habitat in the Yaqui River basin. Given that the model used historical data, it can be considered as a potential distribution, rather than current distribution. Moreover, the MaxEnt model was unable to account for effects of non-native species, such as Channel Catfish, which are widespread (Varela-Romero et al. 2011), suggesting that the current distribution of Yaqui Catfish is smaller than its potential.

To better estimate the current distribution of Yaqui Catfish, especially in relation to non-native Channel Catfish, collecting new data in a robust statistical framework is needed. Factors in the Yaqui River basin make it difficult to use standard sampling techniques, such as electrofishing and netting equipment around steep and rugged terrain in Mexico. Additionally, low reported catch and encounter rates from past attempts and the violence from drug cartels

prevent the development of a rapid survey to describe occupancy of Yaqui Catfish in the Yaqui River basin, Mexico. Environmental DNA (eDNA) is an alternative method for sampling fish that is rapid and efficient and, when conducted within an occupancy modeling framework, can provide inference on local and regional factors that influence presence of target species. Moreover, the high sensitivity of eDNA is especially effective at detecting rare species occurring at low densities (Thomsen and Willerslev 2015; Laramie et al. 2015; Jerde et al. 2011; Pilliod et al. 2013). When compared to traditional organismal sampling, eDNA has been demonstrated to have higher sensitivity, especially at detecting rare and cryptic species, and it has been shown to be more efficient, requiring less equipment and effort (Robinson et al. 2019; Ostberg et al. 2019; McColl-Gausden et al. 2020). Environmental DNA surveys can be more effective than standard sampling in remote desert streams looking for rare species, similar to in the situation in the Yaqui River basin (Robinson et al. 2019). Repeated eDNA sampling can also be used to account for imperfect detection and provide detection probability and allow one to determine the influence of other species on target species (Mackenzie and Royle 2005; Siesa et al. 2011; Hines et al. 2010). This framework makes field data collection easier, and less expensive, while still creating a robust framework from which, species interactions, and habitat use can be generalized across a landscape (Long et al. 2011). Thus, my goal was to apply a multi-scale occupancy model approach that includes local and landscape level-factors with eDNA sampling to investigate the occupancy and detection probability of Yaqui Catfish in the Yaqui River basin, Mexico. I also estimated the occupancy and detection probability of non-native Channel Catfish and their possible effect on Yaqui Catfish distribution in the basin.

Study Area

The Yaqui River basin is located in the states of Chihuahua and Sonora, Mexico, with a small portion in southwestern New Mexico and southeastern Arizona of the US (Figure 1). I focused my modeling in Mexico because the species is extirpated in the wild in the US (Stewart

et al. 2017). The basin is diverse, with arid, desert vegetation in the north and western portion. The Sierra Madre Occidental mountain range runs North to South along the southeast of the basin in the state of Chihuahua. Temperatures in the basin range from 0° C lows in the high, mountainous elevations to 40° C highs in lower, more arid regions. Precipitation averages 48 cm/year, but is variable depending on elevation, being highest in the southeast where snow accumulation is common in the mountain range (Munoz-Hernandez et al. 2011; Hudson et al. 2005). Major rivers in the Yaqui River basin are the Rio Yaqui, Rio Moctezuma, Rio Bavispe, Rio Aros, and Rio Sirupa, which combine to flow into the Gulf of California. Three large dams occur in the basin, the largest of which, El Oviachic, provides water for agriculture in the southern portion of the basin (Hudson et al. 2005). Vegetation in the western, more arid part of the basin is dominated by creosote bushes, yucca, and various cactus species (Hudson et al. 2005). The portion of the basin in Chihuahua is mountainous and less developed for human occupation, with deciduous and coniferous trees at higher elevations, switching to grassland as elevation decreases (Gentry 1942; Abarca et al. 1995). Drug cartels are known to patrol and reside in mountainous areas, making them less accessible, and dangerous to travel. Drug cartel activity (Le Cour Grandmaison et al. 2019) restricted our sampling to the state of Sonora (Figure 2).

Methods

eDNA surveys – Mitochondrial DNA markers specific to Yaqui Catfish were created by Rocky Mountain Research Station (US Forest Service, US Department of Agriculture). Markers were tested for their ability to identify the presence of Yaqui Catfish in hatchery and wild settings. Wild tests in ponds provided early estimates of detection probability from 20% to 40% (Table 1), which represented good field tests because they required multiple filters with less than 5 L of total water, similar to anticipated field conditions in the streams and rivers of the Rio Yaqui basin.

Moreover, these ponds had low densities of fish (Stewart et al. 2017) also similar to anticipated conditions in the Rio Yaqui basin.

To determine sampling locations in the Yaqui River basin, I used a random stratified sampling based on stream order, which was a main factor determining Yaqui Catfish potential distribution based on MaxEnt modeling (see Chapter 1). This stratification resulted in five sampling locations for each stream order in the basin (1-7), for 35 total locations. Samples at each location were taken in an upstream direction, 100 m from the previous sample. I also sampled at a pond with known Yaqui Catfish and hybrids with Channel Catfish (A. Varela-Romero, Universidad de Sonora, personal communication) to confirm the marker's ability to detect both species in the case of a hybrid.. Detection of both Channel Catfish and Yaqui Catfish from a survey would indicate a higher probability of hybrid detection than detection of only Yaqui Catfish or Channel Catfish. The base hydrologic layer used to determine sampling locations was downloaded from the Instituto Nacional de Estadística y Geografía website (http://antares.inegi.org.mx/analisis/red_hidro/siat/, accessed 8 December 2019). To sample eDNA from streams I followed protocols created by Rocky Mountain Research Station (Carim et al. 2016) and filtered either five liters of water or three filters, whichever occurred first depending on water clarity debris in the sample. I also sampled in a number of reservoirs, following the same protocols as stream sampling with at least 100 m separating samples, along the shoreline, in depths accessible with waders. Based on preliminary detection probability estimates as low as 20%, I considered a survey to consist of three to five samples. I defined a sample as a location in the site where I filtered water and measured habitat covariates, whereas a survey comprised multiple samples. Covariates measured for each sample included water depth, flow velocity, secchi tube depth, water temperature, large woody debris presence, channel unit (riffle, run, pool), in-stream substrate size, and overhead canopy cover (Table 2). After samples were geolocated, I included longitude as an additional covariate because of an east-west gradient in

elevation, temperature, precipitation, and vegetation as the Sierra Madre Occidental ends and transitions to a more desert climate. I also added landcover types, which consisted of either cropland or natural vegetation at a 30x30 m scale at my sampling locations (North American Land Change Monitoring System <http://www.cec.org/north-american-environmental-atlas/land-cover-2010-landsat-30m/>, 28 September 2018).

Occupancy modeling - I developed 13 *a priori* candidate models related to abiotic, biotic, and landscape-scale factors I considered biologically important for species and compared them to a null model without covariates. The *a priori* models were based on knowledge known about the basin, and what factors may be important for Yaqui Catfish occupancy and detection. To estimate co-occurrence of interacting Yaqui Catfish and Channel Catfish, with imperfect detection, I adopted the dominant/subordinate classification of Waddle (2010). I classified native Yaqui Catfish being subordinate to nonnative Channel Catfish, where the occurrence of subordinate species depends on the occurrence of dominant species. However, occurrence of dominant species is independent of subordinate species. The development of the model included estimation of species detection and occupancy, given occurrence of dominant species. This method estimates subordinate and dominant occurrence, in addition to potential factors affecting occupancy, while independently modeling and accounting for imperfection detection (Royle and Dorazio 2008). The eDNA histories for both species were summarized in a matrix Y of binary observations y_{it} and conditional on a state process z_{it} , where the observation model is

$y_{it}|z_{it}, p_{it} \sim \text{Bernoulli}(z_{it}p_{it})$. The state process is the result of a Bernoulli trial indicating the latent occupancy state of Yaqui Catfish or Channel Catfish at site i , replicate observation t , with $z = 1$ indicating presence and $z = 0$ indicating absence. The detection probability p_{it} is conditional on $z = 1$. Here, I denote the Y matrix of binary observations (y_{it}^A, y_{it}^B) and state variables (z_{it}^a, z_{it}^b) for species $A = \text{Yaqui Catfish}$ and $B = \text{Channel Catfish}$. Therefore,

$\psi^B = Pr(z^B = 1) = \text{probability of occurrence of Channel Catfish};$

$$\psi^{A|B} = Pr(z^A = 1 | z^B = 1) =$$

conditional probability of occurrence of Yaqui Catfish given that Channel Catfish is present; and

$$\psi^{A|\bar{B}} = Pr(z^A = 1 | z^B = 0) =$$

conditional probability of occurrence of Yaqui Catfish given that Channel Catfish is absent. U

sing these parameters, the joint probability of the occupancy of species Yaqui Catfish and

Channel Catfish can be estimated following these Bernoulli processes (Waddle et al. 2010):

$$z_i^B | \psi_i^B \sim \text{Bernoulli}(\psi_i^B)$$

$$z_i^A | z_i^B, \psi_i^{A|B}, \psi_i^{A|\bar{B}} \sim \text{Bernoulli}\left(z_i^B \psi_i^{A|B} + \psi_i^{A|\bar{B}} (1 - z_i^B)\right)$$

This shows that occupancy of species Yaqui Catfish depends on occupancy of Channel Catfish,

which is based on two probabilities: 1) the probability that Yaqui Catfish is present based on the

presence of Channel Catfish $\psi^{A|B}$, 2) the probability that Yaqui Catfish is present based on the

absence of Channel Catfish $\psi^{A|\bar{B}}$ Using these parameters, each element of the encounter history

of Yaqui Catfish (A) is modeled as:

$$y_{it}^A | z_i^B, \psi_i^{A|B}, \psi_i^{A|\bar{B}}, p_{it}^A \sim \text{Bernoulli}\left(p_{it}^A \left\{ z_i^B \psi_i^{A|B} + \psi_i^{A|\bar{B}} (1 - z_i^B) \right\}\right)$$

I modeled the detection probability of each species as a logit function of site-level, replicate-level, and watershed-level covariates on detection probabilities for each species and represented generally as:

$$\text{logit}(p_{it}) = \alpha_0 + \sum_{v=1}^w a_v x_{v,i}$$

I also incorporated potential covariate effects in the occupancy model using a logit link specified as:

$$\text{logit}(\psi_i) = \beta_0 + \sum_{v=1}^w \beta_v x_{v,i} + \gamma_i + \varepsilon_i$$

where x_v are predictors $v = 1, 2, \dots, w$ measured at site i . The α 's and β 's are the intercept and slope parameter estimates and ε is the independent error term. The γ term is a latent spatial random error, where $\gamma \sim N(0, \theta)$ and θ takes the form of a conditional autoregressive model represented as

$$\theta = \sigma_\theta^2 (1 - C)^{-1} M$$

Here, spatial dependence $C = \{c_{ij}\}$ and $M = \{m_{ij}\}$ is a diagonal matrix, where m_{ij} is proportional to the conditional variance γ given all of its neighbors. The spatial dependence matrices are developed as $C = pW$, where W is a weights matrix and p controls the strength of dependence (Tognelli and Kelt 2004).

To accurately model occupancy and detection, three assumptions need to be met: the population is closed during sampling (no immigration or emigration), the species may not be detected falsely, and sampling must be independent (detection of target species at one site is not influenced by detection at another site; Mackenzie et al. 2003). By conducting multiple samples for a survey in one day, as well as filtering water for eDNA to keep disturbance to a minimum to avoid “spooking” fish, I met the assumption of site closure. Markers specific to Yaqui Catfish and Channel Catfish were developed and tested for specificity by USFS (T. Franklin, personal communication) to prevent false positives, meeting the assumption of no false detections. Finally, I accounted for spatial dependence of sample surveys in sites in our model to meet the assumption of independence.

Prior to creating models and to avoid multicollinearity among covariates, I estimated Pearson correlation coefficients of all predictor variables and used only uncorrelated variables

within any given model set (≤ 0.7) (Table 3). I modeled both occupancy and detection simultaneously and included models with and without the effect of dominant Channel Catfish on subordinate Yaqui Catfish. The models incorporated parameters affecting Yaqui Catfish occupancy, parameters affecting Channel Catfish occupancy, parameters affecting Yaqui Catfish detection, and parameters affecting Channel Catfish detection. Each part was independently modeled, with no effect on the other models, where both species have unique values for occupancy and detection. I assigned prior probability functions to variables for both occupancy and detection parameters in the model, and standardized continuous parameters. I fit the models using Markov chain Monte Carlo (MCMC) implemented in WinBUGS version 1.4 in R (R core team. 2013; Lunn et al. 2000). Models were fit using 50,000 iterations with a burn-in of the first 5,000 iterations and thin of one. I calculated Deviance Information Criterion (DIC) to rank models, which is a hierarchical modeling generalization of the Akaike Information Criterion (AIC) based on posterior distribution of the model (Plummer 2007), and I considered models with $\Delta DIC (\leq 4)$ to be plausible (Burnham and Anderson 1998).

Results

I collected water samples from 35 survey locations located throughout much of the Yaqui River basin, Mexico. Sixteen locations were occupied by both species, five were occupied only by Yaqui Catfish, three were occupied by only Channel Catfish, and neither species was detected at the remaining 11. The models with the lowest DIC included the effect of Channel Catfish on Yaqui Catfish occupancy. The top-performing model included presence reservoirs, longitude, elevation, landcover and downstream link as influences on occupancy, with temperature and time affecting detection, though most parameter estimates had 95% confidence intervals overlapping with 0, suggesting weak support for these variables. Estimated detection probability in the top performing model with species interactions was 55% (95% confidence interval from 46% to 64%) for Channel Catfish and 64% (95% CI from 54% to 73%) for Yaqui Catfish; estimated

occupancy for the same model was 62% (95% CI from 61% to 67%), and 64% (95% CI from 64% to 67%), respectively. Detection estimates of the top performing model without species interactions were 55% (95% CI from 45% to 64%), for Channel Catfish, and 60% (95% CI from 51% to 68%), for Yaqui Catfish, occupancy estimates were 62% (95% CI from 61% to 67%), and 67% (95% CI from 61% to 69%), respectively. Environmental DNA results from samples of the pond with known Yaqui Catfish and hybrids indicated the presence of DNA from both Channel Catfish and Yaqui Catfish.

The best ranked models all included a biotic interaction effect of Channel Catfish on Yaqui Catfish and most ranked better than the null model (Table 4). However, of nine models developed with species interactions, only one was considered plausible ($\Delta\text{DIC} \leq 4$). The one plausible model included downstream link, elevation, and longitude that affected occupancy whereas channel unit (i.e., pool, riffle, run) affected detection (Figure 4). However, many of these variables include 95% confidence intervals that overlapped 0, suggesting weak effects (Figure 5). Beyond the relationship of Channel Catfish on Yaqui Catfish occupancy, downstream link size was negatively associated, meaning streams discharging into smaller streams had higher likelihood of Yaqui Catfish occupancy. In addition, increased water clarity (secchi tube depth) was associated with increased occupancy probability. The positive relationship between Channel Catfish and Yaqui Catfish occupancy likely reflected both species occupying the same areas (Figure 6).

Of the models without species interactions, only the null model was considered plausible ($\Delta\text{DIC} \leq 4$; Table 5). Estimated detection probabilities for the null model was 56% (95% confidence interval from 47% to 65%) for Channel Catfish and 59% (95% CI from 49% to 69%) for Yaqui Catfish. Estimated occupancy rates for the same model was 71% (95% CI from 69% to 75%) for Channel Catfish and 56% (95% CI from 56% to 61%) for Yaqui Catfish.

Discussion

The eDNA markers developed for this survey were based on mitochondrial DNA (mtDNA), which is more common than nuclear DNA, making it more prevalent in the environment than nuclear DNA. However, mtDNA is maternal, creating uncertainty in interpreting results. Detecting both species in the same sample could mean both species are present, or it could mean the species detected is a hybrid between Yaqui Catfish and Channel Catfish (Bylemas et al. 2018; Evans and Lamberti 2018). In my study, I considered the presence of both species at a site to indicate a high probability of hybrids at the location given their documented propensity to hybridize (Varela-Romero et al. 2011). At the border of Sonora and Chihuahua, two of five survey locations with only Yaqui Catfish presence were documented, which was at the base of the Sierra Madre Occidental in an area of lower human development, and could provide an area of refuge for Yaqui Catfish. Even further east, in the state of Chihuahua, Yaqui Catfish have been historically encountered (Varela-Romero et al. 2011), suggesting this region could be targeted for further sampling with the goal of conserving habitat for Yaqui Catfish.

Compared with MaxEnt results (see Chapter 1), which estimated potential distribution, eDNA results confirmed some locations that were predicted as suitable for Yaqui Catfish occurrence. Cajon Bonito, in particular, along with portions of the southeastern basin at the border of Sonora and Chihuahua states, showed high correspondence between modeling approaches. Three of five locations with Yaqui Catfish only detections were all contiguous in this part of the basin, potentially explaining the role of longitude and downstream link on occupancy results. These two modeling tools in concert thus demonstrates their utility for providing information to guide sampling strategies and refining factors affecting species distributions, given limited information.

Results from MaxEnt compared to Bayesian hierarchical models presented some conflicting results regarding factors affecting the distribution of Yaqui Catfish in the Yaqui River basin. MaxEnt results suggested positive effects of stream size (stream order and sum of upstream length) on Yaqui Catfish occurrence, whereas occupancy models found that stream size (downstream link) was a negative factor affecting Yaqui Catfish occupancy. Reasons for this may be a result of sampling bias from MaxEnt results. Accessibility in the Yaqui River basin is very limited, with roads typically following the larger rivers of the basin, making sampling big rivers easier than traveling to roads where smaller streams would be located. The opportunistic strategy of sampling the Yaqui River basin in historic presence records used in MaxEnt model likely show a bias toward large rivers, where more sampling occurs, which may explain the strong positive effects for stream size. Using a random stratified sampling approach based on stream order for the eDNA survey reduced stream size as a potential bias, enabling other metrics to become important.

Historically, Yaqui Catfish distribution covered the entire Yaqui River basin, demonstrating their high tolerance of temperatures and harsh desert environments (Hendrickson et al. 1980). The negative association of longitude with Yaqui Catfish occupancy may be driven by factors such as temperature, water availability, non-native introductions, and habitat availability. Many streams and rivers go completely dry during certain times of the year forcing species to move to more reliable sources (Campoy-Favela et al. 1989; Hudson et al. 2005). Moreover, temperature, precipitation, and elevation of the Yaqui River basin decreases longitudinally from east to west, where the eastern part of the basin receives more precipitation and has lower temperatures on average than the west (Abarca et al. 1995; Munoz-Hernandez et al. 2011; Hudson et al. 2005). Finally, reservoirs in the basin tend to be constructed on larger rivers in the western portion of the basin and are often stocked with non-native Channel Catfish. All of these factors combined help explain our results of where Yaqui Catfish have persisted in the river basin.

Beyond abiotic variables, the presence of Channel Catfish appears to be the largest driver of Yaqui Catfish occupancy in the Yaqui River basin. Non-native introductions can create a suite of challenges for native fishes adapted to specific environments and circumstances, whether it be from interspecific interactions (Gozlan et al. 2010; Britton et al. 2011) or hybridization (Varela-Romero et al. 2011). Channel Catfish were first stocked in the Yaqui River basin in reservoirs for recreational fishing and as a food source (Varela-Romero et al. 2011) and have now expanded their distribution from reservoirs into mainstem rivers, and even to headwater streams. The mechanism driving Channel Catfish effects on Yaqui Catfish (e.g., niche similarity, competition) is unknown, but effects likely include decreased growth rate and abundance (Cucherousset and Olden 2011), increased exposure to predation (Blanchett et al. 2008), and competitive exclusion (Fisk et al. 2007). The presence of non-native species and their hybrids will likely complicate conservation, because further steps will be necessary to ensure species identity in areas of restoration or conservation. Studies focused on the extent of hybridization on the landscape is a logical next step to Yaqui Catfish conservation. Investigation interactions between Yaqui Catfish and Channel Catfish also appears necessary for understanding how Channel Catfish affect Yaqui Catfish in their native environment (Hata et al. 2019; Montanari et al. 2016; Hendrickson and Varela-Romero 2002; Rosenfield et al. 2004).

Should conservation agencies be interested in developing conservation areas for Yaqui Catfish, identifying areas of relatively 'pure' Yaqui Catfish populations would be critical. Moreover, areas of refuge, separated from streams and rivers connecting to the basin to safeguard from nonnative species invasions could further ensure long-term stability of such areas. This idea is mirrored in the goals of the recovery plan for native fishes of the Yaqui River basin to eradicate non-native species, protect critical habitat, and protect and conserve groundwater (USFWS 1995). Because efforts to breed Yaqui Catfish in captivity have been mostly unsuccessful (Varela-Romero et al. 2011; Stewart et al. 2017), creating refuge areas in their native range could be

prioritized. Such refuges have been shown to be effective for other threatened fishes (Saunders et al. 2002; Williams 1991; Abell et al. 2007). From our results, the most likely refuge areas include the upper reaches of the Tejaquia sub-basin, in the southern portion of the Rio Yaqui basin at the border with the state of Chihuahua and the area in the northern part of the basin at Cajon Bonito, which is currently under active conservation measures to preserve portions of native ecosystems (Serrano et al. 2005). Additional surveys, including the use of eDNA, could better identify specific areas that could be targeted for protection. Based on my results regarding the role of channel unit (riffle, run, pool) affecting detection, future eDNA sampling efforts could increase efficiency when deciding specific locations to sample. Because DNA degrades more quickly in warm, slow moving water, which are more common in run and pool environments (Balasingham et al. 2018), focusing on riffle habitats where detection estimate were highest, when available, would decrease time spent at any one specific location, enabling a greater number of locations across the basin to be sampled.

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Table 3.1. eDNA summary test results from wild populations maintained at San Bernardino National Wildlife Refuge and near the refuge, Douglas Arizona.

Pond (date)	N samples	N positive	% Detection
Big Tank (11/29)	5	2	40%
Big Tank (12/13)	5	1	20%
House Pond (12/12)	3	1	33.3%

Table 3.2. Parameters used for models of Yaqui Catfish and Channel Catfish in the Yaqui River basin, Mexico, measured in the field, and from geospatial information.

Covariate	Modeled	Scale modeled
Depth	Detection	m
Secchi tube depth	Detection	m
Substrate	Detection	mm
Temperature	Detection	°C
Flow	Detection	m/s
Canopy cover	Detection	Percent
Channel unit	Detection/occupancy	Riffle, pool, run
Time	Detection	24 hour period
Large woody debris	Detection/occupancy	Presence
Landcover	Occupancy	Cropland or vegetation
Elevation	Occupancy	m
Slope	Occupancy	Δ stream length
Stream order	Occupancy	Strahler
Interaction with Channel Catfish	Detection/occupancy	Presence
Downstream link magnitude	Detection/occupancy	integer
Reservoir	Detection/occupancy	Presence
Longitude	Occupancy	Decimal degrees

Table 3.3. Pearson Correlation coefficient of variables used in models, with variables ($\leq|0.7|$) highlighted in bold. dlink; downstream link size (an indicator of stream size); turb, secchi tube depth (meters); elev, elevation (meters); lc, landcover type (cropland or natural vegetation); long, geographical longitude; res, reservoir presence or absence; temp, water temperature ($^{\circ}\text{C}$); depth, water depth (m); sub, stream substrate size (mm); LWD, large woody debris presence or absence at a survey; canopy, overhead vegetation canopy (%); order, stream order; class, channel classification;

	long.	temp.	depth	flow	turb	canopy	sub	dlink	lc	order	elev.	long	res	LWD
long.	1.00													
temp.	-0.26	1.00												
depth	-0.12	-0.06	1.00											
flow	-0.17	0.02	-0.03	1.00										
turb	-0.01	0.03	-0.11	-0.05	1.00									
canopy	0.44	-0.28	-0.21	-0.06	0.06	1.00								
sub	-0.39	0.00	-0.04	-0.01	-0.07	-0.17	1.00							
dlink	-0.16	0.30	0.07	-0.10	0.19	-0.21	0.16	1.00						
lc	-0.13	0.03	-0.16	0.09	-0.30	0.38	0.09	-0.33	1.00					
order	0.25	0.22	0.16	0.15	0.26	-0.03	-0.24	-0.02	0.01	1.00				
elev.	0.21	-0.35	-0.10	-0.01	-0.18	0.29	-0.20	-0.81	0.25	-0.20	1.00			
class	0.11	-0.08	0.00	0.00	0.01	0.36	0.09	-0.18	-0.06	0.45	0.02	1.00		
res	-0.09	-0.05	-0.05	-0.13	-0.11	-0.08	0.13	-0.06	0.09	-0.34	0.18	-0.09	1.00	
LWD	-0.21	-0.16	0.20	-0.01	-0.26	-0.11	-0.21	-0.12	0.19	0.05	0.18	-0.21	0.39	1.00

Table 3.4: Models with Channel Catfish affecting Yaqui Catfish distribution. ψ_{yc} , Yaqui Catfish occupancy; ψ_{cc} , Channel Catfish occupancy; cc Channel Catfish as a parameter in the model; p_{yc} , detection model of Yaqui Catfish, p_{yc} , detection model for Channel Catfish; dlink; downstream link size (an indicator of stream size); turb, secchi tube depth (meters); elev, elevation (meters); lc, landcover type; long, longitude; res, reservoir presence or absence; temp, water temperature ($^{\circ}\text{C}$); depth, water depth (m); sub, stream substrate size (mm); LWD, large woody debris presence or absence at a survey; canopy, overhead vegetation canopy (%); time, time of day (24 hr.).

Models with $\Delta\text{DIC} \leq 4$ were considered plausible.

Model	Deviance Information Criteria (DIC)	Δ DIC	W_i
$\psi_{yc} = cc$ $p_{yc} = dlink + turb$ $\psi_{cc} = elev + long$ $p_{cc} = riffle + run + pool$	327.6	0	0.93
$\psi_{yc} = cc$ $p_{yc} = dlink + turb$ $\psi_{cc} = elev + long$ $p_{cc} = riffle + pool$	333.4	5.8	0.05
$\psi_{yc} = cc$ $p_{yc} = dlink + turb$ $\psi_{cc} = dlink + long$ $p_{cc} = riffle + pool$	335.9	8.3	0.02
$\psi_{yc} = LWD + sub + depth + canopy + cc$ $p_{yc} = riffle + pool$ $\psi_{cc} = sub + depth$ $p_{cc} = temp + time$	343.7	16.1	0
Null model	345.9	18.3	0
$\psi_{yc} = long + elev + cc$ $p_{yc} = temp + time$ $\psi_{cc} = flow + depth + res$ $p_{cc} = temp + flow + depth$	349.3	21.7	0
$\psi_{yc} = res + dlink + cc$ $p_{cc} = LWD + subs$ $\psi_{cc} = temp + elev + order$ $p_{cc} = LWD + canopy$	354.4	26.8	354.4 0
$\psi_{yc} = reservoir + cc$ $p_{yc} = temp + CC + turb$ $\psi_{cc} = riffle + run + pool$ $p_{cc} = riffle + run + pool$	364.8	37.2	0

$\psi_{yc} = cc$			
$p_{yc} = riffle + run + pool$			
$\psi_{cc} = LWD + subs + depth +$ $canopy + lc$	396.9	69.3	0
$p_{cc} = time + temp + flow + turb +$ $depth$			
$\psi_{yc} = cc + dlink + res$			
$p_{yc} = LWD + subs$			
$\psi_{cc} = canopy + lc + long$	399.0	71.4	0
$p_{cc}: flow + temp + depth + turb$			

Table 3.5. Models without Channel Catfish affecting Yaqui Catfish occupancy. ψ_{yc} , Yaqui Catfish occupancy, ψ_{cc} , Channel Catfish occupancy; cc, Channel Catfish as a parameter in the model; p_{yc} , detection model of Yaqui Catfish, p_{cc} , detection model for Channel Catfish; dlink; downstream link size (an indicator of stream size); turb, secchi tube depth (meters); elev, elevation (meters); lc, landcover type; long, longitude; res, reservoir presence or absence; temp, water temperature (°C); depth, water depth (m); sub, stream substrate size (mm); LWD, large woody debris presence or absence at a survey; canopy, overhead vegetation canopy (%); time, time of day (24 hr.) Models with $\Delta DIC \leq 4$ were considered plausible.

Model	Deviance Information Criteria (DIC)	ΔDIC	W_i
Null model	345.9	0	0.84
$\psi_{yc} = \text{long} + \text{res} + \text{dlink}$ $p_{yc} = \text{temp} + \text{time}$ $\psi_{cc} = \text{long} + \text{elev} + \text{res}$ $p_{cc} = \text{temp} + \text{time}$ $\psi_{yc} = \text{lc} + \text{long}$ $p_{yc} = \text{flow} + \text{depth} + \text{turbidity}$ $\psi_{cc} = \text{res}$ $p_{cc} = \text{substrate} + \text{LWD}$	350.7	4.8	0.07
$\psi_{yc} = \text{long} + \text{lc}$ $p_{yc} = \text{cc} + \text{pool}$ $\psi_{cc} = \text{elev} + \text{res}$ $p_{cc} = \text{turb}$	350.8	4.9	0.07
$\psi_{yc} = \text{temp} + \text{elev} + \text{order}$ $p_{yc} = \text{canopy} + \text{time}$ $\psi_{cc} = \text{long} + \text{res} + \text{elev}$ $p_{cc} = \text{temp} + \text{time}$	355.7	9.8	0
	361.3	15.4	0

Figure 3.1. Map of Yaqui River basin with major dams and rivers indicating locations sampled for Yaqui Catfish and Channel Catfish with eDNA.

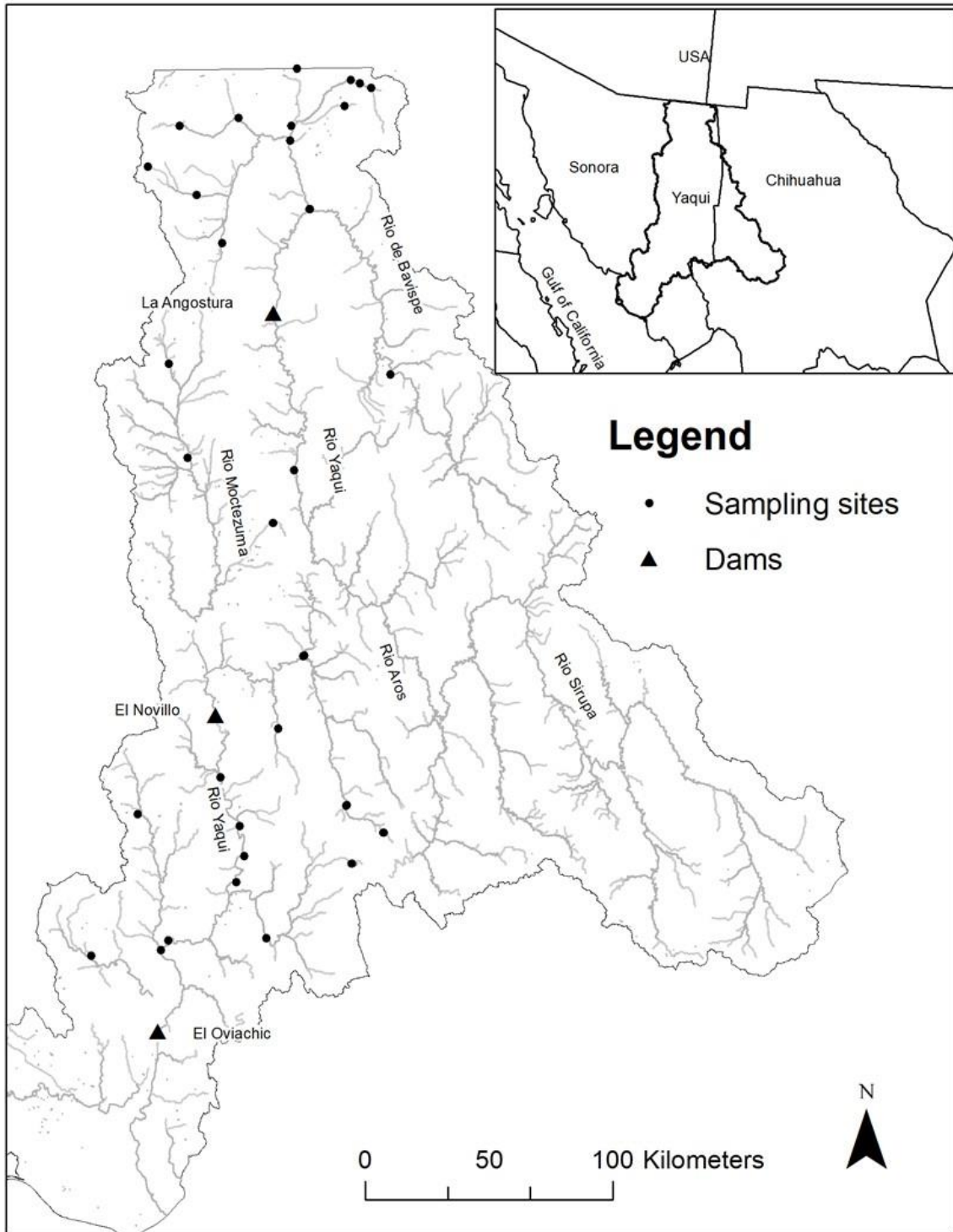


Figure 3.2: Presence locations of Yaqui Catfish and Channel Catfish based on eDNA samples.,
Hatching in southeast basin represents area not sampled due to drug cartel activity.

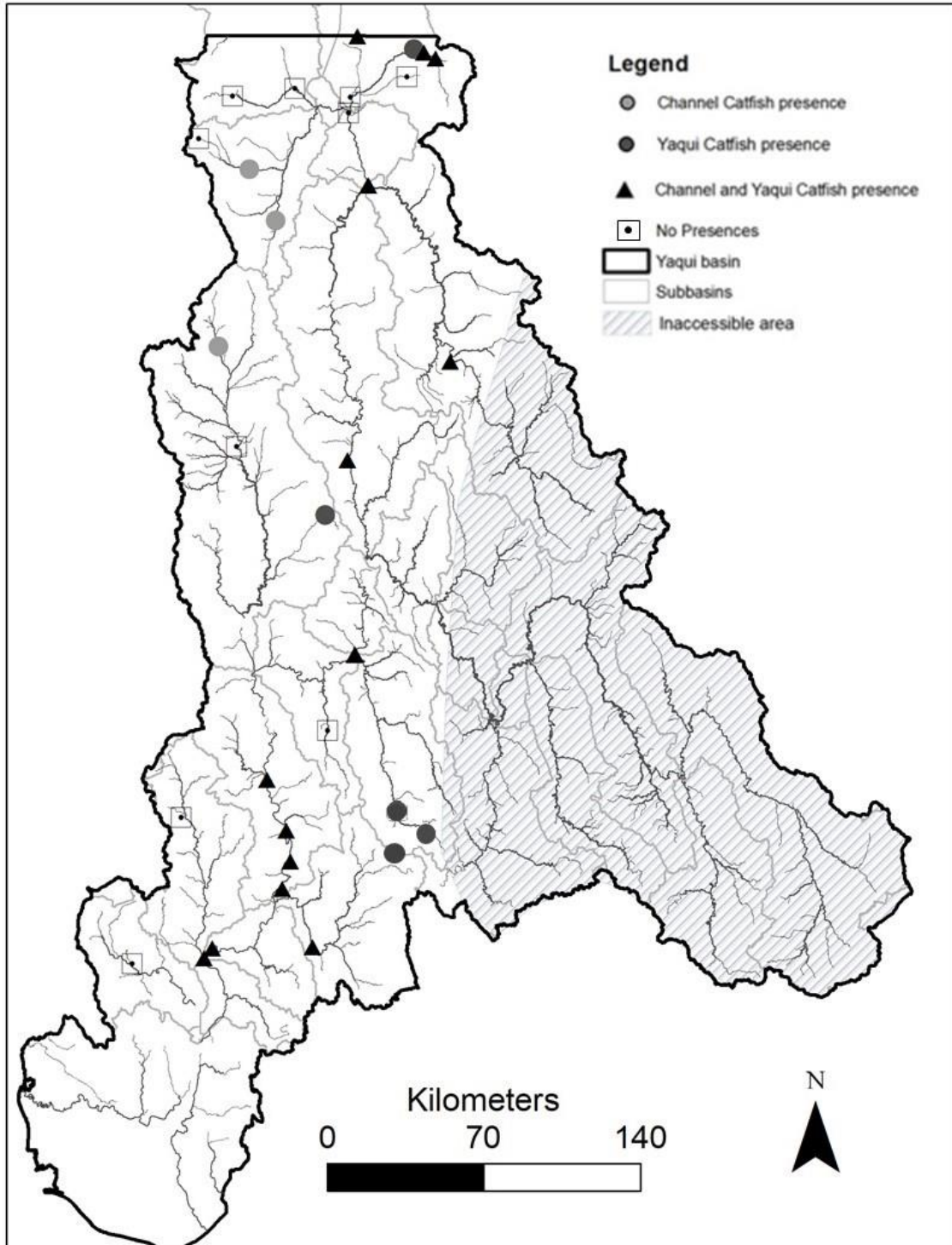


Figure 3.3: Parameter estimates ($\pm 95\%$ confidence intervals) of continuous variables for detection for top-ranked model with species interactions. turb, secchi tube depth (meters); Temp, temperature; Sub, substrate size, Depth, water depth; Time, time of day (24 hour period); Flow, water velocity (m/s).

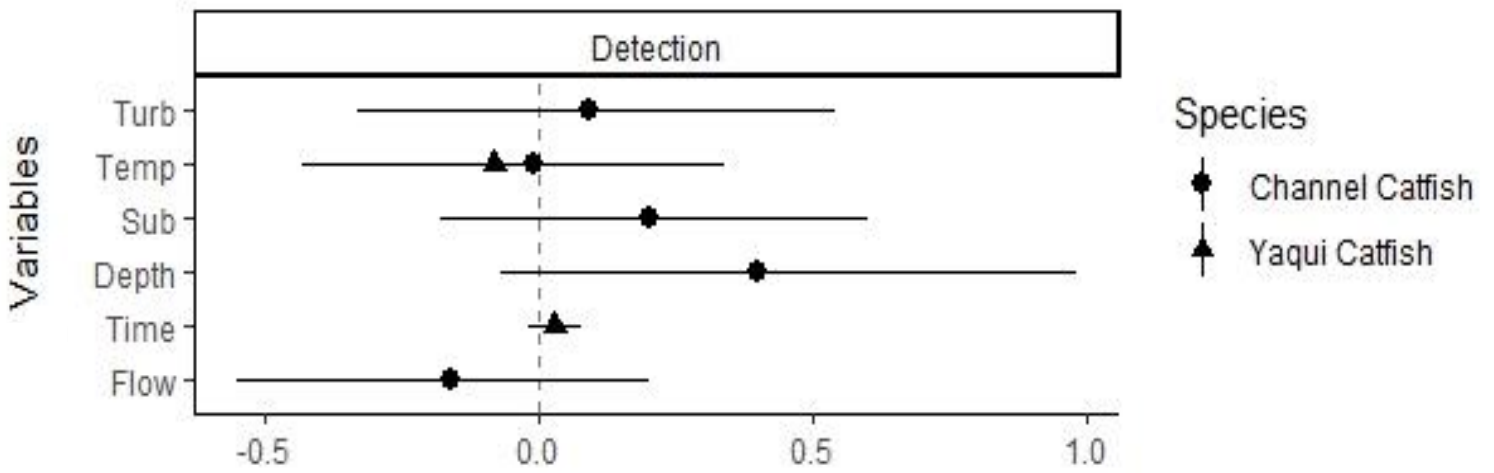


Figure 3.4. Parameter estimates ($\pm 95\%$ confidence intervals) of stream classifications for detection of Channel Catfish of top ranked model with species interactions. Absent signifies parameter when the variable was absent, and present is parameter estimate when the variable was present.

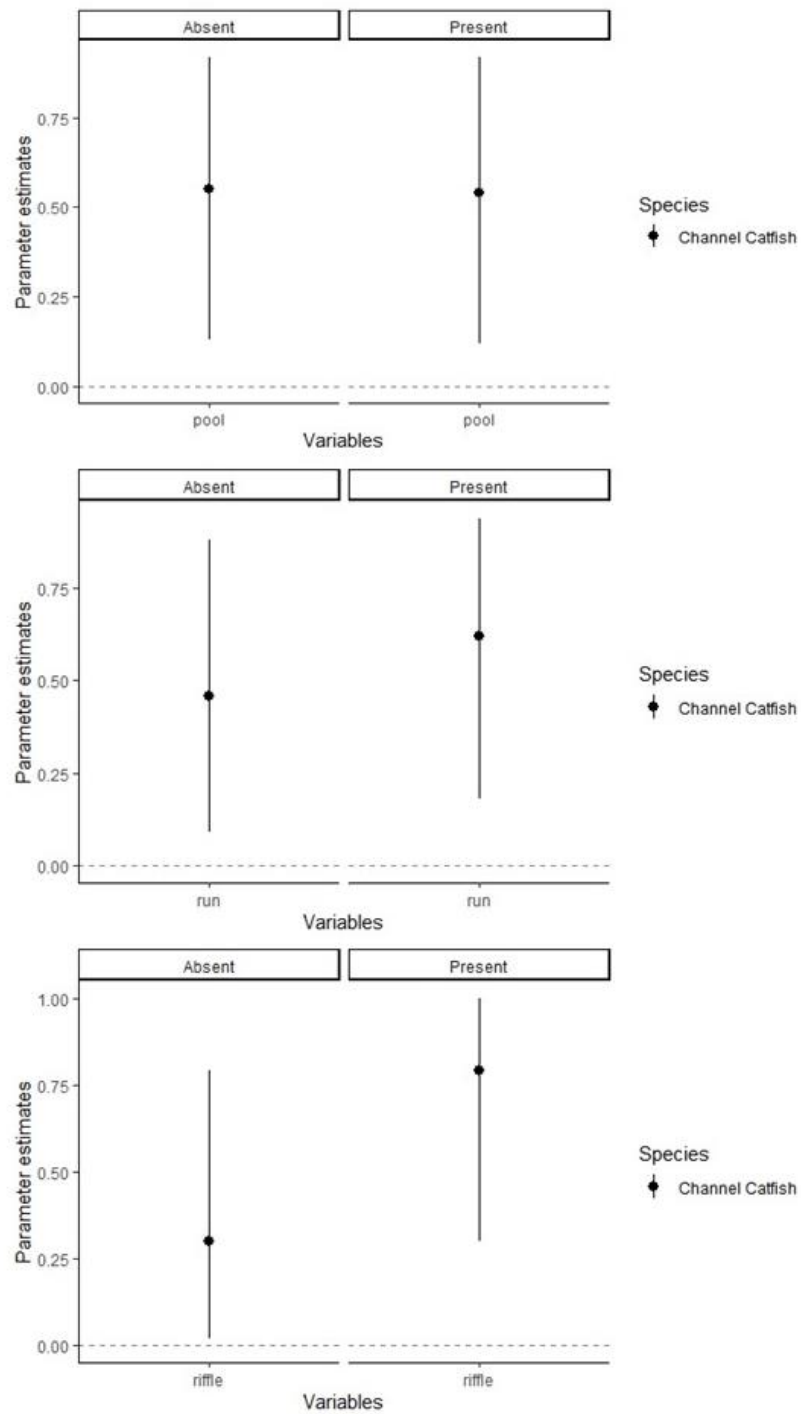


Figure 3.5. Parameter estimates ($\pm 95\%$ confidence intervals) of continuous variables of highest ranked model with species interactions. Occupancy represents variables modeled affecting Occupancy probability. Occupancy with variables modeled affecting occupancy of species. Dlink; downstream link size (an indicator of stream size); turb, secchi tube depth (meters); Elevation (meters)..

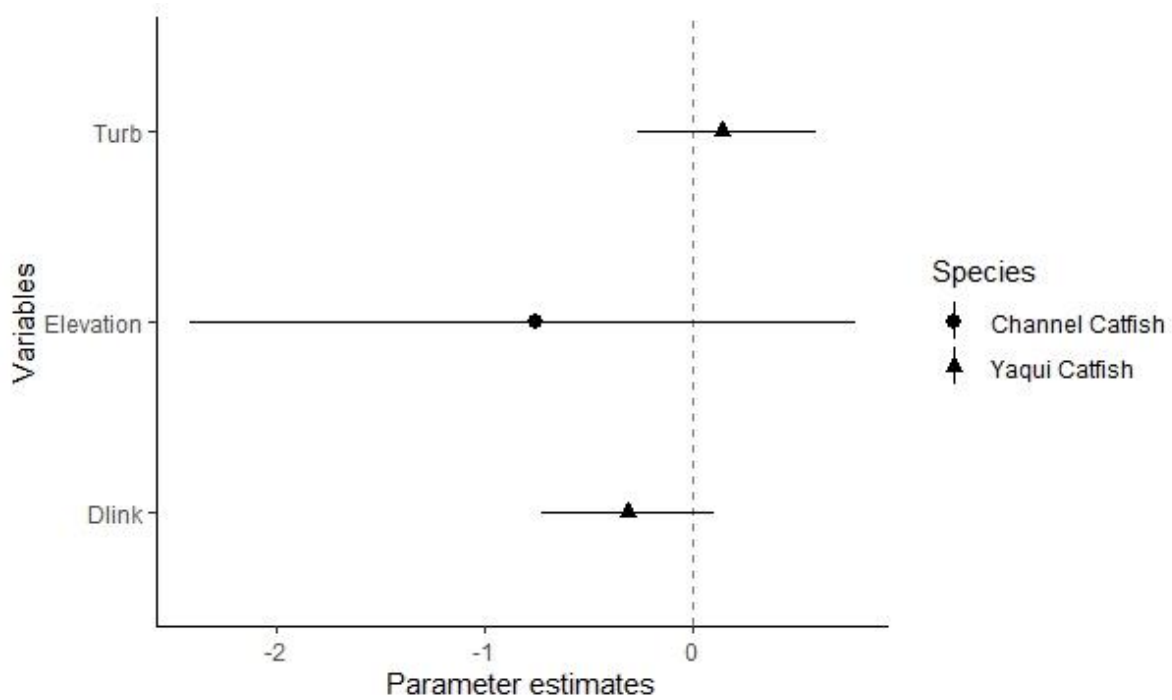
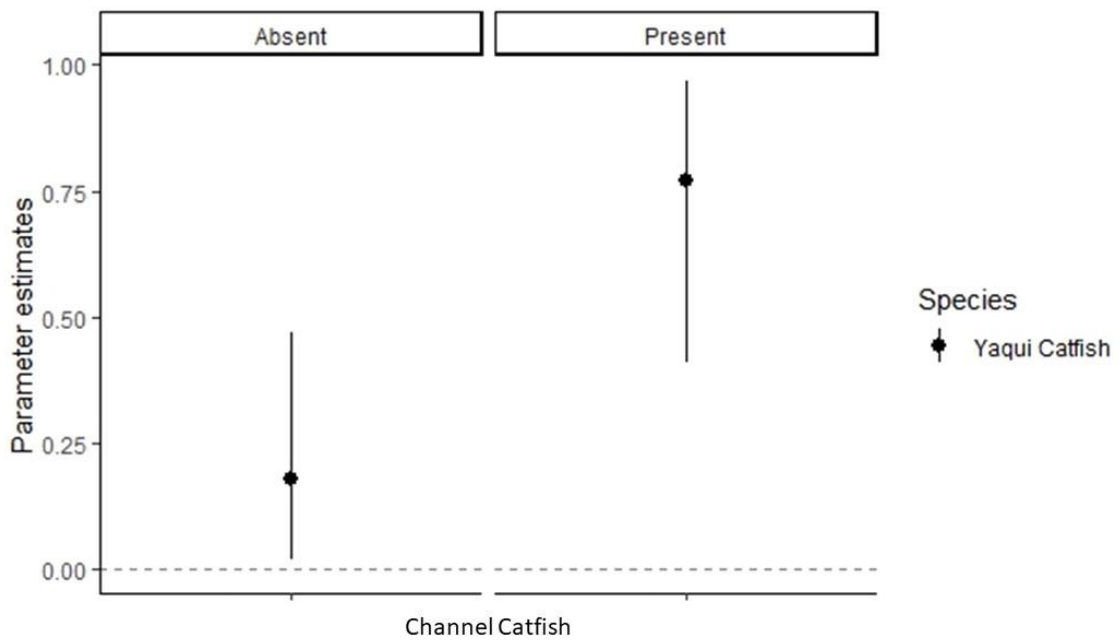


Figure 3.6. Parameter estimates ($\pm 95\%$ confidence intervals) of binomial variable of highest ranked model with species interactions. This describes the probability of a Yaqui Catfish being present at a site having Channel Catfish.



APPENDIX

Table 1. Correlation matrix of landscape variables considered for MaxEnt modeling. Variable pairs with correlation coefficients $\geq|0.70|$ are indicated in bold. Rip = riparian; precip = precipitation.

	Stream order	Dry precip.	Elevation	Mean precip.	Slope	Tree landcover	Shrubland	Grassland	Agriculture	Barren land
Stream order*	1.000									
Dry precip.	-0.017	1.000								
Elevation*	-0.133	0.747	1.000							
Mean precip.	-0.064	0.735	0.465	1.000						
Slope	-0.311	0.300	0.341	0.331	1.000					
Tree landcover*	-0.077	0.412	0.247	0.529	0.402	1.000				
Shrubland	0.024	-0.331	-0.225	-0.443	-0.272	-0.683	1.000			
Grassland	-0.029	-0.205	-0.066	-0.207	-0.100	-0.507	-0.116	1.000		
Agriculture*	0.123	0.002	0.033	-0.067	-0.234	-0.273	-0.067	-0.049	1.000	
Barren land	0.024	-0.020	-0.012	-0.022	-0.013	-0.037	-0.005	-0.004	0.007	1.000
Urban	0.021	0.004	-0.005	0.000	-0.042	-0.055	-0.005	-0.009	0.027	0.001
Rip. deciduous	-0.002	-0.040	-0.040	-0.058	-0.031	-0.033	-0.009	0.004	-0.002	0.002
Rip. coniferous	-0.052	0.414	0.245	0.527	0.380	0.913	-0.646	-0.452	-0.237	-0.033
Rip. shrubland*	0.013	-0.332	-0.223	-0.441	-0.260	-0.647	0.919	-0.084	-0.049	-0.001
Rip. grassland	-0.027	-0.205	-0.066	-0.204	-0.097	-0.447	-0.090	0.864	-0.037	-0.002

Rip. agriculture	0.092	0.005	0.037	-0.063	-0.214	-0.230	-0.047	-0.036	0.804	0.012
Rip. barren	0.017	-0.023	-0.012	-0.025	-0.012	-0.035	0.001	-0.002	0.014	0.740
Rip. urban	0.014	0.004	-0.006	0.003	-0.040	-0.044	0.006	-0.006	0.043	0.002
Rock type*	-0.015	-0.361	-0.351	-0.187	-0.120	-0.085	0.046	0.040	0.019	0.002

	Urban	Rip. deciduous	Rip. coniferous	Rip. shrubland	Rip. grassland	Rip. agriculture	Rip. barren	Rip. urban	Rock type
Stream order*									
Dry precip.									
Elevation*									
Mean precip.									
Slope									
Tree landcover*									
Shrubland									
Grassland									
Agriculture*									
Barren land									
Urban	1.000								
Rip. deciduous	-0.001	1.000							
Rip. coniferous	-0.040	-0.033	1.000						
Rip. shrubland*	-0.001	-0.009	-0.679	1.000					

Rip. grassland	-0.004	-0.004	-0.501	-0.120	1.000				
Rip. agriculture	0.040	-0.004	-0.282	-0.070	-0.052	1.000			
Rip. barren	0.001	0.004	-0.037	-0.005	-0.005	0.009	1.000		
Rip. urban	0.522	-0.002	-0.062	-0.003	-0.009	0.035	0.002	1.000	
Rock type	0.002	0.009	-0.085	0.047	0.038	0.019	0.001	0.001	1.00

*Variable used in model

Figure 1. Map of river basins in Mexico where Yaqui Catfish were historically located.



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