Native and nonnative fish community and food-web dynamics in dryland streams of the American Southwest

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Abstract

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Freshwater biodiversity is at once the most diverse and the most imperiled among the world's ecosystems. In the southwest, regional biodiversity and endemism face challenges imposed by declining water availability and widespread nonnative species proliferation. In this dissertation, I explore how these challenges affect fish community dynamics and native species persistence in dryland rivers, and explore the effectiveness of nonnative removal programs toward native fish conservation. The overarching questions motivating my research are: (1) How are fish communities responding to a changing climate? (2) How does flow intermittence and species origin shape freshwater fish beta diversity across dryland riverscapes? (3) Can we restore native species food-web dynamics through invasive species management? (4) Do strategic and opportunistic removal programs result in measurable, and if so comparable, benefits to native

species conservation? Demographic models linking native and nonnative populations to flow dynamics predicted that contemporary declines in the frequency of peak flows, and increases in drought frequency are likely to result in nonnative dominant fish assemblages and diminished native fish populations. I found that intermittent and perennial streams play complementary roles in supporting fish beta diversity, and that contributions of intermittent streams to overall beta diversity were relatively consistent through time, primarily supporting a unique composition of native fishes. Although nonnative species control and removal programs are a common management strategy they have not always been successful. However, I found that nonnative removal efforts allowed native species to recover in their food-web dynamics, by returning to higher trophic levels and isotopic niches comparable to individuals that did not co-occur with nonnative fishes. In a model informed by long-term monitoring programs, I also found that both opportunistic and strategic removal strategies were predicted to decrease native fish extinction probabilities. These results were encouraging, and demonstrated that removal programs can meet recovery goals even over large areas and long after nonnative species are established.

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DEDICATION

For my mom, Alice, who instilled the value of education. “Knowledge is the only thing you take with you anywhere you go, and the only thing no one can take away.”

Chapter 1. **Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model**

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1.1 Abstract

Understanding how novel biological assemblages are structured in relation to dynamic environmental regimes remains a central challenge in ecology. Demographic approaches to modeling species assemblages show promise because they seek to represent fundamental relationships between population dynamics and environmental conditions. In dryland rivers, rapidly changing climate conditions have shifted drought and flooding regimes with implications for fish communities. Our goals were to (1) develop a mechanistic multispecies demographic model that links native and nonnative species with river flow regimes, and (2) evaluate demographic responses in population and community structure to changing flow regimes. Each fish species was represented by a stage-structured matrix, and species were coupled together into a multispecies framework through density-dependent relationships in reproduction. Then, community dynamics were simulated through time using annual flow events classified from gaged streamflow data. We parameterized the model with vital rates and flow-response relationships for a community of native and nonnative fishes using literature-derived values. We applied the simulation model to the Verde River (Arizona, USA), a major tributary within the Colorado River Basin, for the past half century (1964 – 2017). Model validation revealed a match between model projections and relative abundance trends observed in a long-term fish monitoring dataset (1994 – 2008). At the beginning of the validation period (1994), model and survey observations showed that native species comprised approximately 80% of total abundance. Model projections beyond the survey data (2008 – 2017) predicted a shift from a native dominant to a nonnative dominant assemblage, coinciding with increasing drought frequency. Trade-offs between native and nonnative species dominance emerged from differences in mortality in response to the changing sequence of major flow events including spring floods, summer high flows, and droughts. In conclusion, the demographic approach presented here provides a flexible modeling framework that can be readily applied to other stream systems and species by adjusting or transferring, when appropriate, species vital rates and flow-event thresholds.

Key words: assemblage; climate change; community; demographic model; drought; freshwater fish; hydrology; invasive species; multi-species model; non-native species; non-stationarity; stochasticity.

1.2 Introduction

Novel biological assemblages, comprised of species combinations differing from the past, are increasingly widespread across the world (Hobbs et al. 2009). Mounting evidence suggests that novel assemblages do not arise from a random reshuffling of species, but from heterogeneous rates of species losses and gains over time and space (Zavaleta et al. 2009, Dirzo et al. 2014, Moore and Olden 2017). Species invasions and climate change are primary contributors to novel assemblages, causing changes in species composition and non-systematic reductions in species richness (Dornelas et al. 2014). Consequently, modeling changes in community structure in response to non-stationary climate regimes, particularly in light of on-going species invasions, is a primary research challenge.

Demography-based approaches to modeling communities show promise because they represent fundamental relationships between population dynamics and environmental conditions (Keith et al. 2008, van de Pol et al. 2010, Yen et al. 2013, Lytle et al. 2017). Demographic models utilize knowledge regarding the autecology of a species, such as rates of birth, growth, fecundity, and mortality of individuals (i.e., vital rates) to project population dynamics through time. Causal mechanisms can be readily incorporated by allowing vital rates to change as a function of environmental stochasticity or density-dependence (Caswell 2001). Unlike modeling approaches that largely rely on combining single-species predictions to infer community change between two points in time, demographic approaches can model population responses to specific sequences of environmental events. This makes demographic approaches useful for understanding community responses to environmental change (Lytle and Merritt 2004, Yen et al. 2013, Wheeler et al. 2017). Representative communities can be modeled by linking individual species together via density-dependence in space requirements, food, or some other limiting resource. The demographic community models are “interaction neutral” in the sense that pairwise species interactions arise from the model structure itself, rather than being specified *a priori* as parameters (Lytle et al. 2017; Tonkin et al. 2018). This community-wide approach has demonstrated an ability to recover realistic patterns of community dynamics in freshwater ecosystems and shows promise for revealing how species interact under novel environmental conditions.

A rapidly changing climate that includes more frequent and severe droughts and flooding is poised to reshape fish communities of temporary and perennial rivers in dryland regions (Datry et al. 2014, Kominoski et al. 2018). Climate models project that decreased snow accumulation and higher evapotranspiration rates in spring and summer months will lead to more frequent and severe droughts in the southwestern United States, especially when combined with growing human water demands (Christensen et al. 2004, Seager et al. 2013, Udall and Overpeck 2017). In fact, climate-driven changes to streamflow in the Colorado River Basin have already been observed (Solander et al. 2017), where increased low-flow anomalies and decreasing habitat connectivity threaten native fish persistence (Jaeger et al. 2014, Ruhí et al. 2015) and may favor nonnative fishes in the future (Ruhí et al. 2016). Life-history traits have proven useful to understand past (Gido et al. 2013) and predict future responses of native and nonnative fishes to environmental change (Whitney et al. 2017). Thus, we expect that demographically-based community models that account for species-specific relationships with hydrology will help to predict past and future changes in fish assemblages.

Dryland rivers of the southwestern United States are a flashpoint for the conservation challenges associated with changing river hydrology and a proliferation of introduced species. Widespread dam construction, flow diversions, and surface and groundwater abstraction for growing human populations have significantly altered environmental regimes in the region, creating conditions that threaten native species persistence and promote nonnative fishes (Minckley and Deacon 1968, Olden and Poff 2005, Strecker et al. 2011). As a result of nonnative species introduction and their establishment and proliferation from reservoirs, the number of nonnative species equals or exceeds native species in most watersheds throughout the southwestern United States (Pool et al. 2010, Walsworth and Budy 2015).

Here, we developed a mechanistic multispecies demographic model to evaluate how native and nonnative fish populations change in response to changing flow regimes. We modeled a fish community by examining species-specific vital rates that varied as a function of flow regimes describing patterns of drought and flooding. Density-dependent relationships coupled populations together into a multispecies framework, and community dynamics were simulated through a sequence of flow events using the streamflow record. We validated the model by comparing model projections to empirical data from a long-term fish monitoring program. We then examined how contemporary climate-driven hydrologic change in the sequence of drought and flood events affect the composition of native and nonnative species in the community. Results from this study provide important insight into how changing flow regimes and invasive species may threaten the future of endemic native fishes in the Colorado River Basin, and broadly highlight the utility of multispecies demographic modeling approaches in ecology.

1.3 Methods

1.3.1 *Study system and species*

The Verde River, a tributary within the Colorado River Basin, drains over 17,000 km^2 of central Arizona (Fig. 1). The perennial mainstem river runs approximately 270 km through private, state, tribal and United States Forest Service lands, originating in Big Chino Wash (1325 m a.s.l.) and flowing to its confluence with the Salt River north of Phoenix, Arizona (402 m a.s.l.). We focused our study on the unregulated upper Verde River mainstem, where development is primarily limited to livestock grazing and reductions in baseflows are a result of groundwater withdrawals (Garner et al. 2013).

Highly valued for its natural beauty and management priorities as a Wild and Scenic River, the Verde River is a focal point for the conservation of endemic native fishes (Averitt et al. 1994, Turner and List 2007). At least twelve fish species were historically native to the system, but the fish assemblage is changing rapidly, and only five native species have been observed since 1997 (Rinne 2005). By contrast, numerous nonnative fishes are present in the Verde system, including several species of centrarchids, ictalurid catfishes and minnows (Rinne 2005). The Verde River has been the focus of detailed monitoring efforts starting in the 1990's, where fish community composition in relation to flow and habitat requirements have been examined annually for the period 1994-2008 (Stefferud and Rinne 1995, Rinne and Miller 2006, Neary et al. 2012). These surveys included seven sites in the upper Verde River, encompassing a spatial extent of approximately 60 river kilometers and representing all valley types and habitats occurring within the Verde River (Fig. 1; Neary et al. 2012). River discharge representative of our study area has been measured in the mainstem upper Verde River continuously since 1963 (USGS gage 09503700).

We examined the seven most common fish species in the upper Verde River, collectively representing, on average, 87% of stream reach biomass (Gibson et al. 2015). Native fishes included desert sucker (*Catostomus clarki*), Sonora sucker (*Catosotmus insignis*) and roundtail chub (*Gila robusta*); species that are endemic to the Colorado River Basin. Nonnative fishes included yellow bullhead (*Ameirus natalis*), green sunfish (*Lepomis cyanellus*), smallmouth bass (*Micropterus dolomieu*), and red shiner (*Cyprinella lutrensis*); species with known ecological impacts (e.g. Ruppert et al. 1993, Dudley and Matter 2000, Propst et al. 2015). These seven species represent a range of body sizes and major life-history trade-offs between size and age at maturity (growth), juvenile survivorship (survival), and fecundity (reproduction) (Olden, Poff and Bestgen 2006). This range of functional traits is represented in dryland streams throughout the western U.S.

1.3.2 *Modeling framework*

All seven species populations were modeled simultaneously to represent the fish community of a one-kilometer river reach. The foundation was a stage-structured matrix population model for each species, modified to incorporate environmental variability and density-dependent relationships (Caswell 2001). The general model structure was adapted from a multispecies matrix population model originally designed to model riparian vegetation population dynamics as a function of river hydrology (Lytle and Merritt 2004, Lytle et al. 2017, Tonkin et al. 2018), but with a number of important modifications described below. Model implementation followed four major steps: parameterization, simulation, validation, and perturbation analysis. Parameter values were based on the flow regime, species biology, and biomass estimates. Model simulations projected fish community composition at annual time steps for each water year in the flow record (1964 – 2017). Model validation compared population and community model projections against the entire record of long-term fish surveys for the seven upper Verde sites from 1994 – 2008. Finally, perturbation analysis evaluated the effect of uncertainty in parameter estimates on the model output. These steps are described in detail below.

1.3.2.1 Parameterization: Streamflow, fish and flow-response relationships.

Hydrology in the upper Verde River mainstem is characterized by relatively steady, spring-fed baseflow, with high-flow events that vary in magnitude and timing among years in response to winter and summer storm runoff (Fig. 2A, Goetz and Schwarz 2018). Each time-step in the model represented one year. Using the historical flow record, each year was classified into a flow-event year-type according to the timing, magnitude, and duration of flows for a water year (1 Oct – 30 Sep) from USGS gage number 09503700 near Paulden, AZ. Flood events were defined using discharge thresholds based on recurrence intervals, and drought events were defined by the duration of baseflow (Fig. 2B). *Spring high-flood events* were years in which the maximum of late winter/early spring discharge (1 Jan – 30 Apr) exceeded 19.8 m^3s^{-1}, which has a 4-yr return interval during the spring time window (following Brouder 2001). *Spring medium-flood events*, corresponded roughly to bankfull flows, had a maximum discharge that exceeded 6.2 m^3s^{-1}, with a 2.5-yr recurrence interval in the spring (Phillips and Ingersall 1998, Neary et al. 2012). *Summer (and monsoon season) high-flow events* (1 May – 30 Sep) exceeded a maximum discharge of 5.7 m^3s^{-1}, representing a 4-yr recurrence interval in the summer. *Drought events* were categorized by the absence of floods, when low-flow conditions (i.e., 25th percentile of flows following Bêche et al. 2009) persisted for a continuous duration of 40 or more days (i.e., exceeding the 75th percentile duration of low-flow events). *Nonevents* occurred by default if years were otherwise not defined by flood or drought. A year type with both spring flood and summer high-flow events was possible, but all other flow events were mutually exclusive. This resulted in six possible years: spring high flood, spring medium flood, summer high flow, spring flood and summer high flow, drought, and nonevent (Fig. 2B).

The life-history adaptations of fishes to the flow regime are directly related to their vital rates (Lytle and Poff 2004). Because of the relationship between growth, survival, reproduction and the flow regime, the use of vital rates inherent to each species supports the transferability of our model to other riverine systems (Mims and Olden 2012, Chen and Olden 2018). We conducted an extensive literature search of peer-reviewed articles, graduate theses, and professional reports for each species, or closely related congeners, to determine parameter estimates for the vital rates used in the model (Table 1, Appendix S1).

Our integrated approach to demographic modeling requires knowledge of how these vital rates vary according to key components of the hydrologic regime. In another literature search, we reviewed studies about fish responses to flow components, specifically low-flow (drought) and high-flow (flooding) events in the Colorado River Basin as much as possible. Limiting our review to the Colorado River Basin minimized variability in vital rates that would be introduced by nonnative fish responses observed in other physiographic regions (Chen and Olden 2018). The breadth of information revealed in this literature review included observed relationships between abundance and discharge, effect sizes on changes in abundance in response to high- and low-flow events, and timing of reproductive behavior (Table 2). This analysis allowed us to assign different vital rates according to types of flow-event years.

The riverine flow regime affects two key life stages that ultimately shape fish population structure and dynamics: juvenile survival and recruitment, and adult survival to reproduction (Schlosser 1985, Humphries et al. 1999). Thus, we allowed the vital rates for each species to vary according to literature-informed relationships between major flow events and fish abundance. To implement this, we used species-specific flow modifiers to adjust baseline vital rates for each year type in the flow record (Appendix S1: Table S1.1). For example, juvenile survival and recruitment of roundtail chub and smallmouth bass are influenced by the magnitude and timing of high-flow events. Spring flooding increases recruitment of juvenile roundtail chub, whereas elevated summer flows increase mortality of juvenile smallmouth bass (Brouder 2001, Smith et al. 2005). Adult survival is most affected by extended droughts. Low-flow events reduce survival and abundances of species (e.g. Stefferud and Stefferud 1998, Ruhi et al. 2015). Droughts typically create conditions where fish suffer because of limited resources and degraded water quality conditions as stream reaches are reduced to shallow isolated pools (Deacon and Minckley 1974, Lake 2003). The magnitude of these flow modifiers is set to reduce or increase mortality by a factor related to trends and effect sizes that were obtained from studies conducted in the region, and occasionally from other watersheds when data for nonnative species were otherwise unavailable (Table 2, Appendix S1: Table S1.1).

1.3.2.2 Model structure and simulation

Each fish species was represented by a three-stage demographic matrix containing species-specific vital rates (Fig. 3, Table 1). The three life stages in the life cycle model represented important ontogenetic shifts for each species. These stages corresponded to: year-1, juvenile recruitment into the population; year-2, sub-adults at first maturity; and year-3 or older adults of fully mature and reproductive individuals (Fig. 3). The parameters within the life-cycle model were adjusted by species to reflect real differences in population stage structure and traits such as lifespan and age at maturity (details follow). Individuals in each stage of the model occupied biomass calculated from length-weight relationships (Appendix S1: Table S1.2). Lengths at each stage corresponded to literature reported values of young-of-year and/or immature fish (stage 1), average length at age of maturity (stage 2), and the average length of mature adult individuals from samples in the Upper Verde River (Appendix S1, unpublished data from Gibson et al. 2015).

Transition probabilities in the matrix differed according to the major flow-events, which allowed recruitment and survival to vary according to the hydrologic conditions in a particular year. The seven single-species demographic matrices were coupled via density-dependent relationships in reproduction, limited by the total biomass carrying capacity of a representative river reach. In this way, the reproductive output of each species declined as the total aggregate fish biomass of the entire community approached a reach-wide carrying capacity (see below). This generalized density-dependence is analogous to exploitative competition experienced by organisms competing for a single limiting resource (Hardin 1960). A similar approach has been implemented in multispecies models using spatial density-dependence (Lytle et al. 2017).

The model had several assumptions regarding carrying capacity and vital rates. First, we assumed that the carrying capacity of the reach was limited by the amount of total fish biomass that could be sustained. Carrying capacity, K, was set to the average total biomass found in a 1-km reach from surveys in nine replicate 100-m sampling sites located in the Upper Verde River and conducted in 2012 (Gibson et al. 2015). We chose to use average total biomass because some reaches will naturally be more or less productive and suitable for fishes than others. Second, population growth was limited by a density-dependent function in the reproductive term (fecundity, F) so no recruitment occurred if total biomass in the reach was greater than or equal to K (see below). Third, baseline mortality was the same for all life stages within each species, except for the egg and larval phase. The combination of egg and larval mortality was calculated as part of fecundity so that the starting population of adults produced sufficient offspring to equal their replacement after stage 1 and stage 2 baseline mortality was taken into account. Last, all species had a 1:1 sex ratio, and an individual's life cycle could be completed in a 1-km reach for all species. This is a reasonable assumption given that fishes in the Verde River typically occupy small home ranges and most fish move less than one kilometer (Jaeger et al. 2014, Comte and Olden 2018).

Species' biomass, rather than species abundances, was the currency for the model framework (although abundance and biomass values were interchangeable using the stage-specific weight of individuals). For each species *j* at each stage *i* for a given year type *k*, the biomass change from time *t* to time *t*+1 was given by:

$$\begin{pmatrix} B_{1j} \\ B_{2j} \\ B_{3j} \end{pmatrix}_{t+1} = \begin{pmatrix} F_{1\mathrm{j}} & F_{2\mathrm{j}} & F_{3\mathrm{j}} \\ G_{1jk} & 0 & 0 \\ 0 & G_{2jk} & P_{3jk} \end{pmatrix} \times \begin{pmatrix} B_{1j} \\ B_{2j} \\ B_{3j} \end{pmatrix}_{t} \tag{1.1}$$

where *Bij* was the total biomass (*g*) of the species at the corresponding life stage. Stage-specific fecundity (*Fij*) was linearly density-dependent on the total fish biomass in the community:

$$F_{ij} = \begin{cases} f_j \times (K - \sum_{i=1}^{m}\sum_{j=1}^{n} B_{ij}) \times K^{-1} \times D_{ej} \times D_{ij}^{-1} \; if \; \sum_{i=1}^{m}\sum_{j=1}^{n} B_{ij} \le K \\ 0, \; otherwise \end{cases} \tag{1.2}$$

$$f_j = 0.5 \times GSI_j \times \left(1 - M_{ej}\right) \tag{1.3}$$

where $i = 1, 2, \ldots, m$ was an index representing stages for each of $j = 1, 2, ..., n$ species in the community. Reach-wide carrying capacity *K* was the maximum aggregate biomass attainable for all species in all stages combined. Species began spawning at the stage that corresponded to the age of first maturity (Appendix S1, Fig. 3). Therefore, in each species' matrix, the number of fecundity (*F*) terms corresponded to the number of years the species can reproduce and was zero otherwise. For example, red shiner may begin reproducing in its first year of life, so the matrix had three fecundity terms, whereas yellow bullhead begin reproducing in their third year of life, so they had one fecundity term at stage 3.

The proportion of egg biomass (f_j) produced by all females in the population after accounting for mortality during the first year depended on the Gonadal-Somatic Index (*GSI*), the proportion of gonad mass to total body mass, the proportion of female individuals (0.5), and the vital rate or combined egg and larval mortality (M_{ej}). The egg biomass of each species was converted to stage 1 biomass to account for fish development and growth. We converted egg biomass using egg density (D_{ej}) in units of number of eggs per gram and the average weights of stage 1 idividuals (D_{1j}^{-1}; Table 1).

Egg density of each species was the average value calculated from literature reported values (Appendix S1) of the number of mature eggs in ripe females, divided by the total ovary mass. Ovary mass was reported or calculated using her length-weight relationship and *GSI*. If the relationship between total length and number of mature eggs was not published, egg density was estimated from the means of reported values.

The growth rate and survival probability (G) transitions from stage 1 to stage 2 and stage 2 to stage 3 were:

$$G_{ijk} = \left(1-(M_{ij} \times \mathrm{Y}_{ijk}\right)) \times \mathrm{D}_{ij} \times D_{(i+1)j}^{-1} \tag{1.4}$$

Survival was one minus mortality (M_{ij}) multiplied by a flow modifier Y_{ijk} for stage i at species j for flow event k (Table 2, Appendix S1: Table S1.1).

The probability of surviving and remaining in the adult stage was related to the literature-reported lifespan of each species:

$$P_{ijk} = (1-(M_{ij} \times Y_{ijk})) \times \left(1-a_{3j}\right) \tag{1.5}$$

where the probability that adults stay in stage 3 (a_{3j}) is the reciprocal maximum age of species j after accounting for the first two life stages of the model. At the end of each model run, biomass output was converted to abundance for subsequent data analysis and interpretation.

We ran 1,000 iterations of the model, simulating the community from 1964 through 2017. Each iteration began with different initial population sizes to account for spatial variation in abundance. Initial abundance for each species was sampled from a negative binomial distribution with mean λ and dispersion parameter κ calculated from the mean and variance in relative abundance of the long-term Verde dataset for all seven sites and 15 years of data (n = 105). As with a Poisson distribution, the negative binomial is appropriate for counts of organisms that occur randomly over time or space, but the negative binomial allows the variance to exceed the mean.

1.5.1.1 Model validation.

Model validation was performed by comparing population and community projections to data from long-term fish surveys from seven sites in the Upper Verde River between 1994 and 2008 (Stefferud and Rinne 1995, Rinne et al. 1998, Rinne 2012). Data from 2002 were omitted from the analysis because only two of seven long-term sites were surveyed. Relative annual species abundances, averaged across the seven sites, were compared to model projected relative abundances according to the sum of non-juvenile (stage 2 and 3) individuals because juveniles (stage 1) are underrepresented by electrofishing survey methods due to their more cryptic behavior and small body size (Bonar et al. 2009). Relative abundance was chosen over absolute abundance because survey effort was not reported and was not always consistent between years, despite the use of a standardized collecting protocol. The strength of association between observed and modeled relative abundances was assessed using Spearman rank correlations. Spearman rank correlations are reported for each species across years and each year across species between 1994 and 2008, again omitting 2002. We also reported root mean square error (RMSE) and coverage (C), the percentage of 95% confidence intervals that overlap true values, to evaluate model performance.

1.5.1.2 Perturbation analysis

The influence of model uncertainty was evaluated with respect to mortality rate, GSI, flow event thresholds, and biomass carrying capacity. These values were chosen because they are the most likely to affect transitions between life stages (i.e., mortality rate), fecundity/reproduction (i.e., *GSI*), species responses to environmental changes (i.e., flow-event thresholds), and outcomes in species dominance (i.e., biomass carrying capacity). We conducted a direct perturbation analysis (*sensu* Regan et al. 2003, Bond et al. 2014) to estimate the effects of parameter uncertainty by adjusting each value by ±10% of the starting value. Flow-events were evaluated by adjusting thresholds of spring and summer high-flow events and duration of low-flow drought events. Uncertainty was quantified by the proportional change in species' relative abundances in response to parameter adjustments. Perturbation analysis was favored over analytical sensitivity analysis (via partial differentiation of a vital rate with respect to population growth rate) because it can be used to evaluate uncertainty in non-matrix elements, such as carrying capacity, and it does not require calculation of the long-term population growth rate (Akçakaya et al. 2003, Stott 2016). The model simulation and all analyses were performed with program R v.3.4.0 (R Core Team 2017).

1.6 Results

Model population projections reflected compositional trends observed in the long-term fish surveys conducted from 1994 to 2008 (Fig. 4). During this validation period, trends in observed relative abundances of green sunfish, smallmouth bass, yellow bullhead, and roundtail chub were aligned with the simulated model populations (Fig. 4C, D, F, G). Model performance was best for green sunfish, with highest values for correlations (*r*), coverage (C), and lowest prediction errors (RMSE) (Fig. 4F). The remaining species demonstrated varied correlations, coverage, and prediction errors. Predictions for relative abundance for roundtail chub and smallmouth bass were significantly correlated with observed data and had low to moderate prediction errors (Fig. 4C, G). Both smallmouth bass and yellow bullhead had high coverage (Fig. 4D, G). Desert sucker predictions correlated moderately well with observations and had moderate prediction errors and coverage (Fig. 4A). By contrast, the model tended to overestimate Sonora sucker and underestimate red shiner relative abundances (Fig. 4B, E). Relative abundances of red shiner, a species with small maximum body size that often occurs patchily in large schools of individuals, varied greatly among sites, evidenced by the large error bars (Fig. 4E). Sonora sucker had the lowest correlation with survey data and lowest coverage because the model did not capture an observed shift toward lower relative abundance in the middle of the survey period.

Community structure shifted from native dominant to nonnative dominant over the course of the model simulation period. Native species comprised approximately 80% of total abundance at the beginning of the validation period (1994) for both model and survey data (Fig. 5). Then, after a series of drought and nonevent flow years, there was a marked transition toward nonnative dominance. At the end of the observed survey data, after a spring high-flood event in 2005, native species rebounded to represent 50-60% of the assemblage abundance (Fig. 5). Model simulations followed the general trend of decreasing, then increasing native abundances, but the magnitude of the model fluctuations was dampened compared to survey observations (Fig. 5). Despite some differences in magnitude, overall there was a strong correlation between rank order abundances of species between model projections and survey observations (mean $r \pm$ SE: 0.67 ± 0.018) with significant annual correlations for half (7 out of 15 years) of the validation period (Appendix S1:

Table S1.3). The model performed poorly between 1999 and 2005, coinciding with a period in the flow record from 1996 to 2004 that lacked spring flood events, which are important for juvenile (stage 1) survivorship of native Sonora sucker, desert sucker, and roundtail chub (Table 1, Appendix S1: Table S1.1). Beyond the period of the fish survey (post-2008), the modeled community projection, in response to observed streamflows, continued to gradually shift from native to nonnative dominant assemblage to the end of the flow record in 2017. Put in the perspective of flow events, the last ten years of the model had a drought frequency of 30%, compared to 9% drought frequency of the full flow record (Fig 2B).

Perturbation analysis on species vital rates had the largest effects on overall community composition, a larger effect than was seen by perturbing flow thresholds or biomass carrying capacity (Table 3). Perturbation of desert sucker and green sunfish mortality and red shiner reproduction (GSI) had the largest influence on community composition overall, but the most affected species was always the one whose parameter was being perturbed. For example, when desert sucker’s mortality rate experienced a 10% decrease, their relative abundance increased by 58% while other species compensated for this increase with a decline of 14% to 23% relative abundance. A decrease in red shiner’s GSI parameter resulted in a 44% decrease in their relative abundance with a compensatory increase of 6% to 30% for the other species. This species, with its short lifespan, small body size, and high reproductive rate, was the most influential among changes in GSI, but also the most influenced by increased carrying capacity. When carrying capacity for a reach was increased, red shiner relative abundance increased by 17%, due to its high reproductive rate. Other members of the community had smaller changes in relative abundance, with declines of 4% to 9%.

Perturbation analysis in flow event thresholds demonstrated that community composition was most influenced by increasing the threshold of spring medium-flood events and decreasing the threshold of summer high-flow events. By increasing the spring threshold, two fewer spring flow events and two more nonevent years occurred during the hydrologic record. This influenced community composition by increasing yellow bullhead and green sunfish relative abundance by 39% each, accompanied by smaller increases in relative abundance for the other nonnative species, and decreases in relative abundance for the native species (Table 3). By contrast, decreasing the threshold for summer high-flow events resulted in three fewer nonevent years and a decrease in yellow bullhead and green sunfish relative abundance by 35% and 52%, respectively, but with minor or no changes to the relative abundance of the other species (Table 3).

1.7 Discussion

Demographic models provide new opportunities to better understand species responses to shifting environmental conditions such as climate-induced changes to hydrologic regimes and human-caused flow alteration (Shenton et al. 2012, Bond et al. 2018). Approaches that enable temporally specific predictions of species responses to specific flow sequences are likely to be most useful in practice (Wheeler et al. 2017). Here, we used a demographic modeling approach to simulate how a hydrologic record of drought and flood events interact with species' vital rates to shape native and nonnative fish composition in a dryland river. Although biotic interactions, such as competition and predation, were not specified *a priori* in the model framework, pairwise species interactions arose from the model structure itself due to the assumption of aggregate density dependence. The approach captured community trends using trade-offs in flow-related mortality of different life stages, as evidenced by predicting ranked abundances of species over a decade-and-a-half time period. Mismatches between modeled and observed numbers were most noticeable for species with vital rates that are difficult to obtain, or arose from potential life histories that lead to observation error associated with field survey methodology. Mechanistically representing trends in community response to environmental drivers using independently published vital rates opens up the possibility for hypothesis testing and scenario analysis for exploring management options for multiple species at once.

In our simulated model of the Verde River, overall patterns in community structure, over a 54 year period, demonstrated that more frequent drought events and fewer spring flood events created conditions where native fishes fared poorly compared to nonnative fishes. This finding is supported by empirical research in dryland rivers of the same region (Propst et al. 2008, Gido and Propst 2012, Gido et al. 2013). In the model, both nonevent years and droughts supported population growth by nonnative species. Nonevents represent years of steady baseflows that favored the survival of all juvenile nonnative fishes and adult life stages of yellow bullhead, red shiner, and green sunfish. Similarly, during drought years, native suckers (Sonora sucker and desert sucker) and roundtail chub experienced high mortality rates in both juvenile and adult life stages. By contrast, nonnative species had lower mortality rates for juvenile life stages, and depending on the species, had higher or lower mortality rates for adult life stages during drought. Higher mortality rates of large native species (i.e., the suckers) during drought years facilitated a compensatory response by nonnative species. That is, newly available portions of carrying capacity in the form of biomass were taken up by small- and medium-bodied fishes with high reproductive and low mortality rates during drought years (i.e., red shiner and green sunfish).

Past research demonstrates that droughts modify the spatiotemporal connectivity of riverine habitats, ultimately driving patterns in the composition and trophic structure of fishes (Matthews and Marsh-Matthews 2003, Rolls et al. 2016). As streamflows decline, fishes move to seek deep refuge pools (Labbe and Fausch 2000, Magoulick and Kobza 2003, Marshall et al. 2016). As pool habitats contract, the density of organisms initially increases with several consequences. First, smaller volumes of water concentrate prey, providing a food subsidy and increasing survival probability for young-of-year fishes for species spawning in warm months, or for extended breeding seasons (Schlosser 1985, Craven et al. 2010). In the Verde River, all nonnative species included in this study spawn during the warm spring-summer months. Of these, red shiner has the longest breeding season being a serial spawner, thereby performing well in drought years. Second, crowding intensifies predation and competition for resources among fishes (Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2006). In rivers of the southwestern USA, nonnative fishes such as smallmouth bass, green sunfish and yellow bullhead, outcompete or consume native fishes, especially juvenile life stages or small-bodied species, leading to local extirpations and community change when streamflow variability declines (Eby et al. 2003, Stefferud et al. 2011). Eventually, the combination of low flows and negative species interactions may lead to local native species extirpation. For instance, in the Verde River, the small-bodied native spikedace (*Meda fulgida*) has already been lost from the system but maintains viable populations where it has been repatriated in streams without nonnative fishes (Neary et al. 2012). As a corollary, high flows tend to favor native species, sometimes at the cost of nonnative species. In particular, spring floods may displace nonnative species and delay their reproduction (e.g. Propst and Gido 2004). This suggests that low-flow conditions favor species invasions (Bêche et al. 2009, Diez et al. 2012) and can have prolonged consequences even after the cessation of drought (Humphries and Baldwin 2003).

In the model results, low frequency or absence of spring flood events was detrimental to native fish populations. As observed in the perturbation analysis, minor increases in thresholds for medium spring flood events increased the number of nonevent years in the hydrologic period of record. This resulted in lower relative abundances of native species, including both sucker species and roundtail chub. The absence of spring flood events for nine years during the model simulation led to lower population growth rates for native species. The lack of spring flood events, which favored juvenile recruitment, resulted in native species experiencing higher mortality rates compared to nonnative species during these times. Therefore, given that the average lifespan of native species in this study range from 5 to 10 years, it is likely that low recruitment potential for the nine-year period was detrimental to the persistence of these fish populations.

We found that native fish populations trended downward as nonnative fishes became dominant during a period of more droughts (three occurrences) and nonevents (two occurrences) starting in 2008. This decline was only punctuated by minor increases in native fish abundances following 2010 and 2015 spring floods. Because our model simulates a closed community with no rescue effects, once native fish population growth rates experienced a precipitous decline for several consecutive years after droughts, species within the model community were more likely to go extinct than in observational studies of riverine fish communities. Unlike our model community, fish communities observed under prolonged and supra-seasonal droughts can be resilient in spatially-connected landscapes. For example, communities may eventually recover to pre-drought composition if deep refuge pools persisted during drought or other locations acted as sources for recolonization following the cessation of drought (Davey and Kelly 2007, Matthews et al. 2013, Rolls et al. 2016). However, persistent low-flow conditions have caused long-term changes in community structure where species adapted to low-flow conditions expanded their range and increased in abundance with complementary reductions in species favored by high flows (Lawson and Johnston 2016).

Demographic models that link species vital rates with hydrology have the advantage of addressing differential responses of native and nonnative fishes to streamflow variability because they leverage mechanistic associations between populations and specific flow events. This modeling approach implicitly includes species interactions via the density-dependent relationship between reproduction and biomass carrying capacity, but does not explicitly include trophic interactions such as predation. For this reason, as with most modeling approaches, the strength of our conclusions depend on how much variability in population and community structure is explained by the unknown true contribution of flow events to demographic responses compared to other factors. Separating the influence of flow conditions independent of other extrinsic environmental factors, including species interactions, is inherently difficult (Chen and Olden 2018). However, a number of observational studies have demonstrated that the importance of biotic interactions in shaping fish communities are often overridden by environmental forcing (Grossman et al. 1998, Ruhí et al. 2015, Giam and Olden 2016, Bino et al. 2017). Our goal was to develop and present a transferable approach to modeling multiple species within a community, an approach that allows for the incorporation of non-stationary environmental change and demographic variability. Continued research will help establish the relative strength of different drivers to demographic and community responses and help improve model performance and interpretation of model results.

A persistent challenge of community modeling is to simultaneously represent all individual species (e.g. Olden, Joy, and Death 2006). Individual species correlations between observed and simulated model data were moderate, but it is important to note that our model predictions were derived from independently reported parameters. In other words, the demographic multispecies model we have presented is unlike a statistical model where empirical data are used to fit model parameters. Rather, model performance depended solely on independent information, including that from literature-based vital rates, initial population sizes taken from a probability distribution, and empirically-informed flow modifiers. Discrepancies between observed and modeled results were at least partially due to uncertainty in parameter estimates. Despite long interest in flow-ecology relationships, the strength of our understanding of these associations for all species in a community remain limited (Davies et al. 2014, Rosenfeld 2017). Vital rate and flow-dependent transition parameters can be adjusted as new empirical knowledge is gained. Although no one method is perfect, natural observations and in-stream or mesocosm experiments remain critical for acquiring vital rate information as a function of streamflow and will help further improve model predictions of community structure (Shenton et al. 2012, Wheeler et al. 2017, Poff 2018).

Discrepancies between model predictions and observed values may also occur because of observation error. For example, we found that model predictions underestimated the abundance of red shiner and overestimated the abundance of Sonora sucker. Together, these discrepancies led to a period where native dominance in the community was overestimated. Models for red shiner demonstrated the poorest performance, which may be due to highly variable sampling efficiencies due to the schooling behavior of this species. Sampling bias may also affect the observation of species with large maximum body sizes such as Sonora sucker and smallmouth bass. Older age groups of these species may be observed less than expected by model predictions because they occupy habitats too deep to sample with standard seining and backpack electrofishing techniques. Although fish surveys document low-recruitment periods during dry years with smaller sample sizes of Sonora sucker in wadeable habitats, model projections of adult Sonora sucker were relatively stable. This apparent stability may reflect mechanisms related to the temporal storage effect, whereby species are able to store up gains during favorable periods to persist during non-favorable periods, enabling multiple species to coexist in variable environments (Chesson and Warner 1981). Here, high-recruitment periods (i.e., spring flood years) allow Sonora sucker populations to remain stable because long-lived adults survive through periods more favorable to other species.

In our model, the sequence of flow events appeared to support long-term multispecies coexistence, by favoring different species in years with different environmental conditions, at least over the 54-year time frame examined in this analysis. In explorations over longer timescales (centuries or longer), the model is expected to eventually predict the complete dominance of a single species - the species with traits that resulted in the highest stochastic population growth rate for that particular hydrologic regime – due to the fact that we are modeling finite populations in a finite reach under stochastic conditions. Body size, age at maturity, and fecundity represent strong trade-offs in the life-history strategies of fishes (Olden et al. 2006). Therefore, one might expect that the largest or earliest maturing species with the highest fecundity or reproductive rate, respectively, would always outcompete all other species in the community (Cushing 1992). However, because modeled vital rates are tightly coupled to flow conditions, patterns reflected observed species coexistence dynamics. In the model, the sequence and frequency of particular flow events played an important role in determining which species persisted over longer timescales.

Demographic models can be applied to any component of river ecosystems to explore species responses to changing hydrology, or other drivers of persistence and mortality. Where vital rates are known, they have been applied to individual species or functional guilds of invertebrates (McMullen et al. 2017), riparian plants (Lytle et al. 2017, Tonkin et al. 2018) and fish (Yen et al. 2013). Demographic models are also flexible because different parameters may be applied to forecast the effects of environmental change in other ecosystems (McMullen et al. 2017). For example, one could apply our model to another stream system by adjusting or transferring, when appropriate, species vital rates and flow event thresholds specific to the hydrograph and ecology of the system of interest. The flexibility of these models, and ability to predict non-stationary temporal dynamics, make them useful for exploring scenarios of environmental change and the outcomes of various flow management interventions into the future. Instream flow management plans to benefit species and ecosystems are often challenged by other competing demands on river flows, and population models that forecast the outcomes of various flow futures are a valuable and much-needed tool for decision makers.

1.8 Acknowledgments

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1.9 Supporting Information

For all code and data required to reproduce the results refer to Metadata S1.

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1.11 Tables

Table 1.1. Model parameter values for species vital rates. Parameters included the Gonadal-Somatic Index (GSI_{ij}), the conversion factor from individuals to biomass for eggs (D_{ej}), stage 1 juveniles (D_{1j}), stage 2 sub-adults (D_{2j}), stage 3 (D_{3j}), egg and larval mortality (M_{ej}), and mortality (M_{ij}) and transition probability of adults persisting in stage 3 (a_{3j}) for each stage i and species j in the model. Species codes are four letter abbreviations of the scientific names for the seven native and nonnative species used throughout the manuscript. References for vital rate parameter estimates can be found in Appendix S1.

Parameter	Native species Desert sucker *(Catostomus clarki)*	Sonora sucker *(Catostomus insignis)*	Rountail chub *(Gila robusta)*	Nonnative species Yellow bullhead *(Ameiurus natalis)*	Red shiner *(Cyprinella lutrensis)*	Green sunfish *(Lepomis cyanellus)*	Smallmouth bass *(Micropterus dolomieu)*
GSI_{ij}	0.08	0.14	0.06	0.06	0.11	0.1	0.07
D_{ej} (eggs/g)	894	345	1000	533	2123	667	484
D_{1j} (indiv/g)	0.28	0.03	0.11	0.07	6.65	0.86	0.23
D_{2j} (indiv/g)	0.113	0.004	0.019	0.009	3.735	0.249	0.010
D_{3j} (indiv/g)	0.014	0.002	0.008	0.007	0.618	0.094	0.007
M_{ej}	0.999154	0.999869	0.999409	0.998945	0.98855	0.99138	0.999367
M_{ij}	0.29	0.212	0.31	0.356	0.32	0.43	0.188
a_{3j}	0.167	0.167	0.2	0.2	1	0.333	0.25
B_3j (λ, κ) start	5284, 1.52	34068, 1.33	2376, 0.44	1306, 0.36	238, 1.78	164, 0.34	4202, 0.66

Table 1.2. Evidence for flow-response relationships in the study region. Information presented includes the directionality of response to generalized flow attributes reported in the literature (+ / -), list of relevant fish species, the dependent response variable to the flow attribute, and supporting references. Flow modifier values assigned according to these relationships are provided in Appendix S1: Table S1.1.

Flow Attribute	(+ / -)	Species	Response Variable	References
High flows (spring)	+	*Catostomus sp., Gila sp.*	Abundance/density	Propst and Gido 2004, Propst et al. 2008, Stefferud et al. 2011, Gido et al. 2013, Ruhi et al. 2015
High spring flows	+	*Gila robusta*	Recruitment	Brouder 2001
High flows (summer, spring, or number of events)	-	*Ameiurus sp., Cyprinella lutrensis, Lepomis cyanellus, Micropterus sp.*	Abundance/density	Minckley and Meffe 1987, Propst et al. 2008, Gido et al. 2013, Ruhi et al. 2015
High summer flows	-	*Micropterus dolomieu*	Recruitment	Smith et al. 2005
Low flows (constant baseflow)	+	*Ameiurus sp., Cyprinella lutrensis, Lepomis cyanellus, Micropterus sp.*	Abundance/density	Propst and Gido 2004, Propst et al. 2008, Gido et al. 2013, Ruhi et al. 2015

Flow Attribute	(+ / -)	Species	Response Variable	References
Low flows	-	*Catostomus sp.*, *Gila sp.*	Abundance/density	Stefferud and Stefferud 1997, Propst et al. 2008, Stefferud et al. 2011, Gido et al. 2013, Ruhi et al. 2015

Table 1.3. Species' relative abundance responses to model perturbation analysis. Relative changes resulted from ± 10% change in parameters for species mortality (M_{ij}), Gonadal-Somatic Index (GSI_{ij}), flow event thresholds, and maximum biomass carrying capacity (K). For each species, the table displays the directional change (i.e., + or -) that had the greatest effect on species responses. Ranked responses represent the largest absolute change in relative abundance across species in descending order. Bold text highlights the species with the greatest response to each affected parameter. Abbreviations for flow event year (SP_HF = spring high flood, SU_HF = summer high flood, SP_MF = spring medium flood, DR_length = length of the drought period)

Parameter	Δ ± 10%	Desert sucker	Sonora sucker	Roundtail chub	Yellow bullhead	Red shiner	Green sunfish	Smallmouth bass	Rank
M_{ij}									
Desert sucker	-	**0.58**	-0.19	-0.19	-0.23	-0.20	-0.21	-0.14	2
Sonora sucker	+	0.13	**-0.29**	0.25	0.13	0.08	0.15	0.20	7
Roundtail chub	-	-0.08	-0.10	**0.88**	0.03	-0.12	-0.09	-0.03	5
Yellow bullhead	-	-0.04	-0.06	0.00	**1.23**	-0.04	0.00	-0.07	4
Red shiner	+	0.17	0.03	0.16	0.10	**-0.28**	0.15	0.12	13
Green sunfish	-	-0.04	-0.13	-0.03	0.00	-0.04	**1.94**	-0.07	1
Smallmouth bass	-	0.00	-0.06	-0.01	-0.03	-0.08	0.12	**0.51**	16
GSI_{ij}									
Desert sucker	+	**0.46**	-0.16	-0.16	-0.03	-0.16	-0.03	-0.05	11
Sonora sucker	-	0.13	**-0.32**	0.21	0.06	0.12	0.24	0.17	6
Roundtail chub	-	-0.04	-0.06	**0.75**	-0.06	-0.08	-0.06	0.00	10
Yellow bullhead	+	-0.04	0.00	0.00	**0.68**	-0.08	-0.06	0.10	14
Red shiner	-	0.21	0.10	0.06	0.19	**-0.44**	0.30	0.15	3
Green sunfish	+	-0.04	-0.03	0.03	0.00	-0.08	**0.97**	0.03	8
Smallmouth bass	+	0.00	-0.03	-0.05	0.00	-0.08	-0.06	**0.63**	15
Flow									

Parameter	Δ ± 10%	Desert sucker	Sonora sucker	Roundtail chub	Yellow bullhead	Red shiner	Green sunfish	Smallmouth bass	Rank
SP_HF	-	0.04	0.00	0.04	**-0.06**	-0.04	0.03	0.02	19
SU_HF	-	0.04	0.06	0.00	-0.35	-0.04	**-0.52**	0.03	12
SP_MF	+	-0.13	-0.06	-0.05	**0.39**	0.08	**0.39**	0.05	9
DR_length	+	0.08	-0.03	0.06	0.10	-0.08	**-0.12**	0.03	18
K									
Biomass	+	-0.06	-0.05	-0.05	-0.09	**0.17**	-0.04	-0.05	17

1.12 Figures

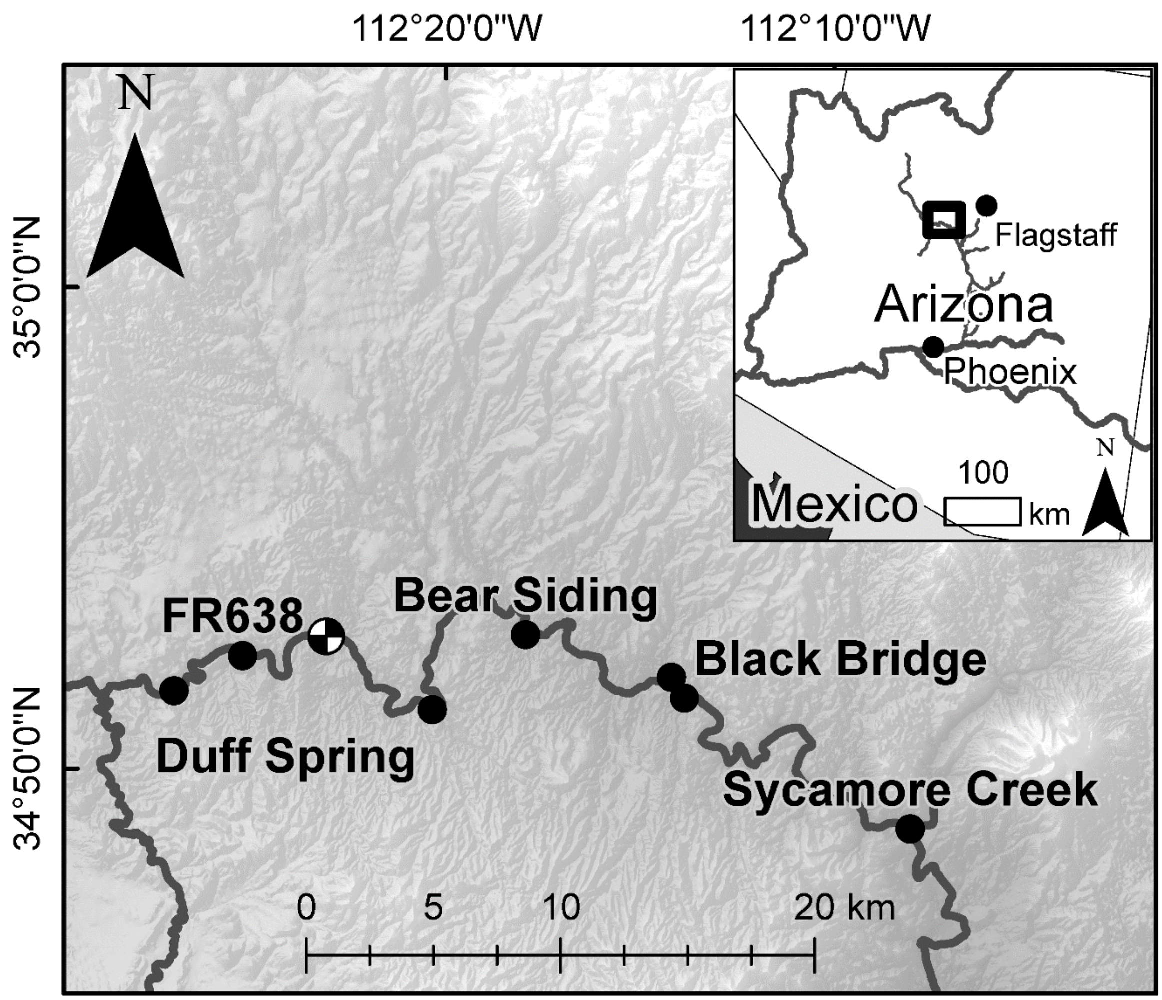

Figure 1.1. Study area map depicting the seven long-term fish survey monitoring sites (black dots) and USGS gage (09503700; black and white checkered circle) on the upper Verde River. The black box in the inset map shows the location of the study area in Arizona, USA.

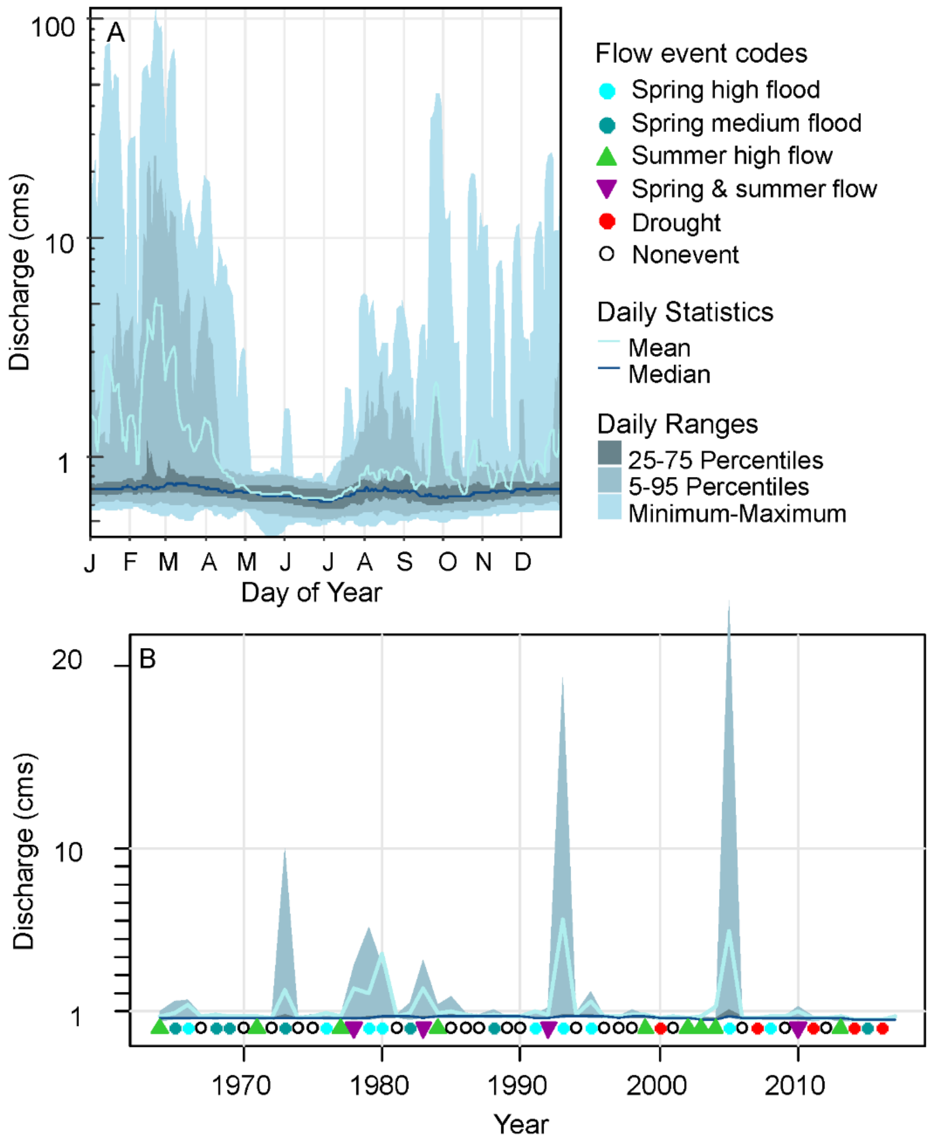

Figure 1.2. Hydrograph for the Upper Verde. Data were sourced from USGS gage (09503700) near Paulden, AZ. The top panel (A) is a summary of daily discharge statistics for a calendar year with a rolling 7 day average window. The bottom panel (B) is a summary of annual flows for the period 1964 – 2017 in cubic meters per second (cm•s^{-1}). Represented values include median annual flows (dark blue line), mean annual flows (light turquoise line), and percentile ranges as explained in the figure key. The min-max range was omitted from the bottom panel for clarity. Symbols below the hydrograph indicate the flow event assigned to each water year (1 Oct – 30 Sep) with colors delineated in the figure key.

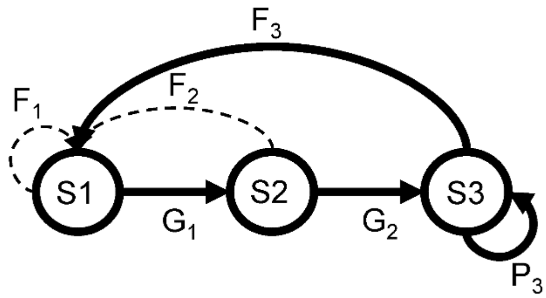

Figure 1.3. Generic life-cycle graph for fish species, with one year projection intervals. Each circle represents a life stage (S_i): juveniles (S1), sub-adults (S2), and mature individuals (S3). Each arrow represents a transition between life stages with probabilities of growth and survival (G_i), surviving and remaining in the same stage (P_i), or reproduction (F_i). All fish reproduce by S3. Dotted lines represent arrows for species who begin reproducing in their first or second year of life, at S1 or S2, respectively.

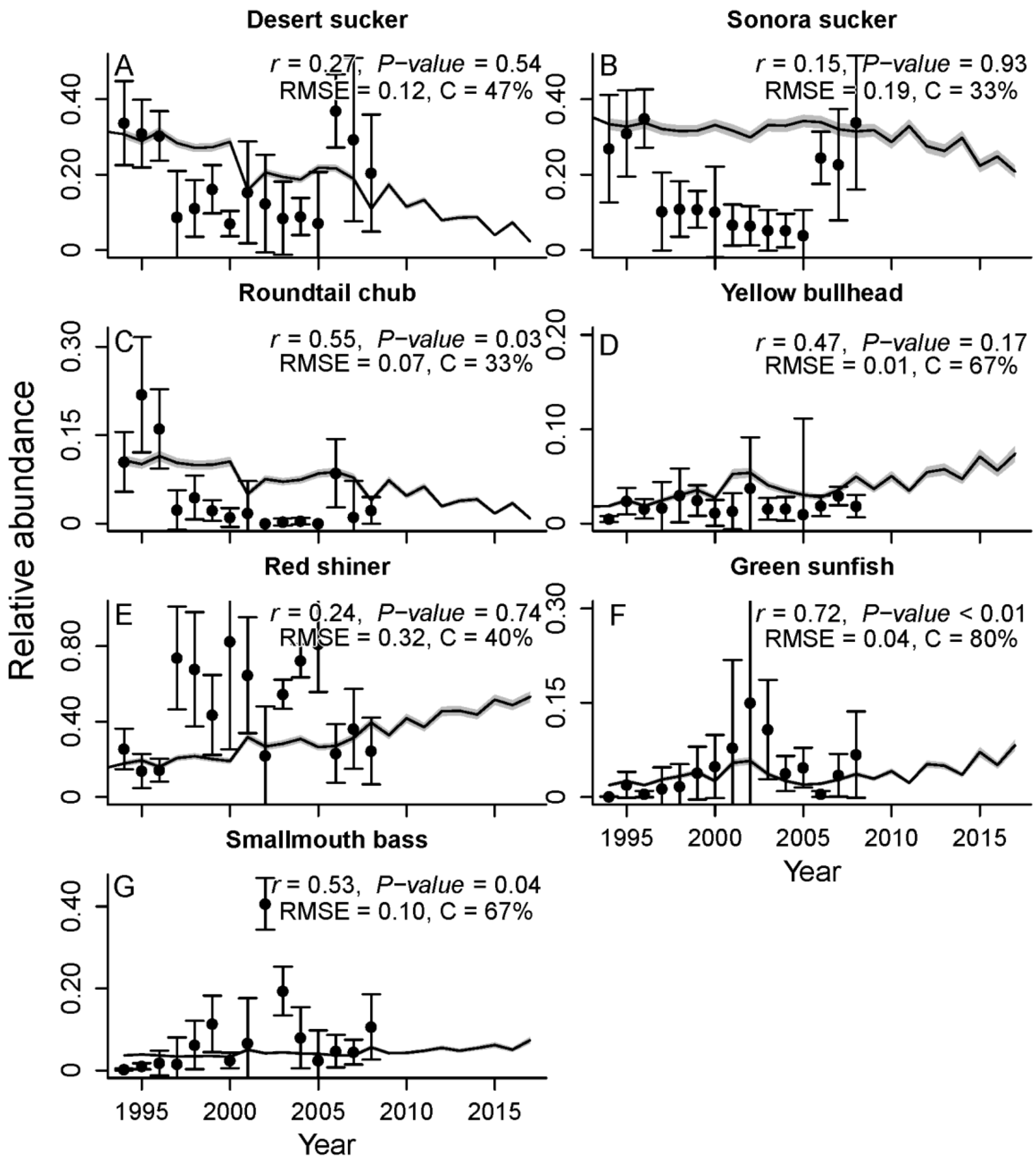

Figure 1.4. Modeled (lines) and observed (dots) relative abundances through time for native (A - C) and nonnative (D - G) fish species. Model and observed data include 95% confidence intervals, grey bands and error bars, respectively. In the upper right corner of each panel, root mean square error (RMSE) is a measure of the difference, and Spearman rank correlations (*r*) is a measure of the association strength, and coverage is a measure of the percent overlap, between observed and model values.

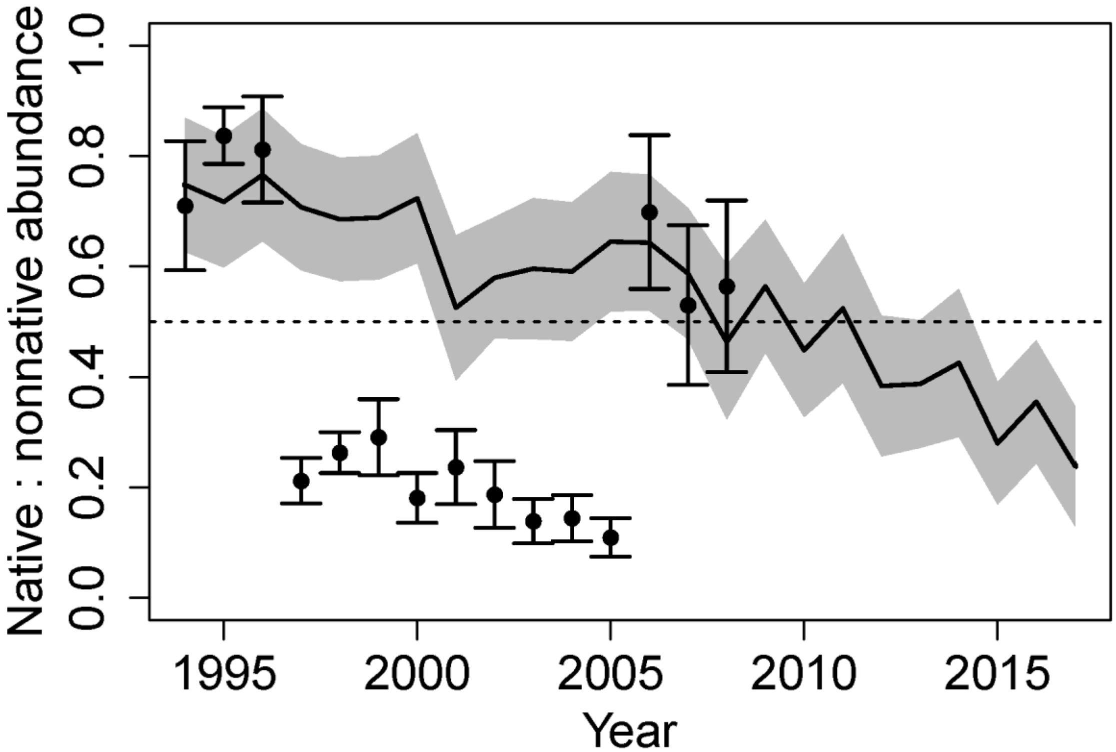

Figure 1.5. Ratio of native species to nonnative species abundance. Presented are model predicted mean (black solid line) and 95% confidence intervals (grey band), and observed mean (points) and 95% confidence intervals (whiskers). Correlations between observed and modeled data for each year are available in Appendix S1: Table S1.3.

1.13 Chapter 1 Appendix

1.13.1 *Supporting Information: Metadata S1*

1.13.1.1 Verde fish model

Code and data associated with Rogosch et al. manuscript examining fish communities in the Verde River, AZ, USA. The model is a community-wide stochastic matrix population model that links population dynamics with river flow regimes.

1.13.1.2 Code files

- `fish-model-all-spp.R`: The core model used to generate results in the manuscript: community-wide stage-structured stochastic matrix population model (7 spp.).
- `make-multiflow.R`: This is code to make a list of all possible future flow regimes. Pulls hydrograph data from USGS. This will then get read into the main model (`fish-model-all-spp.R`) as a list.
- `functions.R`: Some functions used in running the various scripts.
- `fish-model-flowsims.R`: Code used for simulations of spp combinations. This is to be run in combination with shell script (not included in repo) on HPC. This is not part of the Rogosch et al. manuscript.

1.13.1.3 Raw data files

- `vital-rates.csv`: Vital rates needed to run the model.
- `modifiers-all-spp.csv`: Modifiers that act on the vital rates under different hydrograph settings.
- `Rel_Abu_Verde_94-08.csv`: Empirical fish relative abundance data from the Verde River, used to test model.

The remaining data is generated from the various scripts. But generated flow data required to run `fish-model-all-spp.R` is included in the repo.

1.13.1.4 Code and data availability

The model simulation and all analyses in the manuscript were performed with program R v.3.4.0. License information and all code and data required to reproduce the results can be found at https://doi.org/10.5281/zenodo.1309024

1.13.2 *Supporting Information: Appendix S1*

1.13.2.1 References for vital rates

Desert sucker

- Reproductive timing/temperature, clutch size, lengths at life stages (Minckley 1973, Ivanyi 1989, Ivanyi et al. 1995)
- Average adult length, length-weight (Gibson et al. 2015 unpublished data using 143 individuals)
- Longevity (for congeners; Klein et al. 2017)
- GSI, ages and lengths at life stages (for congeners; Carothers and Minckley 1980, McCall 1980, McAda and Wydoski 1983, Propst et al. 2001)

Sonora sucker

- Reproductive timing/temperature, lengths (Minckley 1973, Minckley and Marsh 2009)
- Age at maturity (Frimpong and Angermeier 2009)
- Length-weight (Gibson et al. 2015, unpublished data using 109 individuals)
- Longevity (for congener; Klein et al. 2017)
- Clutch size, GSI, length at maturity (for congeners; Kennedy and Kucera 1978, Hinck et al. 2007, Bowron 2008, Mendoza 2016, Begley et al. 2017)

Roundtail chub

- Reproductive timing/temperature, clutch size, GSI, ages and lengths at life stages, longevity (Brouder et al. 2000, Brouder 2005, Brouder et al. 2006)
- Effects of floods on recruitment (Brouder 2001)

Yellow bullhead

- Reproductive timing/temperature, GSI, lengths and ages at life stages (for congener; Copp et al. 2016)
- Length-weight (Gibson et al. 2015, unpublished data using 22 individuals)
- Age, length, and longevity (Murie et al. 2009)

Green sunfish

- Reproductive timing/temperature, GSI (Kaya and Hasler 1972)
- Clutch size (Carlander 1977)
- Length-weight (Mannes and Jester 1980)
- Age at maturity (Moyle 2002, Wang 1986)

- Lengths at life stages, longevity (Delp et al. 2000, Quist and Guy 2001)
- Resilience to drought (Bêche et al. 2009)

Smallmouth bass

- Reproductive timing/temperature, clutch sizes, GSI (Minckley 1973, Moyle 2002, Dauwalter and Fisher 2007, Blazer et al. 2012)
- Longevity (Smith et al. 2005)
- Length-weight relationship (Lawrence et al. 2015)
- Lengths and ages at life stages (Knotek and Orth 1998, Robertson and Winemiller 2001, Dauwalter and Fisher 2007, Jackson et al. 2008, Humston et al. 2015)

Red shiner

- Reproductive timing/temperature, GSI, clutch sizes (Gale 1986, Marsh-Matthews et al. 2002, Brewer et al. 2008, Herrington and DeVries 2008)
- Longevity (Matthews et al. 2001, Quist and Guy 2001, Yildirim and Peters 2006)
- Length-weight (Franssen et al. 2007)
- Length and ages at life stages (Marsh-Matthews et al. 2002, Brewer et al. 2006, Yildirim and Peters 2006, Herrington and DeVries 2008)

1.13.2.2 Appendix Tables: Information tables about vital rates and references for vital rates

Table S1.1. Flow modifiers derived from flow-ecology relationships in literature (see also Table 2 and main text for references and details). Flow modifiers (Y_{ijk}) act on baseline mortality rates (*Mij*; Table A3) specific for stage *i*, species *j* and flow-event year *k*. Values greater than 1 increase mortality, values less than 1 decrease mortality. Abbreviations for flow event year (SP_HF = spring high flood, SU_HF = summer high flood, SP_MF = spring medium flood, NE = non-event, DR = drought). S1 = post-larval young-of-year fishes, S2 = size at first maturity, S3 = average adult size in population.

Stage	Flow Event	Desert sucker	Sonora sucker	Roundtail chub	Yellow bullhead	Red shiner	Green sunfish	Smallmouth bass
S1	SP_HF	0.1	0.1	0.1	1	1	1	1
S1	SU_HF	1	1	1	2	1.5	2	2
S1	SP_MF	0.2	0.2	0.2	1	1	1	1
S1	NE	1	1	1	0.1	0.3	0.1	0.1
S1	DR	2	2	2	0.2	0.2	0.2	0.2
S2, S3	SP_HF	1	1	1	1	1	1	1
S2, S3	SU_HF	1	1	1	1	1.5	1	1
S2, S3	SP_MF	1	1	1	1	1	1	1
S2, S3	NE	1	1	1	0.1	0.3	0.2	1
S2, S3	DR	3	3	3	1	0.2	1	1.5

Table S1.2. Length-weight relationships. Length-weight relationships used to calculate biomass for individuals at all three life stages based on their lengths at the end of their first year (L_1), length at maturity (L_2) and average adult length (L_3; see also ”References for vital rates” above). Column headings correspond to variables in the length-weight formula ($W = aL^b$).

	a	*b*	L_1	L_2	L_3
Desert sucker	9.76E-06	3.038	68	92	180
Sonora sucker	9.61E-06	3.022	152	282	360
Roundtail chub	7.89E-06	3.022	101	181	237
Yellow bullhead	7.03E-06	2.920	99	200	218
Red shiner	5.75E-06	3.160	25	30	53
Green sunfish	3.31E-05	3.356	45	65	87
Smallmouth bass	1.16E-06	3.020	70	200	222

Table S1.3. Spearman rank correlation between modeled and observed community composition for the validation period. The correlation for each year (*rho*) is based on relative abundances (mean ± (SE)) of adult-life stages (S2 + S3) for modeled (Model) and observed (Obs) data. Asterisks (*) indicate years with significant monotonic correlations between model and observed community composition (*P-value*; for α level of 0.05). Correlation from 2002 was not reported because only two of the seven monitoring sites were sampled that year.

Year	Desert sucker		Sonora sucker		Roundtail chub		Yellow bullhead		Red shiner		Green sunfish		Smallmouth bass			
	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	*rho*	*P-value*
1994	0.337 (0.057)	0.297 (0.006)	0.269 (0.073)	0.336 (0.008)	0.105 (0.026)	0.113 (0.004)	0.005 (0.002)	0.019 (0.001)	0.255 (0.055)	0.179 (0.007)	0.001 (0)	0.016 (0.001)	0.003 (0.001)	0.039 (0.002)	0.93	0.01*
1995	0.309 (0.046)	0.280 (0.006)	0.309 (0.058)	0.329 (0.008)	0.219 (0.05)	0.107 (0.004)	0.024 (0.007)	0.025 (0.001)	0.138 (0.046)	0.196 (0.007)	0.019 (0.011)	0.022 (0.001)	0.010 (0.004)	0.041 (0.002)	0.86	0.02*
1996	0.303 (0.033)	0.304 (0.006)	0.349 (0.039)	0.339 (0.008)	0.161 (0.034)	0.121 (0.005)	0.015 (0.005)	0.019 (0.001)	0.143 (0.031)	0.161 (0.006)	0.005 (0.003)	0.016 (0.001)	0.018 (0.016)	0.039 (0.002)	0.96	0.00*
1997	0.087 (0.062)	0.274 (0.006)	0.102 (0.053)	0.323 (0.008)	0.023 (0.017)	0.109 (0.004)	0.017 (0.014)	0.025 (0.001)	0.737 (0.139)	0.209 (0.008)	0.013 (0.017)	0.024 (0.002)	0.016 (0.033)	0.036 (0.001)	0.86	0.05*
1998	0.110 (0.038)	0.262 (0.005)	0.109 (0.037)	0.317 (0.008)	0.044 (0.019)	0.106 (0.004)	0.030 (0.015)	0.030 (0.002)	0.677 (0.155)	0.219 (0.008)	0.017 (0.018)	0.029 (0.002)	0.062 (0.03)	0.037 (0.001)	0.82	0.03*
1999	0.161 (0.033)	0.264 (0.005)	0.108 (0.025)	0.319 (0.008)	0.022 (0.009)	0.106 (0.004)	0.024 (0.008)	0.036 (0.002)	0.435 (0.108)	0.204 (0.007)	0.038 (0.021)	0.034 (0.002)	0.114 (0.035)	0.037 (0.001)	0.46	0.50
2000	0.070 (0.017)	0.278 (0.006)	0.101 (0.061)	0.333 (0.008)	0.010 (0.008)	0.112 (0.004)	0.011 (0.007)	0.028 (0.002)	0.824 (0.291)	0.192 (0.007)	0.049 (0.026)	0.022 (0.001)	0.025 (0.01)	0.035 (0.001)	0.57	0.20
2001	0.153 (0.069)	0.152 (0.004)	0.066 (0.028)	0.319 (0.009)	0.017 (0.028)	0.054 (0.003)	0.013 (0.01)	0.051 (0.003)	0.646 (0.157)	0.320 (0.01)	0.078 (0.071)	0.048 (0.003)	0.066 (0.056)	0.055 (0.002)	0.54	0.23
2002	0.123 (0.066)	0.199 (0.005)	0.064 (0.026)	0.301 (0.008)	0 (0)	0.081 (0.003)	0.037 (0.028)	0.053 (0.003)	0.219 (0.133)	0.270 (0.009)	0.150 (0.098)	0.050 (0.003)	0.406 (0.032)	0.045 (0.002)	--	--
2003	0.084 (0.049)	0.187 (0.004)	0.052 (0.027)	0.333 (0.008)	0.003 (0.003)	0.076 (0.003)	0.016 (0.006)	0.040 (0.002)	0.545 (0.04)	0.285 (0.009)	0.107 (0.04)	0.032 (0.002)	0.194 (0.03)	0.047 (0.002)	0.07	0.91

Year	Desert sucker		Sonora sucker		Roundtail chub		Yellow bullhead		Red shiner		Green sunfish		Smallmouth bass			
	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	Obs	Model	*rho*	*P-value*
2004	0.089 (0.025)	0.179 (0.004)	0.052 (0.023)	0.331 (0.009)	0.004 (0.003)	0.08 (0.003)	0.016 (0.006)	0.034 (0.002)	0.723 (0.045)	0.309 (0.01)	0.037 (0.014)	0.022 (0.001)	0.080 (0.038)	0.044 (0.002)	0.36	0.27
2005	0.071 (0.069)	0.210 (0.005)	0.039 (0.034)	0.343 (0.008)	0 (0)	0.090 (0.004)	0.010 (0.052)	0.030 (0.002)	0.810 (0.129)	0.266 (0.009)	0.047 (0.016)	0.017 (0.001)	0.024 (0.038)	0.043 (0.002)	0.89	0.44
2006	0.369 (0.049)	0.208 (0.005)	0.244 (0.035)	0.340 (0.008)	0.085 (0.03)	0.093 (0.004)	0.019 (0.006)	0.028 (0.002)	0.231 (0.079)	0.273 (0.009)	0.005 (0.002)	0.018 (0.001)	0.047 (0.02)	0.039 (0.002)	0.57	0.01*
2007	0.293 (0.11)	0.181 (0.004)	0.227 (0.075)	0.322 (0.009)	0.011 (0.031)	0.084 (0.004)	0.029 (0.005)	0.035 (0.002)	0.361 (0.108)	0.315 (0.01)	0.035 (0.017)	0.024 (0.002)	0.045 (0.015)	0.039 (0.002)	0.64	0.20
2008	0.204 (0.079)	0.104 (0.003)	0.338 (0.091)	0.317 (0.009)	0.022 (0.012)	0.043 (0.002)	0.018 (0.006)	0.047 (0.003)	0.244 (0.09)	0.394 (0.012)	0.067 (0.035)	0.033 (0.002)	0.106 (0.041)	0.061 (0.003)	0.82	0.03*

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Chapter 2. **Dynamic contributions of intermittent and perennial streams to fish beta-diversity in dryland rivers**

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2.1 Abstract

2.1.1 *Aim*

To determine the role of flow intermittence and species origin in shaping freshwater fish beta-diversity across dryland riverscapes.

2.1.2 *Location*

Verde and Little Colorado River basins, United States.

2.1.3 *Methods*

Fish beta-diversity was investigated in two large rivers with marked differences in basin-wide flow intermittence. Local site (continually flowing perennial vs. periodically flowing intermittent) and species (native vs. non-native) contributions to beta-diversity were compared within each basin and over multiple decades (1987 – 2013) in relation to changing hydrologic conditions. Metacommunity dynamics were quantified using changes in alpha- (local), beta-, and gamma- (regional) diversity through time.

2.1.4 *Results*

Beta-diversity patterns varied in relation to basin-wide intermittence. Intermittent sites were most influential to beta-diversity where basin-wide intermittence was lower (Verde River), whereas perennial sites were most influential where basin-wide intermittence was higher (Little Colorado River). In intermittent sites, native fish species contributions to beta-diversity tended to

be higher than non-native species contributions. The relative contributions of perennial and intermittent sites within each basin was invariant to annual flow regimes, whether atypically lower or higher than average flows, but somewhat related to intra-annual flow variation. Native species contributions increased in years with high flow conditions in the Verde River. Over time, beta-diversity decreased in the lower intermittence Verde River, indicating taxonomic homogenization, but remained relatively unchanged in the Little Colorado River.

2.1.5 *Main Conclusions*

Investigations of beta-diversity components over time are considered pivotal for conservation prioritization and planning. We found that both intermittent and perennial streams play complementary roles in supporting fish beta-diversity, and that their relative contributions increase as basin wide availability of the habitat type decreases. Moreover, contributions of intermittent streams to overall beta-diversity were relatively consistent through time and supported native fish diversity. Despite weakening policy protections of intermittent streams, these habitats are critical for supporting local species persistence and regional biodiversity.

Keywords: biotic homogenization, metacommunity, long-term data, river, non-native species, invasion, assemblage, richness, hydrology, drought

2.2 Introduction

The global biodiversity crisis is characterized by non-systematic losses and gains of species (Dornelas et al., 2014; Thomas, 2013). Effective conservation and management, needed to bend the curve of future biodiversity loss (sensu Mace et al., 2018), is increasingly reliant on understanding the environmental context by which communities change through time (Bush et al., 2016; Socolar, Gilroy, Kunin, & Edwards, 2016). Acquiring this knowledge is challenged by the fact that community dynamics are often asynchronous among species (Gotelli et al., 2017; Hillebrand et al., 2018), especially among native and non-native species (McGill, Dornelas, Gotelli, & Magurran, 2015; Olden, Poff, Douglas, Douglas, & Fausch, 2004). Thus, scientific inquiry must extend beyond the lens of species richness and incorporate the spatiotemporal processes by which different dimensions of biodiversity are changing (Magurran et al., 2018).

Freshwater ecosystems are spotlighted in the current biodiversity crisis (Harrison et al., 2018), where biotas continue to experience dramatic changes in composition and loss of endemism (Reid et al., 2018). The discrete boundaries and dendritic topology of rivers contribute to the immense diversity of freshwater organisms, including fish, but also make them highly sensitive to multiple interacting threats (Altermatt, 2013; Craig et al., 2017; Olden et al., 2010). Among the most significant threats are changes to hydrologic regimes. For example, more frequent and severe droughts associated with climate change and water withdrawals are poised to significantly alter intermittence for many rivers in dryland regions of the world, with anticipated shifts from continually flowing perennial to periodically flowing intermittent streams, and from intermittent streams to ephemeral streams that rarely flow (Allen et al., 2019; Jaeger, Olden, & Pelland, 2014). This is compounded with the fact that changes to hydrologic regimes may be coupled with species invasions that further threaten native biodiversity. Consequently, it is increasingly important to understand the complementarity by which intermittent and perennial streams in river networks support species persistence through time and contribute to patterns of native and non-native biodiversity (Hermoso, Ward, & Kennard, 2013).

Beta-diversity, a measure of the amount of change in species composition from one location to another (Whittaker, 1972), is a fundamental consideration in contemporary conservation efforts (Socolar et al., 2016). Metacommunity theory has advanced the study of beta-diversity by acknowledging that species turnover is influenced by local habitat conditions and species interactions, as well as organismal dispersal and connectivity among habitats (Leibold et al., 2004). In dendritic river networks, for example, the metacommunity framework has facilitated the understanding of source-sink dynamics, and the relative roles of spatial distances, dispersal modes, and environmental heterogeneity (Brown & Swan, 2010; Tonkin, Altermatt, et al., 2017). Thus, metacommunity theory provides a powerful construct to understand patterns and mechanisms of fish beta-diversity in networks with dynamic patterns in flow intermittence.

By investigating the different components of metacommunity variability we can begin to understand how processes of species gain and loss (nestedness) and species replacement (turnover) over time contribute to spatial patterns in beta-diversity (Anderson et al., 2011, Legendre 2014). For example, unique community composition driven by species turnover may indicate metacommunity structure is influenced by deterministic processes like environmental filters or species interactions at local scales, and suggest the need to protect a portfolio of locations. By contrast, unique community composition driven by species nestedness indicate metacommunity structure is shaped by stochastic processes like disturbance and dispersal, and suggest that locations with the greatest species richness should be prioritized because they may act as sources for other locations within the metacommunity. Investigations of beta-diversity components over space and time are considered pivotal for pinpointing factors driving community variability and can help inform conservation prioritization and planning (Baselga, 2010; Ruhí, Datry, & Sabo, 2017).

This study seeks to disentangle the roles of flow intermittence (intermittent vs. perennial sites) and species origin (native vs. non-native species) in shaping patterns of freshwater fish beta-diversity in Lower Colorado River Basin, United States. Specifically, we compared two large rivers characterized by distinct differences in basin-wide intermittence, ranging from predominantly year-round hydrologic connectivity to predominantly seasonal connectivity. First, we examined spatial beta-diversity components for each basin, comparing individual contributions of intermittent and perennial sites to overall beta-diversity and how these relative site contributions vary across annual flow conditions over a multi-decadal time period. Second, we explored the individual contributions of native and non-native species to overall beta-diversity and asked whether these species contributions differ in intermittent and perennial sites and across years with marked differences in annual flow conditions. Third, we investigated temporal changes in multiple dimensions of diversity using: beta-diversity (β), local diversity (α), and regional (γ) diversity with species occurrence data. Results from this study seek to inform discussions regarding the importance of intermittently flowing streams and rivers for freshwater biodiversity (Datry, Fritz, & Leigh, 2016; Larned, Datry, Arscott, & Tockner, 2010), and the need to support policies aimed to protect these habitats both now, and in the future (Acuña et al., 2014; Marshall et al., 2018).

2.3 Methods

2.3.1 *Study system*

Located in the Colorado Plateau and Central Highlands region of Arizona, United States, the Verde and Little Colorado Rivers share similar climates, but represent different positions along a gradient of flow intermittence due to contrasting groundwater dynamics (Arizona Department of Water Resources 2010). The Verde River demonstrates relatively low intermittence with a perennial mainstem and several perennial tributaries, whereas the Little Colorado River is characterized by high intermittence with an intermittent mainstem and perennial reaches only located in spring-fed tributaries (Fig. 1). The two basins share similar regional species pools, and support local fish communities of mixed origin ranging from 0 to 100% native species by abundance. Approximately two-thirds of the regional species pool is represented by non-native species (see Appendix S1: Table S1.1 in Supporting Information). In the Verde River, 23 species (9 native, 14 non-native) in intermittent sites and 26 species (9 native, 17 non-native) in perennial sites were recorded in the dataset. In the Little Colorado River, 17 species (6 native, 11 non-native) occurred in intermittent sites and 22 species (6 native, 16 non-native) occurred in perennial sites, respectively.

2.3.2 *Study design*

2.3.2.1 Designation of flow intermittence

River reaches were designated into two categories according to flow intermittence: intermittent or perennial sites. This designation was based on the most recent and comprehensive Geographic Information System (GIS) database created by Arizona Game and Fish Department (AZGFD). The database used a map base of U.S. Geological Survey (USGS) topographic digital line graph and revised stream hydrology codes through independent consultations with multiple district, state, and federal agency staff (Arizona Department of Water Resources, 2010; Wahl et al., 1997). Stream reaches are uniquely identified between two incoming tributaries, and have a mean length of 2.2 km (std. dev = 2.6 km). Stream reaches were considered perennial when streamflow typically occurred during all times of the year, and intermittent when streamflow typically occurred for only certain times of the year. Ephemeral stream reaches, those that have surface flow only in direct response to precipitation events, were not included due to lack of fish collection data. These definitions follow those of Jaeger and Olden (2012). The AZGFD GIS database was spatially joined to the National Hydrography Dataset (NHD) for the Lower Colorado River Basin to be used in subsequent analyses (U.S. Environmental Protection Agency & U.S. Geological Survey, 2012). Using this designation, we found 70% of river kilometers in the Verde River Basin (predominantly small tributaries) and 91% of river kilometers in the Little Colorado River Basin (both mainstem and tributaries) are classified as intermittent.

2.3.2.2 Annual hydrology characterization

Annual flow conditions of the Verde and Little Colorado River basins were quantified according to daily discharge records from USGS gages with at least 30 years of data (Fig. 1). Normalized and log-10 transformed hydrographs were used to calculate daily flow anomalies according to discrete Fast Fourier Transform (following Sabo and Post 2008) for each gage on the Verde (n=10) and Little Colorado (n = 9) rivers and then averages across all gages were used to calculate the net annual anomaly (NAA) for each basin. Flow NAA was calculated as the sum of all daily flow anomalies for a water year (Oct 1 – Sep 30) to best correspond to the year preceding the timing of fish surveys. Flow NAA was evaluated as a continuous variable from negative to positive values, where more negative values indicated lower than average flow years, more positive values indicated higher than average flow years, and a value of zero indicated an average flow year. Because intra-annual flow variation is important for shaping network connectivity and fish communities, and is not reflected in NAA, we also evaluated the annual coefficient of flow variation (FV) in daily discharge records for each water year.

2.3.2.3 Fish community data

Fish community data were obtained from the Arizona Game and Fish Department (AZGFD) Fisheries Information Systems (Stewart, Eiden, & Olden, 2015). Survey records were spatially joined to the National Hydrography Dataset for the Lower Colorado River Basin (USEPA & USGS, 2012). This database holds >81,000 and >43,000 fish records covering 340 and 254 unique sites in the Verde River and Little Colorado River basins, respectively, collected over the period 1958-2013. Data was collated from all survey efforts reported in scientific collection permits compiled by AZGFD. Only surveys conducted using seining and electrofishing sampling methods were considered (59,444 and 28,880 records, respectively); both represent standard methods for community sampling in wadeable warm-water streams (Bonar, Hubert, & Willis, 2009). We used incidence data (presence/absence) in all analyses to account for differences in sampling effort among surveyors and over time.

Prior to data analysis, we estimated sample coverage to assess the completeness of surveys in representing the regional community assemblage each year. Sample coverage was calculated based on incidence data using the 'iNEXT' R package (Table S1.2; Hsieh, Ma, & Chao, 2016). This method estimates expected species richness for a given number of sites using the incidence frequency of each species with rarefaction/extrapolation curves. The coverage measure represents the proportion of the total number of species in a community that were sampled within a year (see Chao & Jost, 2012, for details). Because variation in sample completeness can alter estimates of beta-diversity and dissimilarity metrics between communities, only years with sample coverage of 0.95 or greater were included for analysis. This screening process resulted in a final dataset for each basin, as follows: the Verde River with sampling events in 293 unique sites (196 perennial, 97 intermittent) between 1987 and 2012 (annual mean: 45; range: 19 – 82), and the Little Colorado River with 198 unique sites (118 perennial, 80 intermittent) between 1986 and 2013 (mean: 20; range: 4 – 64; excluding 2002, 2003 and 2012) (Fig. 1). Sites were defined according to a unique stream reach identifier from the NHD (ComID), assigned to intermittent or perennial site classification (described above), and to the metric of NAA and FV corresponding to the water year in which the survey was conducted.

2.3.3 *Analysis*

Beta-diversity can be measured as total variance in metacommunity data, which can subsequently be partitioned into unique variation contributed by individual sites and species within the dissimilarity matrix (Legendre & De Cáceres, 2013). This approach is advantageous because beta-diversity is estimated independent of local (α) and regional (γ) diversity, and thus it is possible to compare estimates among communities of a metacommunity (Wilson & Shmida, 1984; Legendre & De Caceres, 2013). Prior to beta-diversity calculations for site and species comparisons, we performed the Hellinger transformation on the species matrix of presence/absence data. A Hellinger transformation results in a Euclidean distance matrix, making the total variance in community composition range between 0 and 1. This allows one to compare individual site and species contributions using a relative scale (Legendre & De Cáceres, 2013).

Beta-diversity was calculated for each river basin to understand the role of flow intermittence and species origin in structuring riverine fish metacommunities. We compared intermittent vs. perennial Local Contributions to Beta Diversity (LCBD) values and native vs. non-native Species Contributions to Beta Diversity (SCBD) values to determine if flow intermittence or species origin were significant factors contributing to beta-diversity. Only the most recent survey data was used to represent community composition for the river reach. We also considered the effect of flow connectivity among sites by examining the unique contribution of sites to overall beta-diversity (LCBD values) in relation to watercourse distance to the nearest perennial stream reach (see Appendix S2). Next, we examined if relative annual LCBD (intermittent vs. perennial) and SCBD (native vs. non-native) demonstrated significant relationships with flow regimes (NAA and FV). Finally, we explored trends in multiple dimensions of diversity through time including alpha- (local species richness), beta-, and gamma-diversity (regional species richness). Beta-diversity values and site and species contributions were calculated using the 'adespatial' package in software program R (Dray et al., 2017).

To determine the relative roles of species turnover vs. nestedness in shaping metacommunity variability, we used a Jaccard dissimilarity matrix on presence/absence data. Total variance in the dissimilarity matrix is decomposed into complementary components of turnover (i.e. species replacement) and nestedness (i.e. species gain and loss) based on the proportion of shared species across pairwise site comparisons following Legendre (2014). The proportion of total beta-diversity accounted for by replacement and richness differences sums to 1. Therefore, these relative indices can be used to determine which of the two processes dominates among sampling sites in a metacommunity. We investigated the proportion of metacommunity variability due to changes in species richness or replacement spatially across all sites, using the most recent survey data, and across all years. Turnover and nestedness components of beta-diversity were calculated using the 'betapart' package in software program R (Baselga, Orme, Villeger, de Bortoli, & Leprieur, 2018).

All direct statistical comparisons made between intermittent and perennial LCBD values or between native and non-native SCBD values were made using t-tests with Satterthwaite approximations. Individual sites and species were assumed to be independent replicates within each factor (i.e., intermittent, perennial, native, non-native). To examine linear trends, across flow anomalies or through time, we used linear models and reported significant Pearson correlation coefficients and corresponding P-values. All analyses were performed in the software program R v.3.4.0 (R Core Team, 2017).

2.4 Results

Perennial and intermittent streams made important, but variable, contributions to fish beta-diversity (Fig. 2). In the Verde River, characterized by higher hydrologic connectivity (i.e., a perennial mainstem and many tributaries), intermittent sites, on average, had more unique species composition than perennial sites (Fig. 1 and Fig. 2a). Site contributions to overall beta-diversity, especially that of intermittent sites, was also positively associated with their watercourse distance from the nearest perennial stream reach (Table S2.4; Fig. S2.1). In intermittent sites, species replacement contributed more (turnover (T) = 0.59) than differences in species richness (nestedness (N) = 0.41) to total beta-diversity, whereas these two processes were essentially equivalent across perennial sites (T = 0.51, N = 0.49). In the Little Colorado River, characterized by lower hydrologic connectivity (i.e., perennial reaches only in spring-fed tributaries), perennial sites, on average, had more unique species composition compared to intermittent sites (Fig. 1 and Fig. 2b). Site contributions to overall beta-diversity was not related to their watercourse distance from the nearest perennial stream reaches (Table S2.4; Fig. S2.1). Pairwise differences in local community composition of both intermittent (T = 0.60) and perennial (T = 0.59) sites was primarily caused by species replacement.

Species of native and non-native origin contributed similarly to observed variability in community composition across perennial and intermittent sites, although in most cases native species tended to have higher beta-diversity contributions than non-native species (Fig. 2c, d). In the Verde River, beta-diversity contributions of native species tended to be higher in intermittent sites (Fig. 2c); a pattern that was driven largely by the process of species replacement rather than differences in species richness (T = 0.65). Non-native species, however, tended to have the highest beta-diversity contributions in perennial sites (Fig. 2c); a result that was equally driven by species replacement and species richness difference (T= 0.50). In the Little Colorado River, native species tended to contribute most to beta-diversity patterns across both intermittent and perennial sites (Fig. 2d). Pairwise differences in native species composition across sites was due more to changes in species richness than replacement at both perennial and intermittent sites (N = 0.54). By contrast, differences in non-native species composition was driven by the process of species replacement across perennial (T = 0.58) and, especially, intermittent sites (T = 0.75).

The relative contributions of intermittent and perennial sites to beta-diversity showed little association with annual flow conditions (Fig. 3). Regardless of the magnitude of annual flow departure from historical average conditions, intermittent sites consistently showed the greatest contributions to beta-diversity, on average, compared to perennial sites in the Verde River (Fig. 3a), whereas the opposite was true for the Little Colorado River (Fig. 3b). However, in the Little Colorado River, intermittent site contributions to beta-diversity increased with higher flow variability (Fig. 3d). Flow variability increased over the period of study in the Little Colorado River but not the Verde River (see Appendix S3: Fig. S3.2).

Annual flow conditions were somewhat associated with differing contributions of native and non-native species (Fig. 4). In the Verde River, native species contributed increasingly more to variability in community composition compared to non-native species as annual flows increasingly exceeded average conditions (Fig. 4a). Native and non-native species beta-diversity contributions did not change with respect to annual flow conditions in the Little Colorado River (Fig. 4b, d).

Beta-diversity decreased over time in perennial sites of the Verde River (Fig. 5a), driven mostly by species replacement (T = 0.61, N = 0.39). Species richness in perennial sites increased over time (Fig. 5c), as a result of non-native species additions that outweighed any native species losses (Fig. 5d). Increasing local non-native species richness appeared to drive the homogenization process (Fig. 5d) because regional non-native species richness remained unchanged while native species richness declined regionally (Fig. 5f). Beta-diversity appeared stable through time in perennial and intermittent sites of the Little Colorado River, indicating no overall homogenization or differentiation (Fig. 6a), although partitioning beta-diversity contributions revealed changes in species richness drove variability in metacommunity patterns through time (T = 0.27, N = 0.73). This result was mirrored by regional declines in species richness across both intermittent and perennial sites (Fig 6e) as a result of regional non-native species loss (Fig. 6f).

2.5 Discussion

Periodic disturbances and dynamic connectivity shape community composition and diversity across many ecosystems by affecting organism dispersal, colonization, and habitat suitability (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017; Zeigler & Fagan, 2014). Here, we explored long-term patterns and drivers of fish diversity in two dryland rivers of the American Southwest. By examining separate stream components based on flow intermittence and species components based on origin (native or non-native), we exposed underlying changes in diversity patterns that would otherwise not have been apparent. We found that native species often played a greater role than non-native species in contributing to beta-diversity in intermittent streams, indicating intermittent streams represent important habitats to support local native fish persistence and contribute to maintaining regional diversity through time (Datry, Moya, Zubieta, & Oberdorff, 2016; Pusey, Kennard, Douglas, & Allsop, 2016). Fluctuations in river flow due to annual or seasonal hydrologic events (e.g. snowmelt run-off or dry-downs) and spatially variable groundwater connections create a landscape of periodic connectivity on which species assembly unfolds. In the less intermittent Verde River basin, perennial sites were perhaps facilitating non-native species range expansion through time, leading to homogenization among these sites. In the more intermittent Little Colorado River Basin, changes in beta-diversity were more muted, but increasing flow variability led to higher differentiation in community composition among intermittent sites.

Flow intermittency was a significant factor in determining patterns of freshwater fish beta-diversity. Basin-wide prevalence of intermittency appeared to dictate the unique contribution of individual sites to overall beta-diversity. Specifically, where the mainstem river was mostly perennial in the Verde River, intermittent stream reaches had significantly more unique species composition compared to perennial stream reaches. The opposite was true in the Little Colorado River, characterized by low mainstem hydrologic connectivity, where perennial streams had more unique species composition. Despite the fact that the strength of our inferences are limited by including just two basins for comparison, these findings support the long recognized value of complementarity in conservation planning (Vane-Wright, Humphries, & Williams, 1991, Brennan et al., 2019).

Intermittent sites provide periodic increases in network connectivity, expanding habitat availability, and facilitating dispersal within riverine metacommunities when flowing (Jaeger et al., 2014). Intermittent site contributions to beta-diversity remained fairly stable through time and were invariant to high or low departures from historical annual flow conditions. Because high flow years showed little association with the relative contributions of intermittent and perennial sites to beta-diversity, species' dispersal and colonization events may have played similar roles in perennial and intermittent sites, or else environmental conditions other than flow may have affected local species composition (Cadotte & Tucker, 2017). Alternatively, the annual temporal resolution of community surveys may have been insufficient to capture intra-annual metacommunity and beta-diversity dynamics in response to seasonal drying and rewetting periods (Datry, Moya, et al., 2016; Ruhí et al., 2017). Intra-annual flow variability increased over the study period in the Little Colorado River, and was associated with greater intermittent site contributions to overall beta-diversity. As connectivity among sites within river networks changes, one would expect the roles of environmental and spatial structuring of metacommunity composition to change as well. The expectation is that dispersal limitation would be most important during low-flow conditions, and environmental filtering being more dominant during high-flow conditions (Heino, Melo, Siqueira, et al., 2015). If within-year flow fluctuations become more common, then the sensitivity of intermittent Little Colorado River communities to these changes might indicate localities will become more isolated and affected by dispersal limitation.

Metacommunity structure is influenced by changing site conditions and species interactions. In the Verde River, native species contributions to beta-diversity were positively associated with high annual flow anomalies, indicating that high flows perhaps triggered dispersal and recolonization or reproductive events during periods of expanded connectivity and habitat availability. Initially, an increasing occurrence of relatively rare species in the landscape could increase overall beta-diversity (Kuczynski, Legendre, & Grenouillet, 2018). Supporting this conclusion, positive relationships between species contributions to beta-diversity and site occupancy have recently been documented in several studies (e.g. da Silva et al., 2018; Gavioli, Milardi, Castaldelli, Fano, & Soininen, 2019; Heino & Grönroos, 2017). Rapid recolonization of formerly dry habitat is likely to occur after the cessation of drought (Lennox, Crook, Moyle, Struthers, & Cooke, 2019). High flow events are known to induce dispersal of native fishes elsewhere in the Colorado River Basin for increased foraging, spawning, or exploring activities (Booth, Flecker, & Hairston, 2014; Cathcart, Gido, & McKinstry, 2015; Cross et al., 2013), leading to decreased probability of local extinction (Budy, Conner, Salant, & Macfarlane, 2015). Years with the highest flow anomalies are also times when extreme spring floods or summer monsoons have occurred, and may have been detrimental to non-native species populations (Bestgen, Wilcox, Hill, & Fausch, 2017; Gido, Propst, Olden, & Bestgen, 2013; Rogosch et al., 2019). These flow conditions, which are more favorable for native species compared to non-native species, additionally benefit native species by providing some release from negative biotic interactions (Propst, Gido, & Stefferud, 2008; Stefferud, Gido, & Propst, 2011). Notably, native species contributions to beta-diversity in the Little Colorado River did not vary according to high flow conditions. This suggests that the spatial configuration of perennial sites that predominantly occur in tributaries and are separated by large expanses of intermittent mainstem habitat, may define patterns in beta-diversity regardless of annual flow regimes (Davey & Kelly, 2007).

In most cases, contributions of nestedness and turnover to patterns of beta-diversity were similar, indicating species replacement and changes in species richness were both important mechanisms driving metacommunity composition in these river basins. Two exceptions to this pattern occurred in intermittent sites where communities tended to have higher turnover components. Intermittent sites of the Verde River, and particularly native species in intermittent sites, had high turnover components. In the Little Colorado River, this pattern was observed with non-native species. Unlike truly isolated habitats, where one would expect low species richness and high nestedness components in metacommunity structure, intermittent reaches appear to be important to support many species. Most intermittent sites were within 10 km of a perennial stream reach, which is broadly within the dispersal range of fishes in the two basins (Fig. S2.1; Jaeger et al. 2014). Thus, local community composition in most intermittent stream localities did not likely result from dispersal limitation and source-sink dynamics (sensu Mouquet & Loreau, 2003; Vanschoenwinkel, Buschke, & Brendonck, 2013). Intermittent reaches of rivers can act as environmental filters, where community composition results from periodic discontinuity discriminating for species uniquely adapted to dynamic flow conditions, high habitat heterogeneity, or along a gradient, for instance, of harshness (e.g. Bestgen et al., 2017; Datry, Melo, Moya, Zubieta, De la Barra, & Oberdorff 2016; Gido, Propst, & Molles, 1997). The high turnover component of intermittent sites suggests a need to protect a portfolio of these locations within the river network to maintain diversity.

Non-native species can mask fish faunal changes, making metacommunity structure appear homogeneous over time despite considerable turnover in native species composition (Erős et al., 2014). This is because non-native species that successfully establish have widespread distributions, dampening variability caused by the occurrence patterns of other species in the metacommunity. In the Verde River, perennial sites became more homogeneous as non-native species replaced native species over time. Native species richness declined both locally and regionally, while regional non-native species richness remained stable. These patterns are indicative of secondary spread and proliferation of non-native species. Given the widespread introduction of non-native species to mainstem rivers throughout the Colorado River Basin (Olden & Poff, 2005), evidence suggests that non-native populations continue to colonize upstream tributaries, and expand their distribution deeper into the branches of the river network (e.g. Pool & Olden, 2015). Consequently, native species persistence may be vulnerable for species that increasingly rely on intermittent tributary habitats to provide refuge from non-native fishes (Bottcher, Walsworth, Thiede, Budy, & Speas, 2013; Cathcart et al., 2015).

As non-native species proliferated and replaced native species in the Verde River, local (alpha) diversity of non-native species declined slightly in the Little Colorado River. The dominance of intermittent streams in the Little Colorado River could hinder the persistence of certain non-native species; a pattern supported by relatively intact native fish faunas in isolated, non-native free, perennial tributaries of the neighboring Bill Williams River (Pool and Olden, 2015), the Virgin River Basin (Cross, 1985), and the Gila River (Propst et al., 2008). Long distances between perennial tributaries may create barriers to range expansion and recolonization within the Little Colorado River network. The pattern of local and regional species losses of non-native species is unusual compared to other more perennial systems in the Colorado River Basin (Ruhí, Olden, & Sabo, 2016).

Diversity is often underestimated in dynamic systems, such as intermittent rivers (Ruhí, Datry, & Sabo, 2017). These rivers may act as strongholds of native species in more perennial river basins or act as environmental filters preventing spread and proliferation of introduced species in more intermittent systems. Identifying the factors that affect variation in community compositions through time will lead to stronger inferences about the dynamics of species richness and replacement to better inform effective management and conservation (e.g. Angeler, 2013). For example, climate change and increasing water withdrawals are predicted to decrease connectivity in the Verde River and other basins in the southwestern United States (Jaeger et al., 2014). As more perennial sites become intermittent and intermittent sites become ephemeral, losing habitat and connectivity is likely to cause significant non-linear losses in species diversity and metacommunity stability (Thompson, Rayfield, & Gonzalez, 2017; Zeigler & Fagan, 2014). Flow-dependent dispersers will be in landscapes with reduced connectivity for spatial rescue effects to take place, and more severe droughts may exceed species' mechanisms of resilience and resistance to temporary habitat loss (e.g., Driver & Hoeinghaus 2015). Therefore, protecting periodic flow connectivity remains critical to protecting diversity in dryland rivers (Hermoso et al., 2013; Perkin, Gido, Costigan, Daniels, & Johnson, 2015).

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2.7 Data availability statement

Community presence/absence data and reach level flow-intermittence designations for the Verde River and Little Colorado River basins are available through an online repository: 10.6084/m9.figshare.8799161

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2.9 Figures

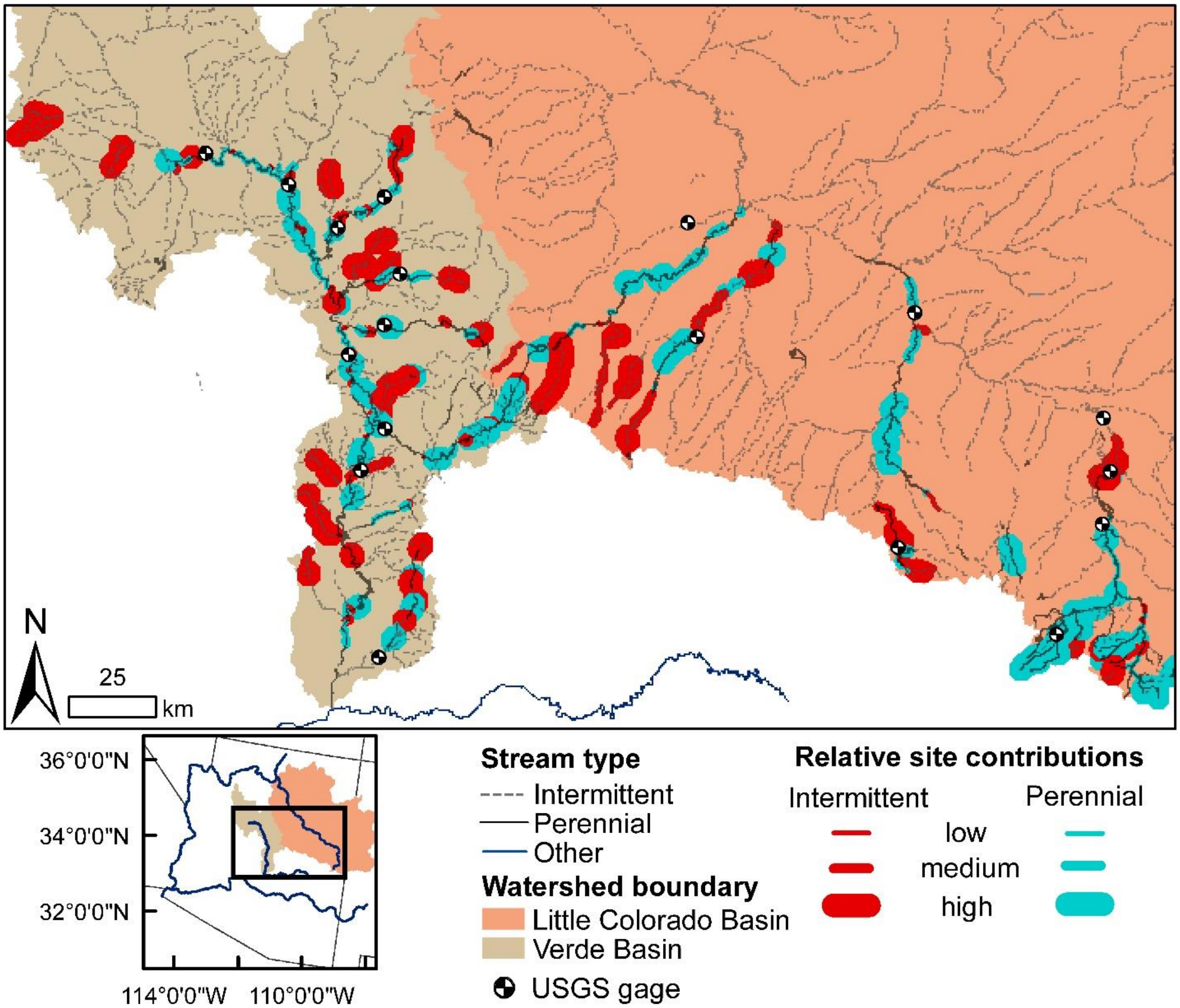

Figure 2.1 Map of Verde and Little Colorado River basins in Arizona, United States. Perennial (solid black line) and intermittent (dashed gray line) flowlines are shown in each river basin along with other major rivers (dark navy line) in the lower Colorado River Basin for reference. Local site contributions to beta diversity (LCBD) in the two study basins are overlayed as perennial (turquoise) and intermittent (red) bands for all stream reaches sampled over the study period between 1987 and 2013. LCBD values are scaled by 33rd percentile bins from low (thin bands) to high contributions (wide bands). Stream gages (checkered circle) used to calculate flow net annual anomalies and variability are also displayed.

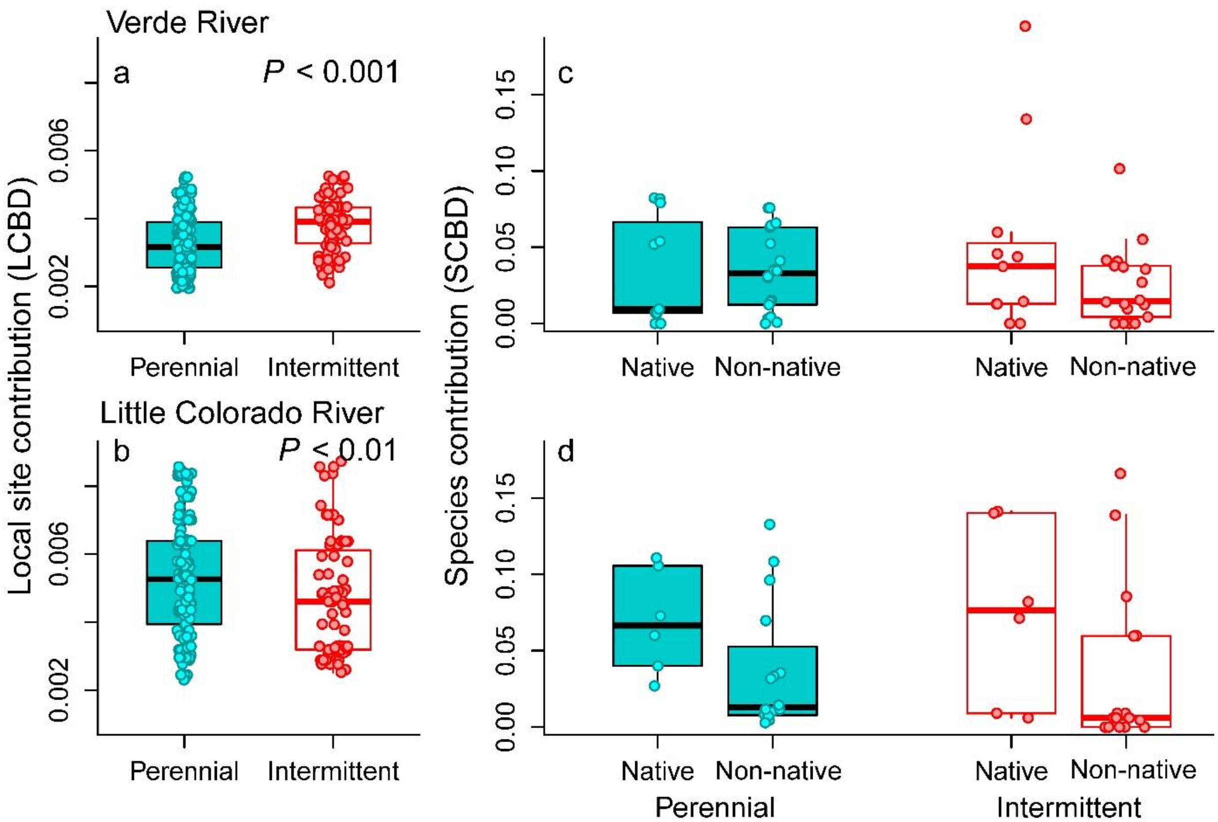

Figure 2.2 Broad patterns in local site (LCBD) and species (SCBD) contributions to beta diversity for the Verde (a, c) and Little Colorado (b, d) river basins. Boxplots cover the interquartile range for perennial (turquoise and black) and intermittent (white and red) sites with data points representing individual sites (a, b) or species (c, d), respectively. P-values are displayed for significant differences between groups.

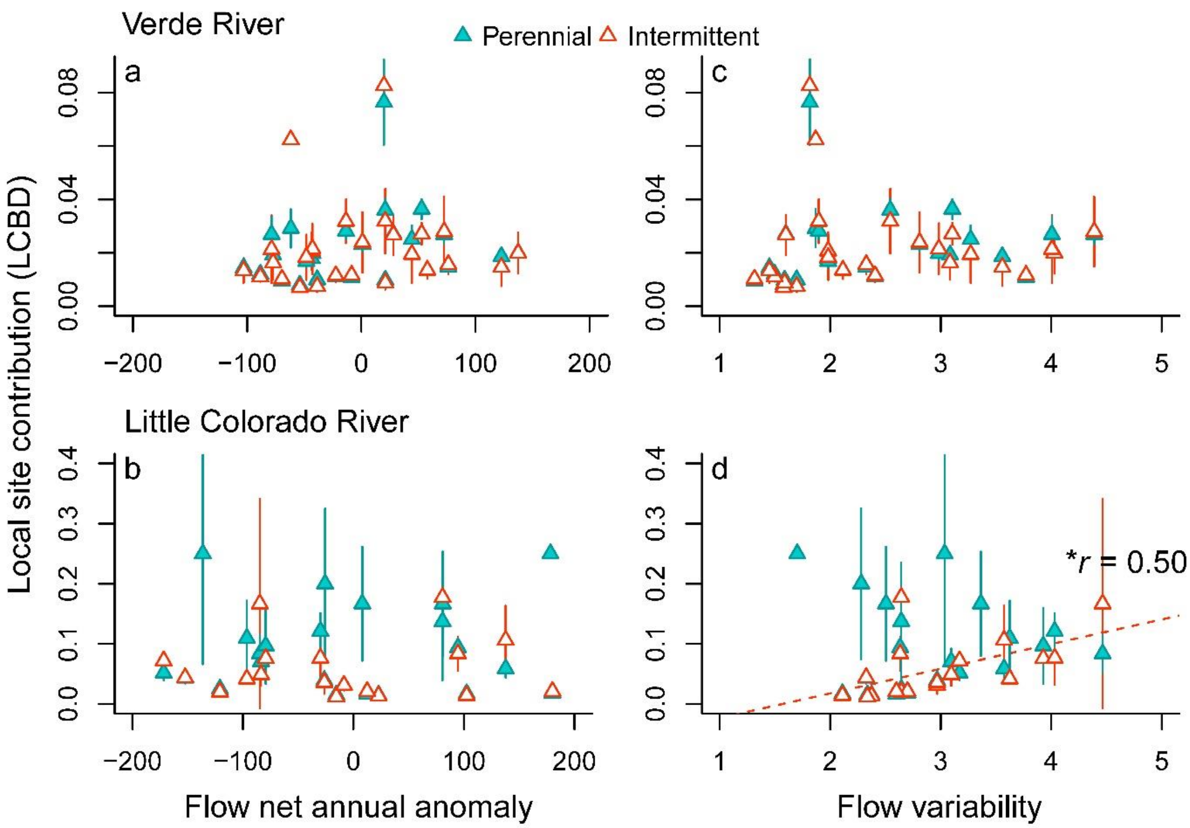

Figure 2.3 Relationship between LCBD values and flow for the Verde (top panels) and Little Colorado (bottom panels) river basins. Perennial and intermittent site LCBD values (mean and 95% CI) are plotted against flow net annual anomalies (a, b) and variability (c, d). Note: The dependent variable axes are different scales for the two basins because fewer sites were sampled in the Little Colorado River than the Verde River in a given year. Asterisks are displayed for significant trends at $P < 0.05$ (*) with a trend line and corresponding Pearson correlation coefficient (r). LCBD values of all sites within a basin sum to 1.

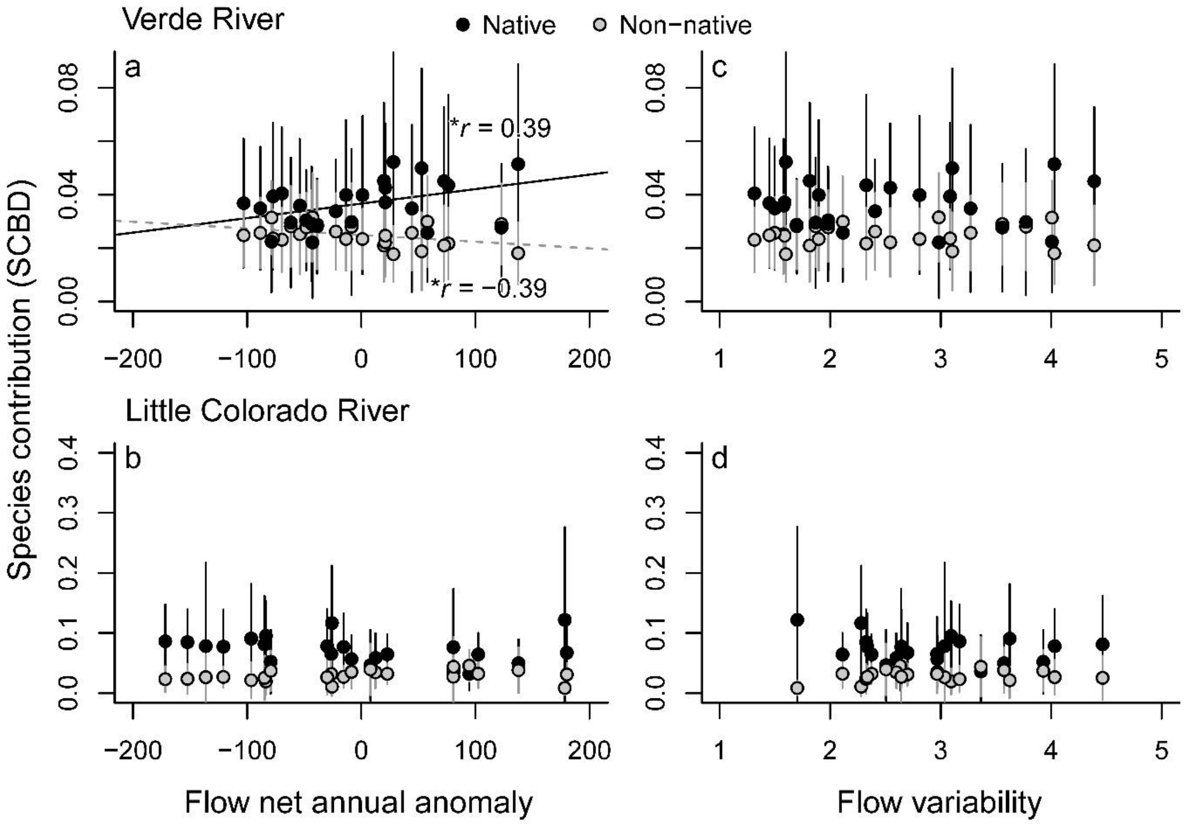

Figure 2.4 Relationship between SCBD values and flow for the Verde (top panels) and Little Colorado (bottom panels) rivers. Native and non-native species SCBD values (mean and 95% CI) are plotted against flow net annual anomalies (a, b) and variability (c, d). Asterisks are displayed for significant trends at P < 0.05 (*) with a trend line and the corresponding Pearson correlation coefficient (r). SCBD values of all species within a basin sum to 1.

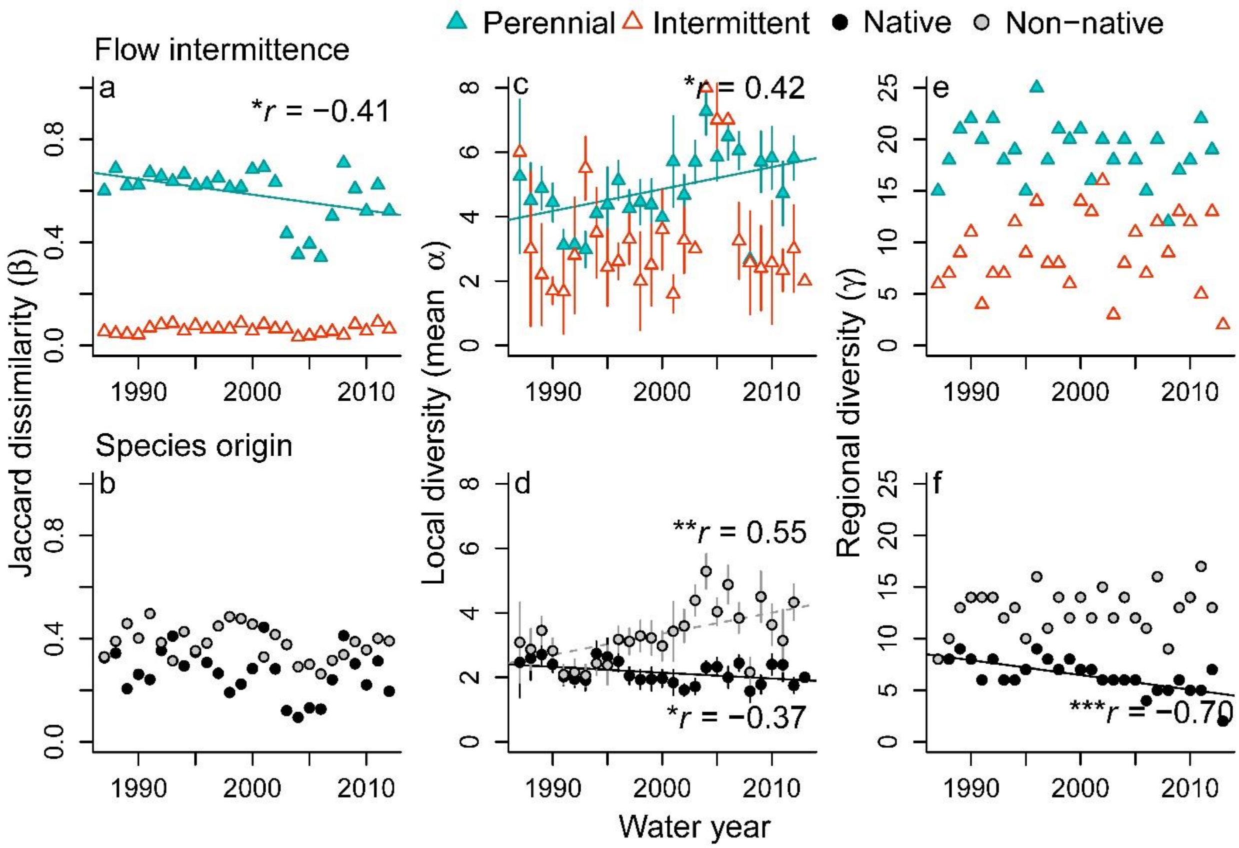

Figure 2.5 Multi-dimensional aspects of diversity in the Verde River through time. Beta (β) diversity (left panels: a, b), average local (α) diversity (middle panels: c, d), and regional (γ) diversity (right panels: e, f) are displayed to compare trends between perennial and intermittent sites (top panels: a, c, e) and native and non-native species (bottom panels: b, d, f). Local diversity reflects the average species richness per site per year (mean and 95% CI). Beta and gamma diversity are total values per year. Asterisks are displayed for significant trends at P < 0.05 (*), P < 0.01 (**), and P < 0.001 (***) with a trend line and the corresponding Pearson correlation coefficient (r).

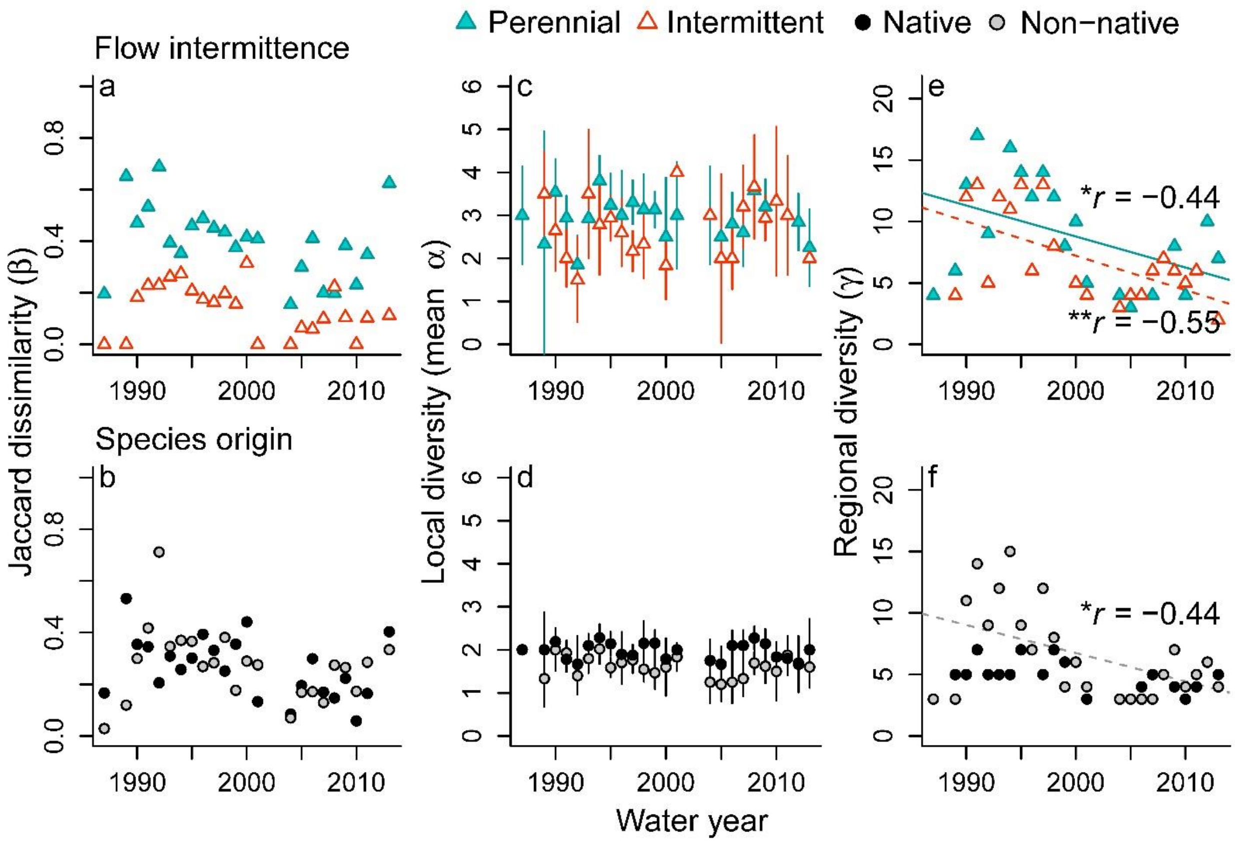

Figure 2.6 Multi-dimensional aspects of diversity in the Little Colorado River through time. Beta (β) diversity (left panels: a, b), local (α) diversity (middle panels: c, d), and regional (γ) diversity (right panels: e, f) are displayed to compare trends between perennial and intermittent sites (top panels: a, c, e) and native and non-native species (bottom panels: b, d, f). Local diversity reflects the average values per reach per year (mean and 95% CI). Beta and gamma diversity are total values per year. Asterisks are displayed for significant trends at $P < 0.05$ (*) with a trend line and the corresponding Pearson correlation coefficient (r).

2.10 Chapter 2 Appendix 1. Species pools and sample coverage

Table S 2.1 Species of the Verde and Little Colorado Rivers collected 1987 – 2013.

Species Name	Common Name	Verde R.	Little Colorado R.	Origin
Agosia chrysogaster	Longfin dace	x		Native
Ameiurus melas	Black bullhead	x	x	Non-native

Species Name	Common Name	Verde R.	Little Colorado R.	Origin
Ameiurus natalis	Yellow bullhead	x	x	Non-native
Ambloplites rupestris	Rock bass		x	Non-native
Carassius auratus	Goldfish	x	x	Non-native
Catostomus clarkii	Desert sucker	x		Native
Catostomus commersoni	Western whitesucker	x		Non-native
Catostomus discobolus	Bluehead sucker		x	Native
Catostomus insignis	Sonora sucker	x		Native
Catostomus latipinnis	Flannelmouth sucker		x	Native
Cyprinus carpio	Common carp	x	x	Non-native
Cyprinella lutrensis	Red shiner	x	x	Non-native
Dorosoma petenense	Threadfin shad	x		Non-native
Fundulus zebrinus	Plains killifish		x	Non-native
Gambusia affinis	Western mosquitofish	x	x	Non-native
Gila robusta	Roundtail chub	x	x	Native
Ictalurus punctatus	Channel catfish	x	x	Non-native
Lepomis cyanellus	Green sunfish	x	x	Non-native
Lepmis macrochirus	Bluegill	x	x	Non-native
Lepomis microlophus	Redear sunfish	x		Non-native
Lepidomeda vittata	Little Colorado Spinedace		x	Native
Meda fulgida	Spikedace	x		Native
Micropterus dolemieu	Smallmouth bass	x		Non-native
Micropterus punctulatus	Spotted bass	x		Non-native
Micropterus salmoides	Largemouth bass	x	x	Non-native
Notemigonus crysoleucas	Golden shiner		x	Non-native

Species Name	Common Name	Verde R.	Little Colorado R.	Origin
Oncorhynchus apache	Apache trout	x	x	Native
Oncorhynchus clarkii	Cutthroat trout		x	Non-native
Oncorhynchus gilae	Gila trout	x		Native
Oncorhynchus mykiss	Rainbow trout	x	x	Non-native
Pimephales promelas	Fathead minnow	x	x	Non-native
Pomoxis annularis	White crappie	x		Non-native
Pomoxis nigromaculatus	Black crappie	x		Non-native
Poeciliopsis occidentalis	Gila topminnow	x		Native
Ptychocheilus lucius	Colorado pikeminnow	x		Native
Pylodictis olivaris	Flathead catfish	x		Non-native
Rhynichthys osculus	Speckled dace	x	x	Native
Salvelinus fontinalis	Brook trout	x	x	Non-native
Salmo trutta	Brown trout	x	x	Non-native
Sander vitreus	Walleye	x		Non-native
Xyrauchen texanus	Razorback sucker	x		Native

Table S 2.2 Sample coverage estimate for each year of the long-term data set (1987 - 2013). Numbers estimate the proportion of species sampled in the metacommunity for the respective year (Chao & Jost 2012).

Year	Sample coverage	
	Verde R.	Little Colorado R.
1985	0.64	NA
1986	0.83	1.00
1987	0.95	1.00
1988	1.00	1.00
1989	1.00	0.97
1990	0.99	0.99
1991	0.98	0.99
1992	0.98	0.58
1993	0.97	0.97
1994	1.00	0.97
1995	0.98	1.00
1996	0.99	0.97
1997	0.99	0.98
1998	0.99	0.93
1999	0.99	0.98
2000	1.00	0.98
2001	0.99	1.00
2002	1.00	NA
2003	1.00	NA
2004	0.98	1.00
2005	0.99	1.00
2006	0.99	1.00
2007	0.99	0.98
2008	0.96	0.96

Year	Sample coverage	
	Verde R.	Little Colorado R.
2009	0.99	0.99
2010	0.97	1.00
2011	0.99	0.99
2012	0.99	1.00
2013	NA	0.97

2.11 Chapter 2 Appendix 2. Associations between spatial connectivity and diversity

We investigated the role of network connectivity in driving local site community composition by examining the association between local contributions to beta diversity (LCBD) among sites and watercourse distance to continually flowing perennial reaches.

Watercourse distances between sites were calculated using the Spatial Tools for the Analysis of River Systems (STARS) and Spatial Stream Network (SSN) package (Hoef, Peterson, Clifford, & Shah, 2014; Peterson & Ver Hoef, 2014). We used a linear mixed effects model to evaluate associations between local contributions to beta diversity and watercourse distance to the nearest perennial reach for each river. This model framework allowed us to separate the distance main effect from variation in site type (intermittent or perennial) that could influence the relationship or absolute magnitude of the response, and accounted for nestedness in the data structure (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The final model was selected using restricted maximum likelihood estimation (REML) among three candidate models, including a null model, and models with different variance structures to account for site type relationship (slope) or absolute value (intercept) effects on the model response. The final model was logit transformed, appropriate for proportional data, to meet the assumption of homogeneity of variance. The amount of variation explained (R^2) by the final model was calculated following Nakagawa and Schielzeth (2013). Model fit was conducted with the package 'lme4' in software program R (Bates et al. 2015). All analyses were performed in the software program R v.3.4.0 (R Core Team 2017).

Watercourse distance to perennial reaches had a strong effect on local site contributions to beta diversity in the Verde River but not the Little Colorado River (Fig. S2.1). In the Verde River, spatial distance alone explained 21% of model variability. When the factor of intermittent and perennial sites was included, the model explained 51% of the variability in site contributions to beta-diversity. Absolute values of LCBD were higher at intermittent than perennial sites, but the slope of the relationship between LCBD and distance to the nearest perennial reach was consistent (Table S2.3, Fig. S2.1a). In general, sites within 10 m distances of perennial reaches exhibited high variability in LCBD values, so the positive relationship between unique site contributions and watercourse distance seems to be driven by sites beyond this distance (Table S2.4, Fig. S2.1a).

2.11.1 *Chapter 2 Appendix 2. References*

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Table S 2.3 Candidate models for the relationship between local site contributions to beta diversity (LCBD) and distance to the nearest perennial reach (P.Dist). A site factor (IPCode) was included to evaluate if the absolute value (intercept) or relationship (slope) between LCBD and distance varied for intermittent and perennial sites. Model selection was evaluated separately for the Verde and Little Colorado Rivers. Asterisks designate the final model selected for plotting and inference.

Model	AIC	logLik	L.Ratio	*p*-value
Verde R.				
P.Dist + IPCode (random intercept)*	248.6	-119.3		
P.Dist + IPCode (random slope/intercept)	261.4	-124.7	34.9	<0.001
P.Dist (null model)	290.3	-142.1	45.7	<0.001
Little Colorado R.				
P.Dist + IPCode (random intercept)	196.3	-94.2		
P.Dist + IPCode (random slope/intercept)	197.0	-92.5	3.3	0.19
P.Dist (null model)*	194.3	-94.2	3.3	0.35

Table S 2.4 Estimated regression parameters, standard errors, t-values and p-values for the linear mixed-effects model describing the relationship between local site contributions to beta-diversity (LCBD) and distance to the nearest sampled perennial site. Marginal (m) and conditional (c) R2 values reporting the amount of variation explained by each model are reported. See also Table 1 for model selection.

	mean	std. error	df	*t*-value	*p*-value	R^2(m)	R^2(c)
Verde R.						0.21	0.51
Intercept	-5.72	0.14	286	-34.3	<0.0001		
P.Dist	0.007	0.0018	286	2.97	0.0032		
IPcode (random)	0.23	0.29					
Little Colorado R.						0.17	0.17
Intercept	-5.34	0.039	170	-136.3	<0.0001		
P.Dist	0.0017	0.0027	170	0.65	0.5		

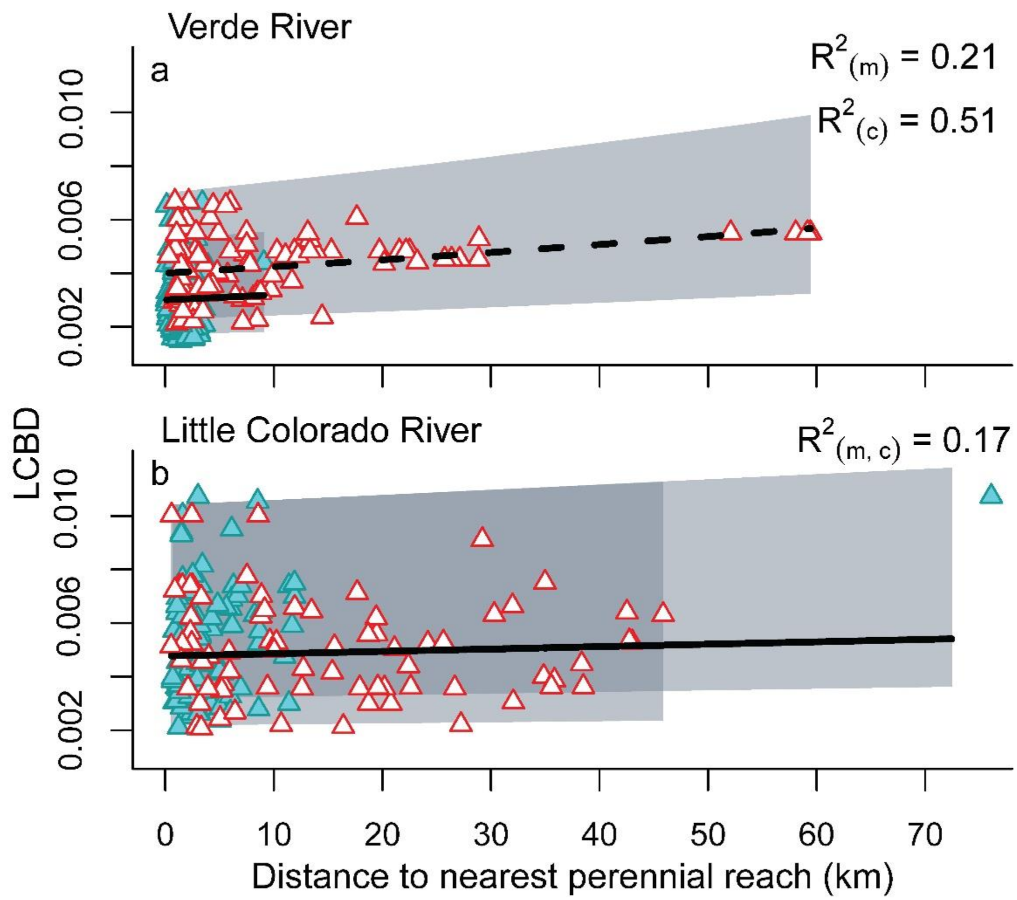

Figure S 2.1 Modeled relationships between LCBD values and the nearest perennial reach for the Verde (a) and Little Colorado (b) river basins. Predictions for the best model fit (Table S2.3 and S2.4) are displayed with separate intercepts for intermittent (dashed line) and perennial (solid line) sites with 95% CI in gray shading. Observed values for the association between LCBD and distance to the nearest perennial reach are displayed for intermittent (open red triangle) and perennial (closed blue triangle) sites. Both marginal and conditional variation explained by model fit (R^2) are displayed in the top right hand corner of the graph. Axis labels are identical for top and bottom panels.

2.12 Chapter 2 Appendix 3. Patterns in flow annual anomalies and intra-annual flow variability through time

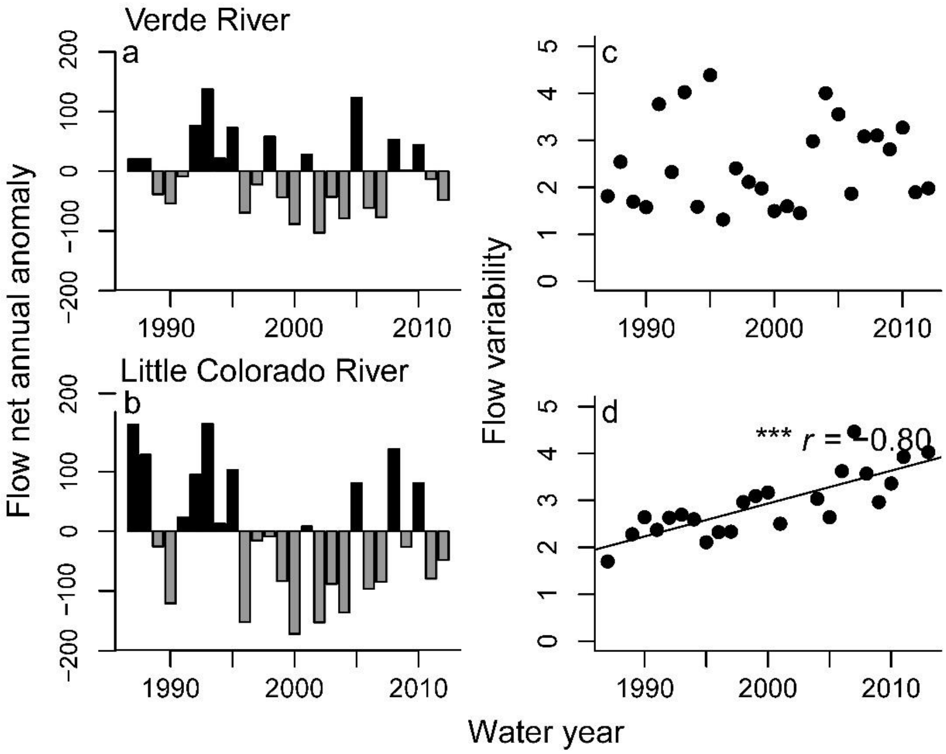

Figure S 2.2 Flow net annual anomalies (a, b) and intra-annual flow variability (c, d) through time. Top panels are the Verde River (a, c), bottom panels are the Little Colorado River (b, d). Asterisks are displayed for significant trends at $P < 0.001$ (***) with a trend line and the corresponding Pearson correlation coefficient (*r*).

Chapter 3. **Invaders induce coordinated isotopic niche shifts in native fish species**

3.1 Abstract

Food-web interactions inform nonnative fish removal efforts aimed at native species recovery. We leveraged a natural gradient of compositional turnover from native-only to nonnative-only fish assemblages, combined with an intensive removal effort, to investigate underlying food-web changes in response to species invasion. Making inferences from carbon and nitrogen stable isotope ratios, we found nonnative species caused coordinated trophic niche displacement in native fish assemblages by inducing resource shifts toward lower trophic levels and enriched carbon sources. In contrast, nonnative fishes did not experience reciprocal shifts. Asymmetrical outcomes indicate native species displacement may result from aggressive competitive or consumptive interactions with nonnative species. Native fishes similar to a nonnative species had the highest niche overlap in mixed assemblages, but a considerable capacity for recovery. Native species' isotopic niches returned to higher trophic levels after green sunfish removal, indicating successful control efforts. Using stable isotope analysis as part of pre-removal assessment provides opportunities to identify asymmetric interactions whereas post-removal assessment could help identify unintended consequences, like mesopredator release. This research is essential to inform adaptive decision making to recover native fish species.

3.2 Introduction

Freshwater ecosystems are susceptible to invasion by nonnative species (Gallardo et al. 2016), and persistent challenges remain to identify and predict potential impacts on food-webs (Jackson et al. 2017). Nonnative species may become integrated into recipient communities, leading to new or modified interactions among resident native and nonnative species (David et al. 2017). Rapidly shifting species assemblages has led to calls to account for food-web structure and species interactions when implementing management strategies aimed at controlling nonnative species (Zavaleta et al. 2001; Ballari et al. 2016). Knowledge of food-web interactions can help prevent unintended consequences and lead to successful restoration outcomes by prioritizing scheduled removal of multiple interacting species (Bode et al. 2015), identifying situations that require simultaneous eradication of multiple invaders (Ballari et al. 2016), or even determining whether eradication actions may do more harm than good (Kopf et al. 2017).

Nonnative invasive fishes are implicated in changing the structure and function of riverine food-webs (Cucherousset & Olden 2011). Longer food chains can result from introduced predators occupying higher trophic levels than resident native species, either by direct consumption, displacing native predators toward lower quality resources, or both (Sagouis et al. 2015). Predators are often successful invaders in aquatic ecosystems (Moyle & Marchetti 2006). Direct predation is the predominant mechanism by which local native species populations decline (Mollot et al. 2017). For native species occupying a similar trophic position as the invader, competition or intra-guild predation may result in a restricted resource base via resource partitioning (David et al. 2017). Native fish that modify their behavior in response to these interactions may suffer decreased growth, reproduction, and/or recruitment rates (Britton et al. 2018).

Trophic interactions between native and nonnative species can manifest through entire food-webs, resulting in ecosystem level impacts and significant economic costs (Lodge et al. 2006). Ecological impacts vary across nonnative species of different trophic levels, but may include changes in species' dominance and distributions, habitat coupling or decoupling across ecosystems, and alterations in primary production and biogeochemical processes (Cucherousset & Olden 2011). Predicting outcomes of introduced species becomes more complicated with multiple nonnative species (Jackson 2015). In some systems, native species persist despite the presence of multiple nonnative fishes (e.g., Propst et al. 2008), whereas other systems document native species declines after a succession of nonnative fish are introduced (e.g., Johnson et al. 2008).

Given complex responses of recipient communities to nonnative species, a food-web perspective is critical to inform management actions seeking to conserve freshwater ecosystems. Numerous native species recovery efforts involve nonnative fish control or eradication through mechanical removal programs (Rytwinski et al. 2019). Removal efforts infrequently alleviate negative impacts or promote native species conservation. Successful eradication efforts tend to be in areas with few nonnative species where barriers prevent subsequent recolonization (e.g., Marks et al. 2010). Most management efforts that control, but not eradicate target populations, have resulted in compensatory responses of target species (Zelasko et al. 2016) or equivocal responses across multiple native and nonnative fishes (Franssen et al. 2014). Unsuccessful removal programs have led to growing recognition that understanding food-web interactions among native and nonnative species may help anticipate management outcomes associated with species removal efforts (Prior et al. 2018).

As is the case for many freshwater ecosystems, nonnative species are a long-standing threat to the conservation of native fishes in southwestern rivers of the United States (Minckley & Deacon 1968). We investigated food-web interactions among vulnerable native and nonnative fishes using a field investigation conducted across a spatial gradient in community composition turnover, coupled with a targeted management effort to eradicate nonnative fishes from a stream system. We leveraged the existence of native-only, mixed-origin, and nonnative-only species assemblages to make inferences about mechanisms underlying food-web changes in response to species invasion. To examine potential differences in species resource use along an invasion gradient, we used natural abundance C and N stable isotope ratios in fish consumers as metrics of basal food-web resources (13C:12C) and trophic positon (15N:14N). Our objectives were to determine (1) changes in native and nonnative species resource use in the presence of each other; (2) degree of isotopic niche overlap and evidence of trophic dispersion in mixed assemblages; and (3) potential isotopic niche recovery of native species upon large-scale mechanical removal of green sunfish (*Lepomis cyanellus*) – a widely distributed invasive species responsible for eliminating or suppressing native fish populations due to predatory and competitive interactions (Lemly 1985; Dudley & Matter 2000). Here we illustrate nonnative fish impacts and highlight insights from food-web perspectives when assessing nonnative species removal approaches to benefit native species conservation.

3.3 Methods

3.3.1 *Study design and sample collection*

The study was conducted in the Bill Williams River Basin, Arizona, United States (Fig. 1). Nonnative fishes occur in greater species richness and higher abundances in more downstream reaches of the watershed, becoming less common toward the headwaters; thus establishing an invasion gradient. The gradient has manifested over the last half century as nonnative fishes spread upstream from initial locations of stocking, predominantly Alamo Reservoir constructed in 1968 (Pool & Olden 2015). This allowed us to identify river reaches (sites) that ostensibly support nonnative-only assemblages (n = 4), mixed assemblages (n = 4), and native-only assemblages (n = 4). Native and nonnative species composition of these assemblages have remained relatively unchanged in recent decades (Pool & Olden 2015), although three of four native fishes are considered species of concern in Arizona, due to habitat loss and impacts from nonnative species.

At each site, we obtained tissue samples from fishes, macroinvertebrates, and allochthonous and autochthonous primary producers to conduct a food-web investigation according to natural-abundance stable isotopes. Using this method, 13C:12C is a proxy for resource use and 15N:14N is a proxy for trophic position. We employed backpack electrofishing along with opportunistic seining and angling to collect fish in 50-m stretches of the river, incorporating riffle and pool habitat. After surveys were completed, we identified 4 native-only, 2 nonnative-only, and 6 mixed sites, separated by at least 500 m to ensure low likelihood of high species exchange among sites. Fish were identified to species, enumerated, and measured for total length (mm) and mass (g). A subset of fish, 10 – 15 individuals, were temporarily held prior to release, in order to remove the distal margin of anal or caudal fins for stable isotope analysis. Collecting fish fins is a less harmful and comparable alternative to collecting muscle tissue (Tronquart et al. 2012). Fin-clipped individuals were representative of captured body lengths in order to incorporate variation caused by ontogenetic, sex, or other individual differences.

Dominant macroinvertebrates were collected using a 500 μm D-frame kick-net deployed on the substrate and in-stream vegetation. Invertebrates were rinsed into a sorting tray where they were separated from large debris and identified to order or family. Primary producers were collected from multiple habitats to represent basal food-web resources. We collected epilithic algae and detritus (fine particulate organic matter [FPOM]) from rocks in pools, filamentous algae (FILALG) from flowing water habitats, and macrophytes and leaf litter (coarse particulate organic matter [CPOM]) from channel margins.

Animal tissues were preserved in salt for later processing. Salt is an effective preservation method for biological samples collected in remote field settings (Arrington & Winemiller 2002) and has been used successfully for stable isotope analysis investigations (e.g. Spurgeon et al. 2015). Following Spurgeon and colleagues (2015), FPOM, FILALG, and CPOM samples were dried in sunlight and stored before processing.

3.3.2 *Nonnative fish removal experiment*

In 2017, we collaborated with Arizona Game and Fish Department to obtain fish and macroinvertebrate tissue samples before and after one year of intensive mechanical removal of nonnative green sunfish (sunfish) at McGee Wash (Fig. 1). McGee Wash is a predominantly intermittent tributary, with a 2 km perennial reach that serves as reliable fish habitat throughout the year, separated by a 3.2 km downstream stretch of intermittent channel before its confluence with the perennial mainstem. Removal efforts occurred along the entire perennial reach commencing in August 2017 and continuing on at least a monthly interval. The effort was part of a conservation and mitigation program to secure existing populations of roundtail chub (*Gila robusta*), a species of conservation concern (USFWS 2011). We sought to determine if sunfish removal would result in native species isotopic niche space being “restored” (i.e., return to what was observed in native-only assemblages). Fin clips of 20 individuals per species were collected when removal efforts were initiated on August 10, 2017 and again on October 3, 2018 representing one year of removal efforts (17 total removal events). Fin tissue turnover time is estimated to be around 30 days (Galván et al. 2015), so collecting the tissues at least 30 days after the year-long removal efforts ensured that native fish tissues reflected suppressed green sunfish populations. Two native species, roundtail chub (chub) and desert sucker (*Catostomus clarkii*) - and one nonnative species, green sunfish, inhabit McGee Wash; notably less speciose than the other study sites.

3.3.3 *Stable isotope processing*

Tissue samples were dried for 24 - 48 h at 60 °C, homogenized with mortar and pestle, and encapsulated in 5 x 9 mm tin capsules (1 mg animal tissue; 6 mg plant tissue). Tissues were sent to University of California-Davis Stable Isotope Facility and analyzed for ratios of stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) using an elemental analyzer (PDZ Europa ANCA-GSL) interfaced to an isotope ratio mass spectrometer (PDZ Europa 20-20; Sercon Ltd., Cheshire, UK). Data are reported as per mil (‰) deviations from standards of Vienna PeeDee Belemnite for carbon and from atmospheric nitrogen, expressed as "δ" units. Long-term standard deviations for natural abundance stable isotope samples at UC Davis is 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

Fin clips of each species were processed to estimate mean and variation among individuals at each site. We selected Diptera-Simuliidae (collector/filterer) and/or Ephemeroptera-Baetidae (collector/gatherer) to represent baseline isotope values for subsequent fish isotopic shift analyses. Isotope values (mean [SD]) of these two macroinvertebrate families overlapped with each other and with FILALG and CPOM values, but were less variable than plant tissues. We used primary consumers as our baseline to account for spatial and temporal variability across a watershed (Jardine et al. 2014), thus representing more robust indicators of resource use (Bunn et al. 2013).

3.3.4 *Stable isotope analysis*

Stable isotopes help indicate nonnative species impacts on food-webs by integrating outcomes of trophic relationships. We examined native and nonnative species shifts in isotopic niche space with directional statistics following Schmidt et al. (2007). Directional statistics calculate magnitude and direction of change in isotopic niche space with estimates of mean and variability comparable to other multivariate analyses. Because C and N isotope values are analyzed simultaneously, this method can reveal insights that may be unclear when focusing on a single element. Factors affecting an individual's isotope values (e.g. trophic discrimination) are not essential to elucidate structural food-web patterns using directional statistics (Layman et al. 2012). For each species, we calculated directional change (θ) and vector magnitude (r) of isotopic niche shifts between individuals in sites with native- or nonnative-only assemblages compared with individuals in mixed sites. Ontogenetic and body-size differences were accounted for by comparing individuals exhibiting the most similar body lengths between assemblage types. We performed 1,000 bootstrap samples of individuals from each species to account for uneven sample sizes among sites and for multiple potential body length matches at corresponding mixed sites. Site-to-site variability was accounted for by calculating directional statistics for pairwise isotopic differences between sites containing native-only or nonnative-only and mixed assemblages, represented as a mean of all bootstrap estimates. For the nonnative fish removal effort, which took place at one location, we calculated directional statistics for pairwise differences of each species between pre- and post-removal sampling events. Among pairwise site comparisons, we performed a Rayleigh test to assess the significance of mean directionality and a Wilcoxon signed rank test to assess significance of vector magnitude from zero. Rao's homogeneity test was performed to assess differences in directionality among species. Circular statistics were performed with package 'CircStats' in software program R (Lund & Agostinelli 2012).

We examined overlap in isotopic niche space using a Bayesian approach to calculate standard ellipse areas, corrected for sample size, as an indicator of potential resource competition, and isotopic diversity indices, as an indicator of trophic dispersion (Jackson et al. 2011). Isotopic niche overlap was examined between native and nonnative species pairs at each mixed site, where species co-occur. To examine trophic dispersion, we tested the probability that pairwise comparisons of native-only, nonnative-only, and mixed assemblages had equal basal resource range ($\delta^{13}C$ range) trophic range ($\delta^{15}N$ range), total trophic area (TA), centroid distance (CD), nearest neighbor distance (NND), and standard deviation in nearest neighbor distance (SDNND) (Jackson et al. 2011). All analyses were performed in software program R v.3.4.0 (R Core Team 2017).

Spatial variation in baseline carbon and nitrogen isotope values need to be controlled for in riverine food-web studies (Jardine et al. 2014). We accounted for site differences in $\delta^{13}C$ and $\delta^{15}N$ values of primary consumer baselines with a normalization procedure: $\delta Xcor_{ij} = \delta Xfish_{ij} - \delta Xbase_{j,\min}$, where *Xcor* represents corrected C or N isotope values, *Xfish* is the isotope value of fish *i* at site *j*, and *Xbase* is the minimum isotope value of assuming macroinvertebrate primary consumers at site *j*. This correction assumes primary consumers have consistent feeding and tissue assimilation of stable isotopes across sites, and thus changes in fish isotope values reflect changes in fish feeding behavior. Although baseline isotope values varied between individual sites, no longitudinal trends were observed (see chapter supplementary material, Appendix 1 Fig. S1 & Fig. S2).

3.4 Results

Individuals occupied different isotopic niche space depending on whether they occurred in native-only, nonnative-only, or mixed assemblages (Fig. 2). Native species demonstrated a marked isotopic niche shift in the presence of nonnative species (Fig. 3a). All native species showed more enriched basal resource use (increased $\delta^{13}C$ value) and lower trophic position (decreased $\delta^{15}N$ value) in mixed assemblages relative to native-only assemblages. All species had a similar and significant directional isotopic niche shifts (Rayleigh's Z = 0.81 – 0.97, 0.0001 < P < 0.001). Directional mean (Rao's test statistic = 2. 5, P = 0.47) nor variance (Rao's test statistic = 6.7, P = 0.08) did not differ among species. The vector magnitude of these isotopic shifted significantly for all species, with the greatest shift of 3.9 ‰ for desert sucker (*Catostomus clarkii*; V = 210, P < 0.0001), followed by 3.1‰ for Sonora sucker (*Catostomus insignis*; V = 21, P < 0.05), and 2.4‰ for speckled dace (*Rhynichthys osculus*; V = 21, P < 0.05) and chub (V = 136, P < 0.0001). Despite our attempt to account for differences in body size, desert and Sonora suckers had a smaller average total length in native than mixed assemblages (Table S1). However, larger body size is typically correlated with higher $\delta^{15}N$ values (Fig S3); the opposite shift in direction from what was observed between native and mixed assemblages.

Nonnative species showed variable isotopic niche shifts in response to native species presence (Fig. 3b). Green sunfish was the only species to have significant changes between nonnative-only and mixed assemblages. Their isotopic niche shifted by a magnitude of 2.2‰ on average (V = 78, P < 0.001), but directional changes were indistinguishable from random (Z = 0.18, P = 0.69). Although not significant, larger-bodied nonnative species like bullhead catfish and sunfish tended to display a higher trophic position (increased $\delta^{15}N$ value) but showed little change in basal resource use. The small-bodied red shiner tended to have a more depleted basal resource signature and trophic position (decreased $\delta^{13}C$ and $\delta^{15}N$ values) when comparing nonnative-only to mixed assemblages.

In mixed assemblages, native and nonnative species demonstrated variable magnitudes of isotopic niche overlap, measured by standard ellipse area (Table 1). Chub overlapped most with nonnative species isotopic niches, followed by speckled dace (dace), desert sucker and Sonora sucker. Chub and dace may have the largest potential to be negatively impacted by competition even after considerable shifts in basal resource use, assuming isotopic niche is a faithful indicator of diet and/or habitat use. Chub and dace overlapped most with nonnative sunfish and bullhead catfish.

Isotopic diversity indices revealed trophic dispersion when native and nonnative species co-occurred (Fig. 4). Mixed assemblages had larger trophic range ($\delta^{15}N$ range; Fig. 4a) than either native (mean difference = 1.77, 95% CI = [1.62, 1.92]) or nonnative assemblages (mean diff. = 1.82, CI = [1.72, 1.92]) but a smaller resource range ($\delta^{13}C$ range; Fig. 4b) than native assemblages (mean diff. = 0.27, CI = [0.08, 0.46]) resulting in larger overall trophic area (mean diff. native = 1.43, CI = [1.18, 1.68]; mean diff. nonnative = 2.03, CI = [1.84, 2.22]; Fig. 4c). This increasing trophic area was accompanied by a higher centroid distance (mean diff. native = 0.18, CI = [0.14, 0.23]; mean diff. nonnative = 0.25, CI = [0.20, 0.30]; Fig 4d), indicating higher richness in isotopic niche space. Estimates of redundancy or evenness indicated no differences among assemblage types using metrics of nearest neighbor distance (NND) and standard deviation in NND.

Native species' isotopic niches showed marked responses to intensive removal of sunfish in McGee Wash, suggesting at least partial recovery, toward pre-invasion (sunfish-free) values. Monthly efforts conducted over one year resulted in a removal of 11,579 sunfish, representing a 97% decline in adult captures between the first and last removal dates (Fig. 5). Following one year of sunfish removal efforts, native species displayed a shift toward higher trophic positions along $\delta^{15}N$ axis, and little change in $\delta^{13}C$ values, relative to fish captured prior to removal (Fig. 6). For chub, but not desert sucker, their isotopic niche shifted significantly in directionality ($Z = 0.92$, $P < 0.0001$) and magnitude (3.0‰, $V = 120$, $P < 0.01$).

3.5 Discussion

Food-web investigations inform management strategies by exposing potential interactions among target nonnative species and other community members that may compromise achieving desired conservation outcomes. This knowledge can be used to help plan nonnative removal (Kopf et al. 2017) or other restoration efforts (e.g., Bellmore et al. 2017, Spurgeon et al. 2015) aimed at recovering native species and restoring ecosystems. Nonnative species are often targets of restoration because they alter trophic interactions leading to changes in food-web structure, energy flow and ecosystem function (David et al. 2017; Jackson et al. 2017). Here, native species, in the presence of nonnative species, shifted to isotope values representing lower trophic levels and more enriched basal resources. Resource shifts resulting from competition or predation may lead to reduced reproduction, growth rates, and survival (Chase et al. 2002). We speculate that, over time, asymmetric competitive interactions are at least a partial mechanism for species replacement occurring in watersheds invaded by introduced fish species, ultimately leading to nonnative-dominated assemblages (Bøhn et al. 2008). In our study, chub, with the largest isotopic niche overlap with introduced species, benefitted most from nonnative removal efforts as indicated by a greater magnitude shift and significant directionality in isotopic niche recovery relative to desert sucker. This suggests nonnative species may affect trophically similar native species most, but these native species are also most likely to benefit from nonnative removal efforts, resulting in desirable restoration outcomes.

Native and nonnative species demonstrated asymmetrical responses to each other's presence. Native species displayed coordinated shifts toward lower trophic levels and more enriched C values, whereas nonnative bullheads and sunfish tended to increase trophic level, though inconsistently. More enriched C values were associated with algal periphyton. Because isotope niches are not equivalent to trophic niches, but rather quantitative indicators of changes in niche, more enriched values could indicate changing habitats, diets, or differences in growth rates, which affect diet assimilation into fish tissues. Therefore, similar isotopic niches may result from either similar resource use or a use of different resources that, when mixed together in consumer tissue, display similar isotope values. Thus, using diet data to corroborate stable isotope values is often recommended as a best practice (Fry 2013). Although we did not collect diet data, to minimize handling time and stress associated with excavating stomach contents of native species, we think resource overlap is likely. Low resource diversity leads to more competition, diet partitioning, and consumption of non-optimal energetic food sources (e.g., Latli et al. 2019). In streams, high dependence on few resources is common, and these resources typically have distinct isotope values to be able to distinguish between them. Most stream consumers depend on algal derived sources of carbon and nitrogen (e.g., Bunn et al. 2013). During restoration efforts in Fossil Creek, a stream with a similar fish community, comparable results were reported. Nonnative smallmouth bass (*Micropterus dolomieu*) and sunfish replaced native dace, chub, and suckers in the highest trophic positions of the food-web (Marks et al. 2010). Concomitantly, chub and desert sucker diets tended to shift away from a diet including predatory invertebrates (Marks et al. 2010).

Establishing interspecific competition is challenging in observational studies because of the difficulty in obtaining repeated measurements of the same individuals to document changes in growth or other vital rates through time. In experimental settings, similar trophic dispersion and niche shifts, as we observed, have been accompanied by reduced native species growth rates, lending stronger evidence for interspecific competition (e.g., Britton et al. 2018). High potential for competition has also been inferred from functional convergence (Arena et al. 2012). Arena and colleagues (2012) showed common native and nonnative fishes at similar trophic levels, exhibited similar prey capture behavior, but nonnative fishes had larger gape width, allowing for potential asymmetric competitive interactions (i.e., intraguild predation). Intraguild predation may be facilitated by ontogenetic shifts in species interactions. In the Colorado River Basin (CRB), nonnative species prey upon small-bodied and young-of-year native fishes (Dudley & Matter 2000; Pilger et al. 2010), and trophically similar adults have been observed to interfere and compete with one another (e.g., Karp & Tyus 1990, Spurgeon et al. 2015), providing additional evidence for this hypothesis. Throughout the CRB, nonnative fishes have been observed to occupy higher trophic levels (Pilger et al. 2010; Walsworth et al. 2013). The available information about mixed assemblages in the CRB, together with our observation that native but not nonnative species shift isotopic niche space in each other’s presence, suggests asymmetric competition is occurring and may reduce local persistence of native species.

After experiencing significant isotopic niche shifts, some native species continued to show considerable overlap with nonnative species. The native sucker species had less isotopic niche overlap with nonnative species than chub or dace. Because suckers have different resource dependencies than nonnative species, they could partition resources more successfully, resulting in greater niche shifts and less niche overlap. When a nonnative and native species have similar ecology, changes in native species behavior may not be enough to offset competitive and/or consumptive interactions with nonnative species (e.g. Ayala et al. 2007). Chub and dace are functionally similar to nonnative species like sunfish and red shiner, therefore, they may be unable to partition high quality resources, activity times, or habitat use, resulting in smaller niche shifts, higher niche overlap, and higher potential for facing detrimental impacts from nonnative fishes. In Fossil Creek, although chub shifted to a diet dominated by small filter feeder invertebrates in the presence of nonnative species, desert sucker diets remained more balanced among feeding groups but included more grazing invertebrates (Marks et al. 2010). High resource overlap between native and nonnative species has been reported elsewhere in the CRB (Walsworth et al. 2013; Spurgeon et al. 2015). Studies combining stable isotope analysis with diet evaluation also demonstrate native and nonnative species share overlapping diets of invertebrate taxa (e.g., Pilger et al. 2010; Whiting et al. 2014). Thus, niche overlap metrics are probably a faithful representation of competition for shared resources and changing diets, not an artifact of using stable isotope values.

Nonnative species introductions commonly result in trophic dispersion (Cucherousset et al. 2012). We found that larger isotopic niche areas in mixed assemblages, compared to other assemblage types, was driven mainly by an increase in trophic ($\delta^{15}N$) range caused by native species displacement to lower trophic levels. Native species shifts in C and N isotope values, unaccompanied by increased values in redundancy (NND and SDNND), signified that resource partitioning was the most likely response of native species to the presence of nonnative species. Although isotopic diversity indices are correlated and sensitive to the number of samples and biased by small sample sizes, our total sample size per community type exceeded the recommended 10 – 30 individuals (Jackson et al. 2011). Even centroid distance, which is less sensitive to species number, considered the "core" niche (Brind'Amour & Dubois 2013), was larger in mixed assemblages relative to native- or nonnative-only assemblages. Our findings are typical of free-flowing ecosystems, where top predator additions increase total area of isotopic niches, primarily by increasing trophic range ($\delta^{15}N$; Sagouis et al. 2015). Contrary to previous studies, however, we found this increased trophic area was associated with native species niche shifts.

Identifying interactions and assessing recovery efforts in freshwater ecosystems using food-web approaches have been valuable in a variety of contexts. In one application involving nonnative species control in rivers, stable isotope and diet analysis suggested trout removal efforts led to increased survival and recruitment of endangered juvenile fishes via reduced predation and resource competition (Coggins et al. 2011; Whiting et al. 2014). Removal of nonnative species can result in quick and substantial food-web recovery of trophically similar native species (Lepak et al. 2006). Nonnative removal efforts in McGee Wash resulted in the apparent recovery of native species with respect to returning to isotopic values typical of native-only assemblages. This could be interpreted as a recovery of their trophic niche. Following nonnative removal, chub and desert sucker increased trophic position, with significant recovery for chub, a state-listed threatened species and candidate for federal listing under the U.S. Endangered Species Act. The larger recovery following removal may indicate chub are more sensitive to nonnative species compared to desert sucker. Similarly, after nonnative removal efforts in Fossil Creek, dace and chub increased in abundance, with densities up to 150 times higher than densities prior to removal efforts, whereas desert sucker densities were about 50 times higher (Marks et al. 2010). Lemly (1985) demonstrated that native fish abundance and biomass were between two and nine times higher after sunfish removal in first order streams in North Carolina. In all of these cases, greater than 90% of nonnative fish populations were removed, so future research exploring the relationship between nonnative species densities and trophic response in native species would provide valuable insights on the level of control needed to have positive effects on native species.

Successful or unsuccessful nonnative removal efforts are influenced by the food-web and ecosystem context, which raises two important considerations of our study. First, the number of species and trophic links in an assemblage affects food-web structure (David et al. 2017). The fish assemblage in the upper Bill Williams River basin is depauperate compared to other temperate rivers, and McGee Wash in particular had a single nonnative species, sunfish, which is a predator and competitor of native fishes. In more speciose food-webs with multiple invaders, a higher potential exists for unforeseen species interactions (e.g., mesopredator release or hyperpredation) and trophic cascades to affect the outcome of nonnative removal efforts (Zavaleta et al. 2001; Ballari et al. 2016). Second, despite not finding longitudinal trends in primary productivity or basal resource isotope values, trophic structure can be affected by changes in productivity alone, without changes in predator composition or introducing new basal resources (McMeans et al. 2015). Thus, we encourage more research on impacts of nonnative species introductions and removal efforts to determine the challenges and opportunities of ecosystem recovery in riverine systems.

In conclusion, nonnative species removal efforts may have positive, negative or neutral outcomes with respect to native species and ecosystem recovery (Prior et al. 2018). Assessing food-web interactions before and after nonnative species removal efforts is recommended for conserving and managing native species biodiversity and ecosystem function (Kopf et al. 2017). Pre-removal assessment will help prevent ecological surprises like mesopredator or competitive release that may result in increases of non-target invasive species. Post-removal assessment, and/or assessment prior to native species reintroduction efforts, will help support functioning populations of native species and overall ecosystem integrity.

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3.8 Tables

Table 3.1 Niche overlap in pairwise species comparisons of standard ellipse area corrected for sample size*.

Nonnative species	Native species			
	Desert sucker (*Catostomus clarkii*)	Sonora sucker (*Catostomus insignis*)	Roundtail chub (*Gila robusta*)	Speckled dace (*Rhynichthys osculus*)
Bullhead spp. (*Ameiurus* spp.)	16.6 (4.7)	7.6 (1.8)	36.0 (1.4)	25.2 (--)
Red shiner (*Cyprinella lutrensis*)	12.6 (--)	9.5 (--)	--	--
Green sunfish (*Lepomis cyanellus*)	18.5 (3.5)	13.6 (8.0)	23.3 (1.8)	22.3 (2.5)

* Overlap is the percent area of 95% prediction ellipses using Bayesian estimation that is shared between two species. Overlap is shown in the body of the table as mean (SE). Species comparisons were made only for sites where two species co-occur in a mixed assemblage. Estimates that could not be made based on sample size or lack of co-occurrence data are indicated by a dash.

3.9 Figures

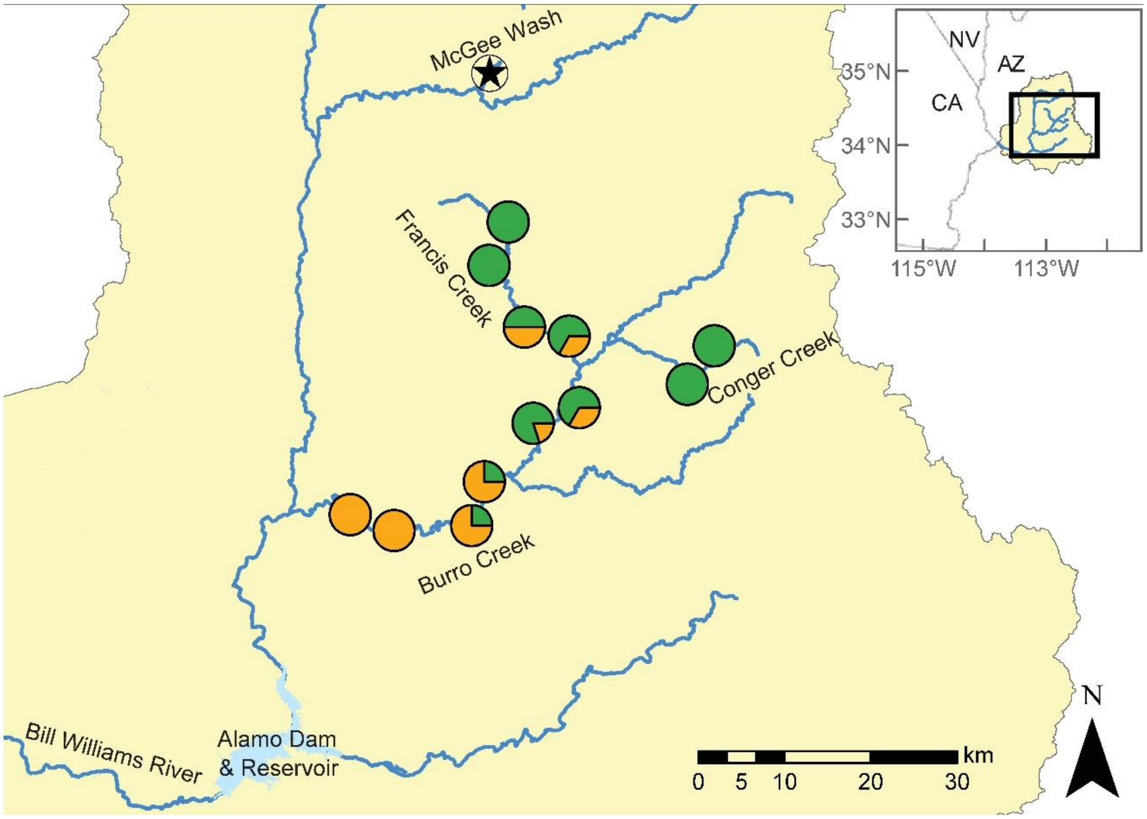

Figure 3.1 Study area map of upper Bill Williams River basin. Approximate sample locations of fish tissue collection surveys are denoted by pie charts showing the proportional richness of native (green) and nonnative (orange) species. Removal efforts, targeting nonnative green sunfish, took place at McGee Wash (encircled star). The inset map shows the location of the Bill Williams River basin and extent indicator of the study area in northwestern Arizona (AZ), USA.

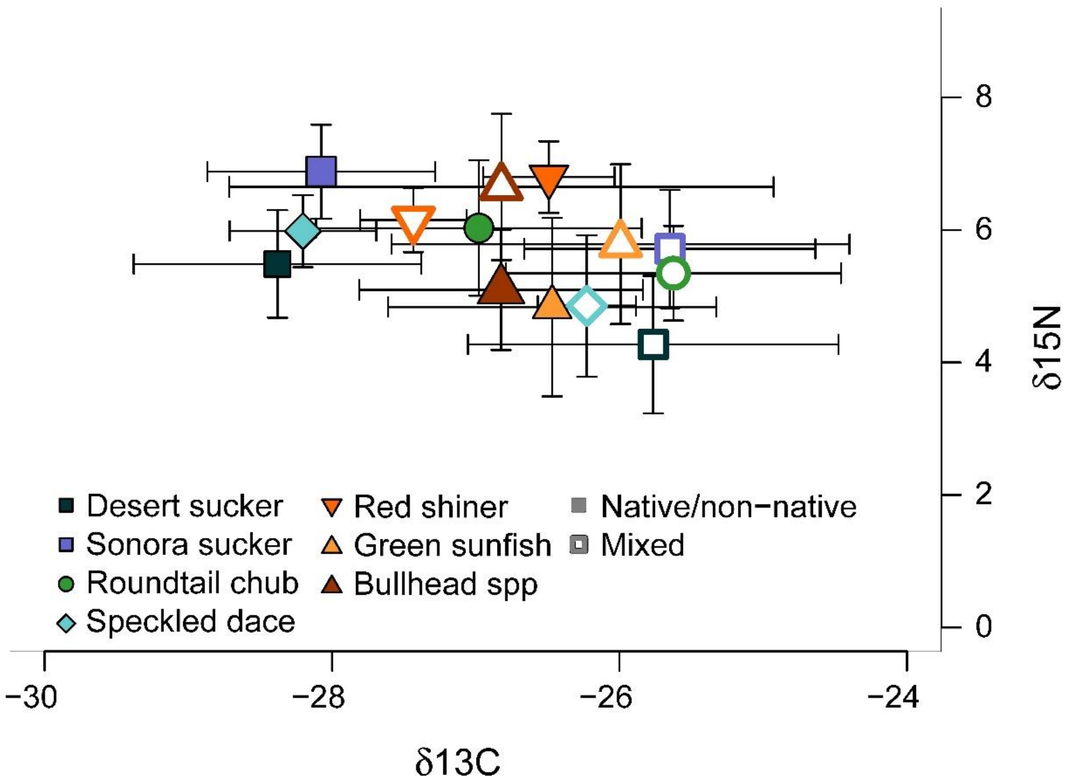

Figure 3.2 Stable isotope bi-plot for ratios of carbon and nitrogen (13C/12C and 15N/14N). Mean isotope values are represented as unique symbols for each species (color, shape) among each assemblage type (pattern) with standard error (arrow bars), as in figure legend key. All values have been corrected using macroinvertebrate primary consumers as a baseline.

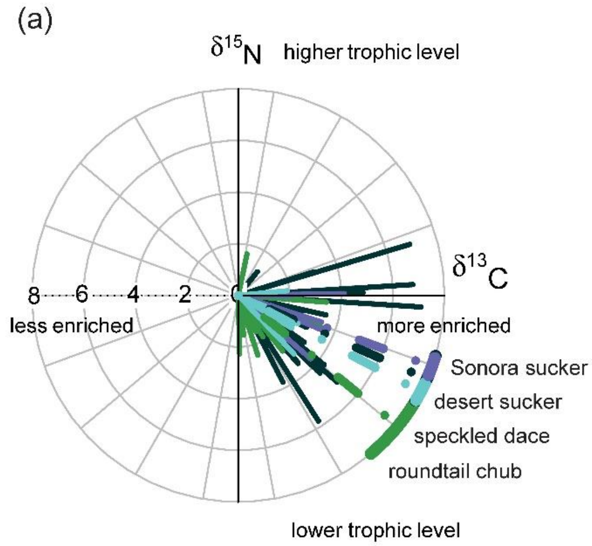

Figure 3.3 Polar bi-plot of isotopic niche shifts between (a) native only and mixed assemblages or (b) nonnative only and mixed assemblages. Vectors (solid lines) represents the mean pairwise isotopic differences of a species between a native- or nonnative-only and mixed sites according to bootstrap sampling (n = 1,000 per species) on individuals of similar body size from each site. Directional isotope differences are represented by the angle of change (θ), where each circular sector is 20°. The length of each vector represents the total magnitude of niche shifts in δ13C and δ15N stable isotopes. Units of magnitude (per mil) are indicated along the plot grid radius. Directional mean (dashed radial line) and variance (arc on circumference) across all pairwise site comparisons are displayed for each species. Each species' isotopic niche shifts are represented by vectors of a unique color indicated by species labels adjacent to the nearest dashed radial line (color codes same as in Fig. 2).

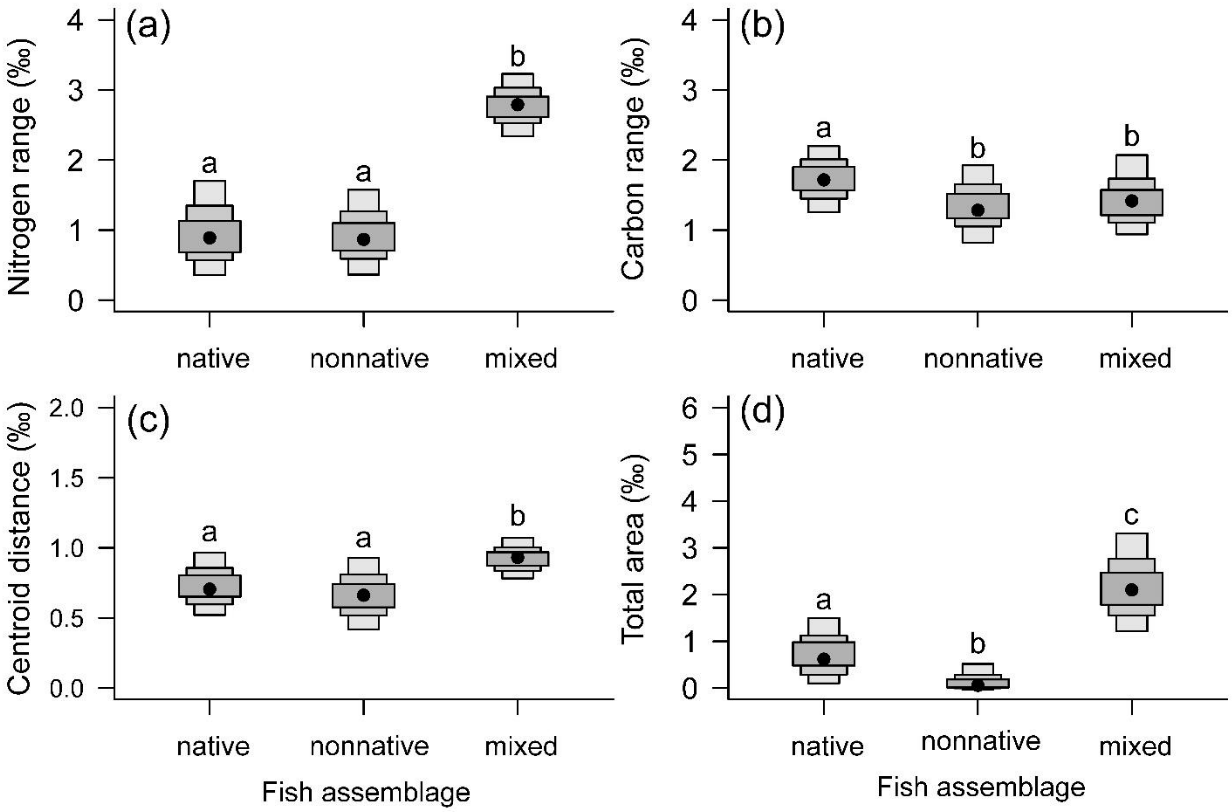

Figure 3.4 Isotopic diversity indices of native-only, nonnative-only, and mixed species assemblages. Diversity indices include (a) nitrogen range, (b) carbon range, (c) centroid distance, and (d) total area in isotopic niche values. The black points correspond to the mean value for each assemblage, and the boxed area reflects the 95, 75 and 50% credible intervals. Letters indicate groups with significant differences.

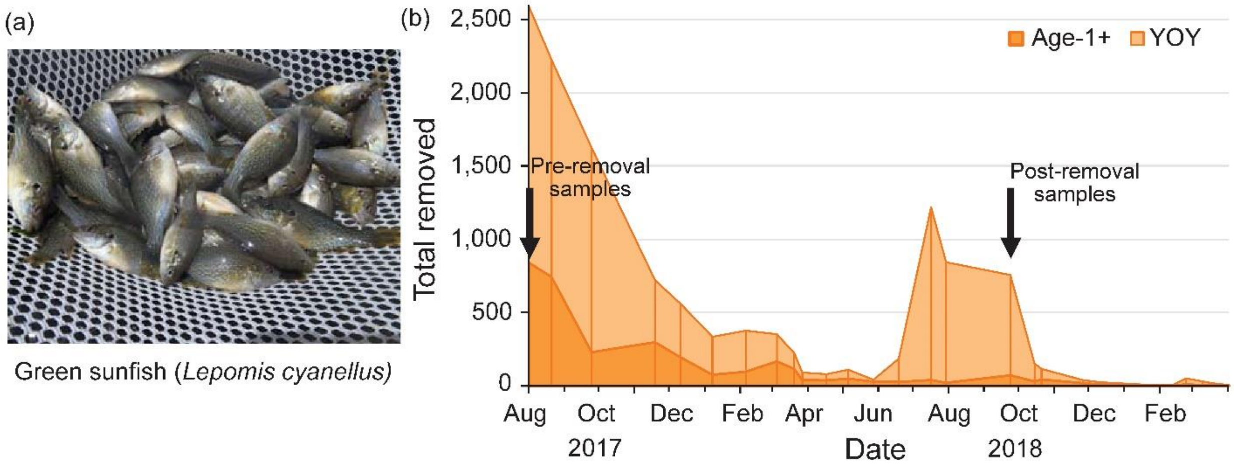

Figure 3.5 Timeline of green sunfish captures during mechanical removal effort, performed by Arizona Game and Fish Department at McGee Wash. Removed green sunfish in a seine (a; photo credit J. Olden), one of many gears used during the mechanical removal efforts. Total number of individuals removed from the start of the removal effort through April 2019 (b) with individuals divided by age/size classes, young-of-year (YOY; ≤ 50 mm) and larger (Age-1+; > 50 mm). Droplines indicate dates on which removal efforts took place. Black arrows indicate when fin clip tissues were collected from fishes for stable isotope analysis for the before and after removal comparison.

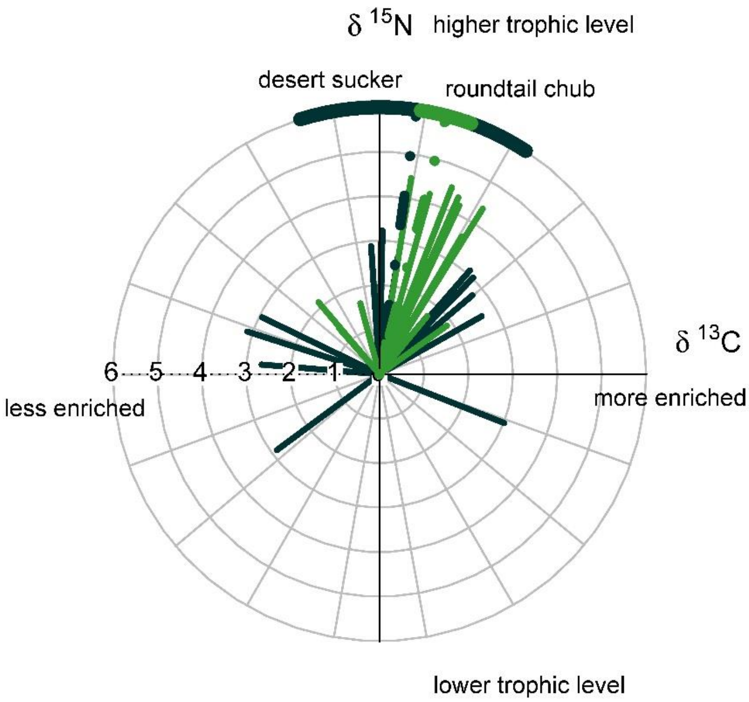

Figure 3.6 Polar bi-plot of isotopic niche shifts of species before and after a year of nonnative removal efforts at McGee Wash. Each solid line vector represents the mean pairwise isotopic differences between individuals of a species before and after removal according to bootstrap sampling (n = 1,000 per species). Directional isotope differences are represented by the angle of change (θ), where each circular sector is 20°. The length of each vector represents the total magnitude of niche shifts in δ13C and δ15N stable isotopes. Units of magnitude (per mil) are indicated along the plot grid radius. Directional mean (dashed radial line) and variance (arc on circumference) across all pairwise individual comparisons are displayed for each species. Each species' isotopic niche shifts are represented by vectors of a unique color as indicated by species labels adjacent to the nearest dashed radial line (color codes same as in Fig. 2).

3.10 Chapter 3 Appendix 1.

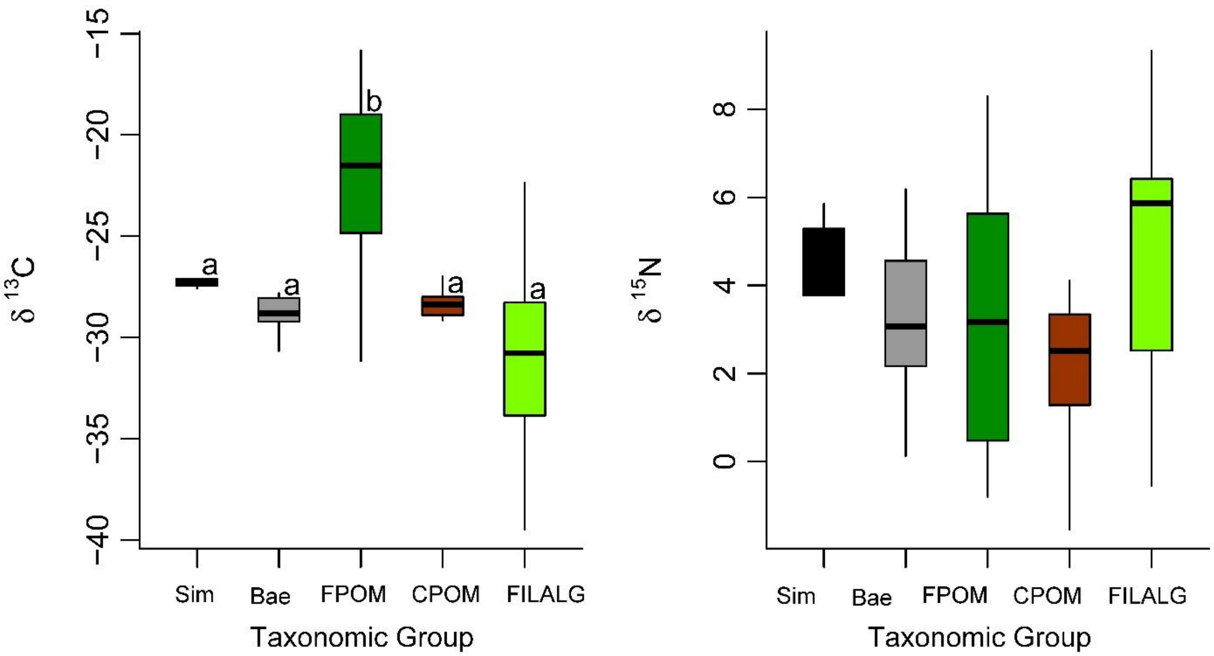

Figure S 3.1 Primary consumer (Simuliidae [Sim], Baetidae [Bae]) and primary producer (FPOM, CPOM, FILALG) values of (a) carbon (δ13C) and (b) nitrogen (δ15N) stable isotopes. Significant pairwise differences ($P < 0.05$) between groups are indicated by different letters, evaluated according to an ANOVA and a post-hoc Tukey's HSD.

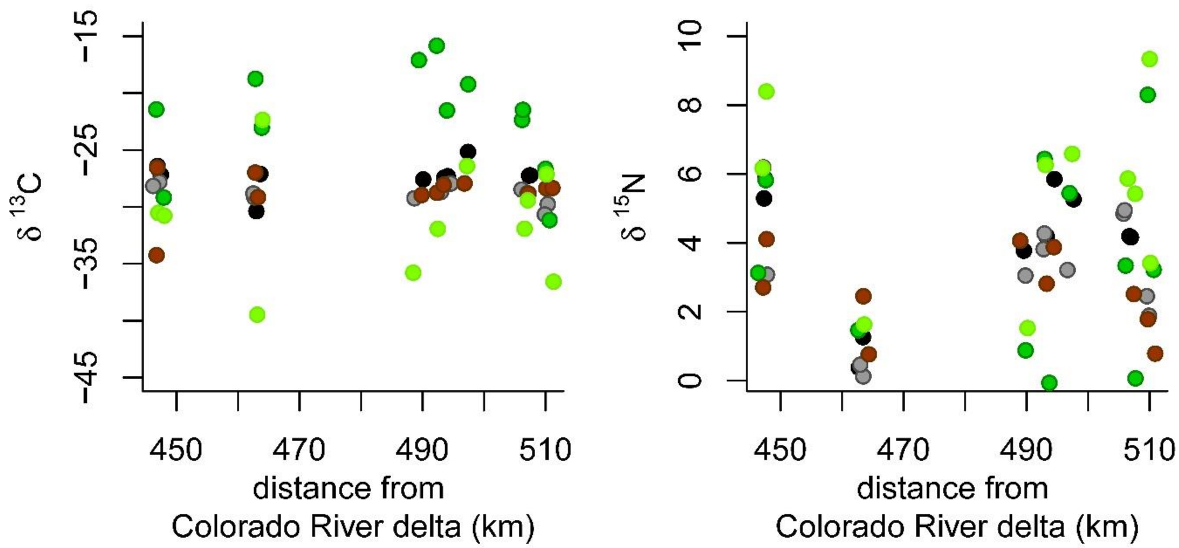

Figure S 3.2 Longitudinal profile of primary consumer and primary producer carbon (a) and nitrogen (b) stable isotope values along the flowline of Burro Creek and its tributaries in the upper Bill Williams watershed. Points were jittered along the x-axis to help make them more visible, but both primary consumers were not always collected at every site. Using Spearman rank correlations (*r*), no significant relationships between river location and $\delta^{13}C$ (r range [-0.43, 0.06]; $P > 0.05$) nor $\delta^{15}N$ stable isotope values (r range [-0.45, 0.31]; $P > 0.05$) were observed. Colors correspond to taxonomic groups as in Fig. S1.1.

Table S 3.1 Total body length (mean [SE]) of native- or nonnative-only assemblages and mixed assemblages. Significant differences between groups were tested with Wilcoxon rank sum tests.

Common name	Total length (mm)		
	Native or Non-native assemblage	Mixed assemblage	Significance
Desert sucker	136.1 (2.5)	144.4 (2.3)	$P = 0.013$
Sonora sucker	139.3 (7.8)	237.6 (11.7)	$P < 0.0001$
Roundtail chub	126.4 (4.6)	135.4 (3.7)	--
Speckled dace	75.5 (1.8)	73.6 (1.3)	--
Green sunfish	80.3 (1.5)	81.6 (1.2)	--
Bullhead spp.	151.8 (4.6)	152.5 (4.5)	--
Red shiner	55.7 (0.8)	55.9 (0.8)	--

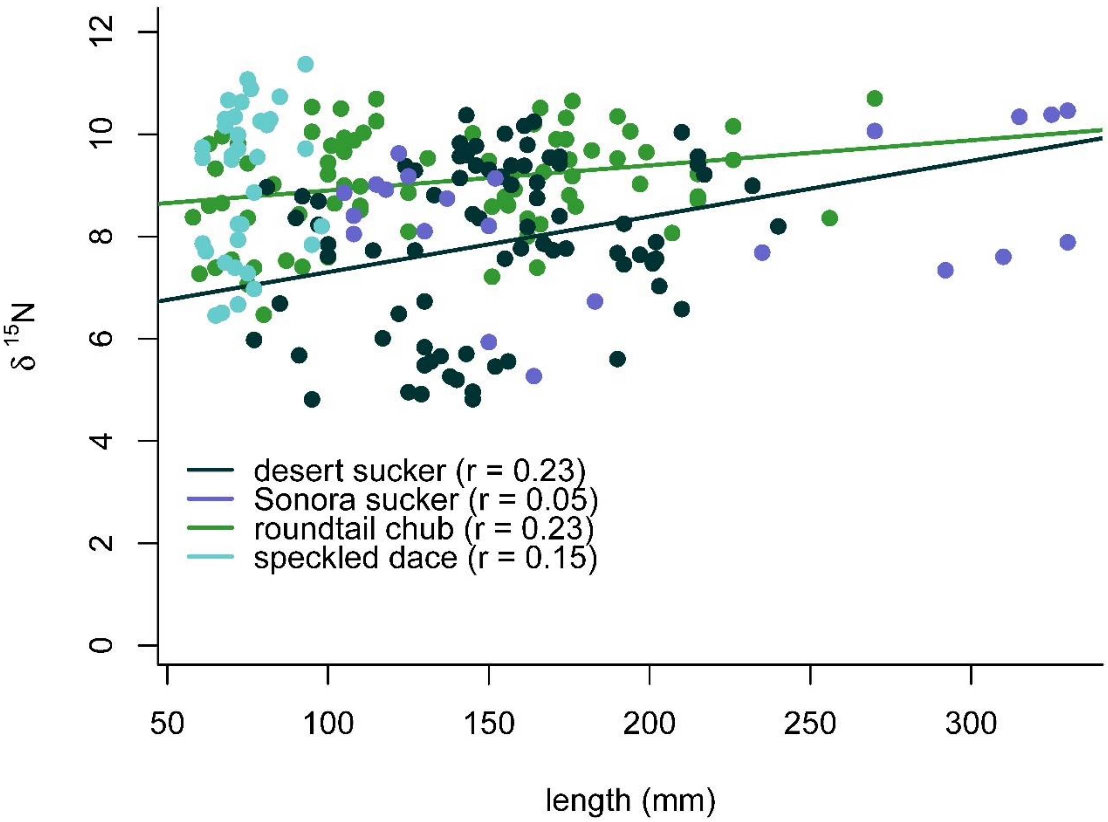

Figure S 3.3 Relationships between body size (total length [mm]) and nitrogen stable isotope values ($\delta^{15}N$). Linear trends are displayed for species with significant Pearson (*r*) correlations (*P* < 0.05).

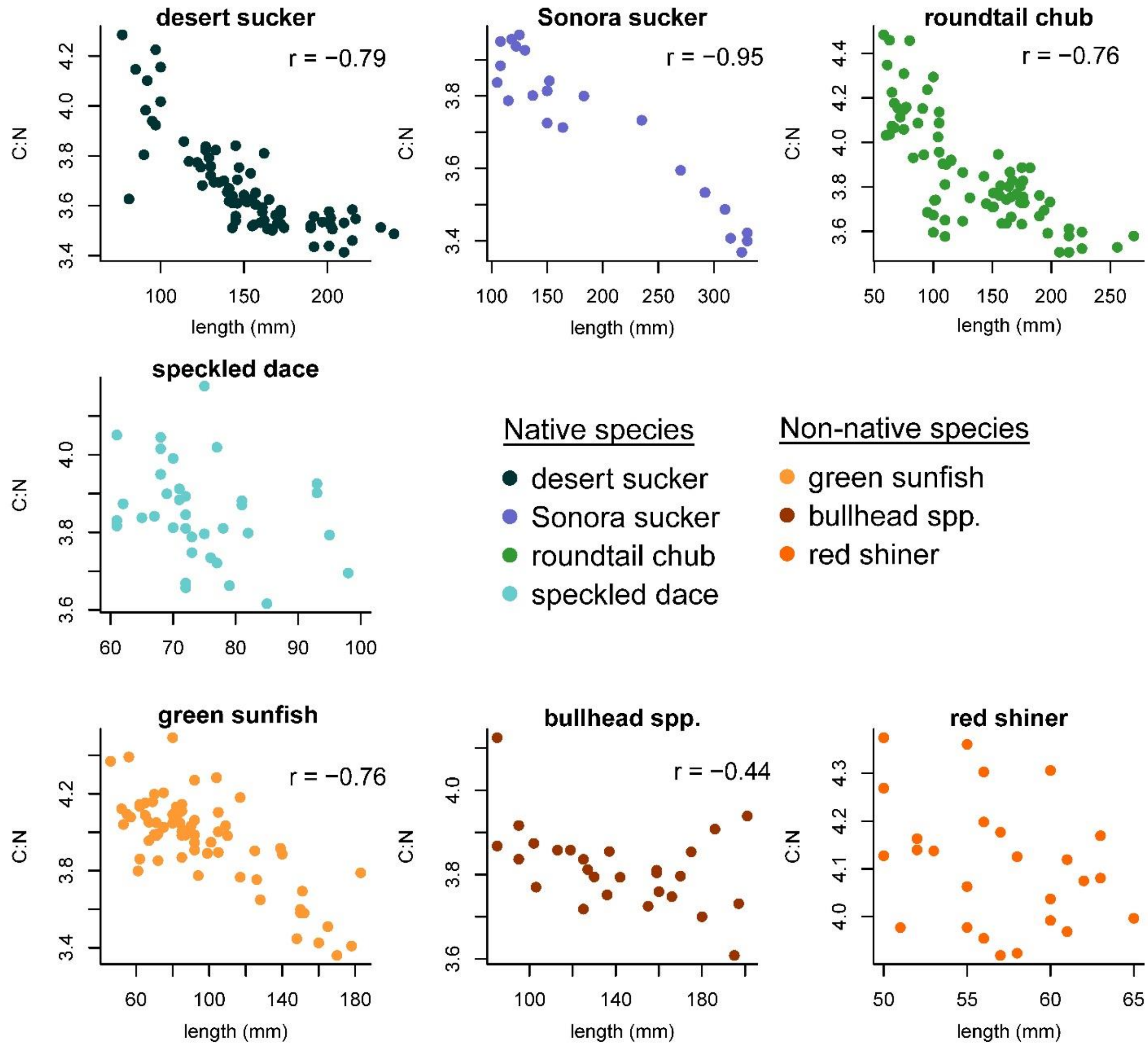

Figure S 3.4 Relationship between carbon to nitrogen ratios in fish fin tissue samples and body length. Pearson correlations (*r*) are shown in the top left corner for species with significant relationships ($P < 0.05$).

Chapter 4. **Dynamic co-occurrence models reveal effectiveness of opportunistic and strategic invasive species removal efforts**

4.1 Abstract

As recognition of the ecological and economic impacts of invasive species grows, so too does the desire for new science to inform management that prevents and counteracts their impacts. A persistent challenge is to identify whether removal programs, which range greatly in their approach, are successful. We were interested in whether strategic and opportunistic removal programs result in measurable, and if so comparable, benefits to native species conservation. We evaluated the roles of interspecific species interactions, hydrologic regimes, and nonnative species removal efforts using dynamic co-occurrence models to examine the ecological processes underlying occupancy dynamics. The model was informed by fish populations monitored at 89 sites in the Lower Colorado River Basin between 1976 and 2018. We used four sets of native-nonnative species pairs to examine interspecific interactions and responses to removal efforts. We modeled two native species of high conservation concern and two other representative native species of the endemic assemblage. Each native species was paired with one of two nonnative fish taxa with demonstrated negative interspecific interactions, centrarchids and red shiner (Cyprinella lutrensis) resulting in four co-occurrence models (chub (Gila robusta) – centrarchids, desert sucker (Catostomus clarkii) – centrarchids, woundfin (Plagopterus argentissimus) – red shiner, and speckled dace (Rhynichthys osculus)– red shiner). We found that native species, especially species of conservation concern, benefitted from both opportunistic and strategic removal programs via increasing colonization and decreasing extinction probabilities. Species interactions also affected predicted colonization and extinction probabilities, particularly during years with low flow anomalies. Although removal efforts had small influences on nonnative species colonization and extinction probabilities, changes in these dynamics incrementally resulted in conservation success. Quantifying dynamics of both native and nonnative fishes in a multi-state dynamic co-occurrence model helped us understand the impacts of opportunistic and strategic invasive species removal efforts. Encouragingly, results from these efforts demonstrated that removal programs can meet recovery goals even over large areas and long after nonnative species are established.

Key words: multispecies occupancy model, dynamic co-occurrence model, invasive species, nonnative, streams, rivers, metapopulation

4.2 Introduction

The global proliferation of invasive species continues, with little evidence of waning (Seebens et al. 2017). As the potential for devastating ecological and economic impacts continues to grow with successful invasion and establishment, so too does the desire for new science to inform management that prevents and counteracts nonnative species impacts (Early et al. 2016). Strategies focusing on invasive species control efforts in natural resource management are growing in particular (Prior et al. 2018, Rytwinski et al. 2019). Mechanical removal of organisms is common practice with the intent to reduce nonnative populations as a means of reversing detrimental impacts such as declining native species, loss of diversity, and altered ecosystem function (Gallardo et al. 2016, Mollot et al. 2017). Despite the best intentions, a persistent challenge is to identify whether removal programs, which range greatly in their approach, were successful (Prior et al. 2018).

Strategies for managing nonnative populations broadly include containment, suppression and eradication (Fig. 1). Containment is used to prevent or control the spread of nonnative species by constructing barriers such as fences or low-head dams (Rahel 2013, Hermoso et al. 2015). Barriers are most effective if they cannot be breached by target nonnative species and if purposeful or accidental introduction into the contained area is avoided (Fig 1a). Suppression and eradication reduce nonnative species populations to different degrees, often sharing a suite of techniques, including introducing new species to serve as biological control agents, mechanical removal of individuals, or chemical treatment of invaded habitats. Suppression is generally used when total population eradication is not feasible or likely due to a large areal extent or high resource requirement (Myers et al. 2000, Baxter et al. 2008). Eradication tends to be most successful in scenarios of early detection and rapid response to a new invasion (Lodge et al. 2006; Fig. 1c). These strategies are not mutually exclusive; for example, containment and eradication are often used together, and eradication is typically more effective in geographic or engineered isolated areas such as islands (Jones et al. 2016), fenced in reserves (Ruykys and Carter 2019), alpine lakes (Tiberti et al. 2019), and streams with barriers (Marks et al. 2010).

Containing, suppressing or eradicating nonnative organisms is a persistent conservation challenge for freshwater biodiversity because of the inherent difficulty in detecting aquatic nonnative species underwater, and their propensity to disperse widely via water currents or transportation vectors (Britton et al. 2011, Simberloff 2014, Reid et al. 2019). Success of nonnative fish removal programs, for example, is highly variable because positive responses in native fish populations hinge on the specifics of the ecology and strength of interactions among species in the community. Native fish responses to restoration actions that include nonnative fish control efforts have been associated with biological traits such as body length, longevity and fecundity, which affect species susceptibility to predation and post-restoration population growth (Propst et al. 2015, Laub and Budy 2015). Indeed, removal efforts often result in positive demographic responses in native populations if targets of removal are predators (Lepak et al. 2006, Marks et al. 2010). However, in situations where interspecific interactions are prevalent and complex, suppressing or eradicating a target nonnative species may result in compensatory responses in non-target species with neutral or negative consequences for native species (Zavaleta et al. 2001, Ballari et al. 2016). Taken together, incorporating interspecific interactions is paramount to improve our ability to predict the conservation outcomes of nonnative species removal programs, including recovery in native species populations.

Enhancing our knowledge of native and nonnative species dynamics is essential for planning removal programs and facilitating long-term achievement of conservation goals. Even if a program is successful at removing target nonnative species, desired recovery of native species populations may not be realized. For example, recovery is less likely when habitat disturbance is the underlying driver of native species declines (MacDougall and Turkington 2005, Prior et al. 2018). Disturbance and propagule pressure are often important factors affecting invasive species removal efforts such that additional restoration activities are needed to shift the balance of recolonization in favor of native species (Buckley 2008). In freshwater systems, hydrologic regimes are a fundamental driver of species life-history, population dynamics and geographic distribution. Native and nonnative fishes can demonstrate different relationships to hydrology because of varying adaptations to the timing, magnitude, and seasonality of flow conditions (Mims and Olden 2012). Thus, local hydrologic context influences native-nonnative species dynamics and consequentially may inhibit or benefit the conservation outcomes of nonnative species removal efforts (Marks et al. 2010, Coggins et al. 2011, Propst et al. 2015).

Nonnative removal efforts span a continuum from fully dedicated strategic programs to opportunistic actions that are temporally periodic and often implemented at smaller spatial scales. A variety of social and economic considerations are infused in the design of removal programs, which ultimately affect both how they are implemented and whether they are successful (Estévez et al. 2015, Crowley et al. 2017). In some cases, conservation action for species federally listed as threatened or endangered leads to multi-agency strategic action plans and funding in support of removal activities with a clearly defined goal, such as local eradication of nonnative species or recovery of native species (Fridell and Bennion 2019). In other cases, state agencies may have limited budgets and personnel to meet multiple management objectives for native and nonnative species (Clarkson et al. 2005, Carey et al. 2011), so nonnative fish removal efforts are limited to opportunistic suppression programs (Propst et al. 2015). Lastly, long-term research programs may result in nonnative species removal actions that are highly sporadic. This raises the question of whether strategic and opportunistic removal programs result in measurable and, if so, comparable benefits to native species conservation.

Models are valuable in designing, implementing and evaluating nonnative species control actions that vary considerably in their effort (e.g., Lohr et al. 2017, Lustig et al. 2017, Messager and Olden 2018). Models complement empirical research by identifying drivers that contribute to latent ecological processes underlying observed patterns. For example, they can help identify factors contributing to colonization and extinction dynamics in the patterns of meta-population distributions (MacKenzie et al. 2018). Using models based on long-term monitoring programs can be particularly useful for species of conservation concern because having data on their vital rates (e.g. survival, reproduction, maturation, etc.) is rare, as is the capacity to examine populations through mark-recapture programs. Thus, long-term data in combination with modeling can provide data-driven estimates to guide adaptive management decisions that include nonnative species control.

The present study evaluates the roles of interspecific species interactions, hydrologic regimes, and nonnative species removal efforts in shaping multidecadal dynamics of native fishes across the Lower Colorado River Basin. We used dynamic co-occurrence models to account for imperfect detection and incorporate these factors to examine the ecological processes underlying site occupancy and rates of colonization and extinction in multiple dryland rivers that are subject to different types of nonnative species control. Dynamic co-occurrence models have demonstrated utility to reveal changes in species distributions and investigate nonnative species influence on native species occupancy through time (Yackulic et al. 2014, Budy et al. 2015). Our objectives were to identify the major factors driving variation in occurrence dynamics and explore evidence for the effectiveness of opportunistic and strategic removal strategies for the suppression of nonnative species and the persistence native fish species occurrence within a large watershed.

4.3 Methods

Our study examined long-term monitoring data from seven locations in the Verde, Gila and Virgin River basins within the Lower Colorado River drainage (USA). These basins share similar native and nonnative fish fauna but differ in their monitoring and nonnative species management, allowing us to investigate the roles of interspecific species interactions, flow conditions, and removal programs. Study locations are subject to different nonnative species removal programs that span containment, suppression, and eradication; these approaches are common to riverine systems more broadly (Fig. 1). Each program has different levels of effort associated with the spatial and temporal scale of removal as well as the frequency of trips, number of personnel, and number of control strategies that are used to fulfill program goals (Table 1). Although this clearly challenges the ability to reveal generality in the effect of different types of removal programs, these conditions reflect the reality of natural resource managers operating to control nonnative species populations across a management mosaic (Epanchin-Niell et al. 2010).

4.3.1 *Removal programs and associated datasets*

The Verde River native species conservation efforts were representative of suppression (Fig. 1b). To model changes in native and nonnative species distributions for the entire Verde River basin, we obtained data from the Arizona Game and Fish Department (AZGFD) Fisheries Information Systems (Stewart et al. 2015). We included only surveys conducted using seining and electrofishing sampling methods, joined spatially to reaches delineated in the National Hydrography Dataset (Rogosch and Olden 2019). Within this database, 41 sites had long-term monitoring data, with at least 10 years of sampling between 1986 and 2012. Surveys were binned into four seasons based on the date of sampling spring (Mar 21 – Jun 20), summer (Jun 21 – Sep 20), autumn (Sep 21 – Dec 20), and winter (Dec 21 – Mar 20), to represent repeat sampling within a year. At two long-term monitoring sites, USFS personnel used mechanical removal efforts to suppress nonnative fishes for nine years (1999-2004, and 2006-2009) (Neary et al. 2012; Table 1). The efforts were opportunistic and experimental, always taking place at the same two long-term monitoring sites, which remained open to recolonization. In 2006, the efforts were expanded to encompass the full 8 km river reach between the two sites.

The Gila River Basin conservation efforts were representative of suppression, containment, and joint containment and eradication programs (Figure 1a, 1b, and 1c; Table 1). This dataset has 24 sites with long-term monitoring between 1988 and 2018. First, in the Gila headwaters of New Mexico (Fig. 2), efforts to suppress all nonnative fish populations occurred each June from 2007 to 2012 (Propst et al. 2015). The control strategy was to use mechanical removal efforts in a reach located between three of six long-term monitoring sites (a downstream mainstem site and two upstream tributaries), which had been surveyed annually in October since 1988 (Table 1). Second, in Bonita Creek further downstream in the basin, a barrier (i.e., containment) was installed in 2008 to prevent further upstream colonization from the source of nonnative fishes via its confluence with the mainstem Gila River. Following barrier installation, a stream renovation to eradicate nonnative fishes occurred in autumn 2008 (Robinson et al. 2009). Monitoring efforts had begun in 2005, prior to the onset of these conservation efforts, and continued after the renovation at 7 fixed sites every April through 2018, including one site located below the barrier, where no effort was made. In the surveys following renovation, some nonnative fishes were observed, so in 2009, mechanical removal efforts were initiated with a focus on eradicating green sunfish (*Lepomis cyanellus*) and yellow bullhead (*Ameiurus natalis*) (Table 1; Blasius & Conn 2015). Third, even further downstream in the Gila River Basin, long-term monitoring sites on the San Pedro River (including a tributary, Aravaipa Creek) had limited nonnative removal effort. To our knowledge, during the period of monitoring data we obtained, the only conservation strategy used in this river was containment, with the construction of a barrier on Aravaipa Creek in 2001 (Clarkson and Marsh 2010).

The Virgin River conservation efforts were representative of a long-term systematic containment and eradication program with the goal of recovering three threatened and endangered species (U.S. Fish and Wildlife Service 1994; Fig. 1c, Table 1). Altogether, 24 sites had more than 10 years of data between 1976 and 2018. The target nonnative species for removal was red shiner (*Cyprinella lutrensis*). Removal efforts primarily took place in the upper Virgin River and were conducted in a stepwise manner moving from upstream to downstream in sections between barriers (Table 1). In addition to removal efforts, the recovery program augmented endangered woundfin (*Plagopterus argentissimus*) and Virgin River Chub (*Gila seminude*) populations through annual stocking programs since 2003. The monitoring dataset came from three sources within the Virgin River Fishes Recovery Team and included datasets from the lower Virgin River Recovery Implementation Team (Golden and Holden 2004, Kegerries et al. 2018), the upper Virgin River Program, and the Utah Division of Wildlife (UDWR; Fridell & Bennion 2019). Seining is the primary gear used to monitor fishes throughout the Virgin River basin. Sampling occurs three to four times a year in this basin, typically spring, summer, and autumn, sometimes winter.

4.3.2 *Focal interspecific interactions between native and nonnative species*

We used four sets of native-nonnative species pairs to examine interspecific interactions and responses to removal efforts and flow conditions through trends in occupancy and occupancy dynamics (colonization and extinction). We chose two native species of high conservation concern: roundtail chub (*Gila robusta*; Page et al. 2017) and woundfin; and two other species representative of the native fish assemblage: desert sucker (*Catostomus clarkii*) and speckled dace (*Rhynichthys osculus*). Roundtail chub has been a candidate for federal listing several times (USFWS 2009) and is considered a species of conservation concern in Arizona. Virgin River chub (*Gila seminuda*) was historically treated as a subspecies of *G. robusta*, but in 1995 it was given individual species status and federally listed as endangered (USFWS 1995). For the purposes of this study, we considered *G. seminuda* as the chub representative in this basin. Woundfin is also a federally endangered species (USFWS 1995). Concern for the persistence of the chub complex and woundfin is based on threats of habitat loss from declining flows and water withdrawals and biotic interactions (competition and predation) with nonnative fishes. Each native species was modeled in a pair with one of two nonnative taxonomic groups: piscivorous centrarchids (green sunfish and basses [*Micropterus* spp.]), or the prolific minnow, red shiner. We chose to use these nonnative groups because they are the most common targets for nonnative species removal efforts and have demonstrable impacts on native fishes. Green sunfish and bass are often targets for removal, not just in the Southwest, but across their introduced ranges, because they are known or suspected predators of many young-of-year and small-bodied fishes (e.g., Lemly 1985; Johnson et al. 2008). Red shiner have been indicated as predators of larvae and potential habitat competitors with small bodied native fishes (e.g., Ruppert et al. 1993; Douglas et al. 1994). The four sets of native - nonnative taxa pairs we modeled were: chub – centrarchids, desert sucker – centrarchids, woundfin – red shiner, and speckled dace – red shiner; for a total of 4 models.

4.3.3 *Flow covariate data*

Annual flow conditions were quantified according to daily discharge records from USGS gages nearest to each site, with flow records that encompassed the monitoring period for that site (Fig. 1). Normalized and log-10 transformed hydrographs were used to calculate daily flow anomalies according to discrete Fast Fourier Transform (following Sabo & Post 2008) for each gage on the Verde River (n=5), the Gila River (n=5), and the Virgin River (n=13). Flow net annual anomaly (NAA) was calculated as the sum of all daily flow anomalies for a calendar year. Negative values indicated low flow anomalies, positive values indicated high flow anomalies, and a value of zero indicated an average flow in a given year. This flow covariate was transformed to a z-score prior to analysis.

4.3.4 *Modeling framework*

We used multi-state dynamic occupancy modeling for co-occurring species (Fidino et al. 2019) to model the presence of each native/nonnative species at a site as a function of the other native/nonnative species (species pairs provided above), flow, and removal covariates. Dynamic co-occurrence models account for imperfect detection and can incorporate multiple covariates to examine the ecological processes underlying site occupancy and rates of colonization and extinction (Dorazio et al. 2010). We rationalize the joint modeling of the three subbasins to provide a more robust evaluation of occupancy patterns and dynamics because native and nonnative fish species demonstrate similar associations with hydrologic conditions across these river basins (Chen and Olden 2017). The model assumes that sites are in one of four mutually exclusive states (*m*): unoccupied (U), occupied by a nonnative species only (A), occupied by a native species only (B), or occupied by both species. Formally the underlying random variable for the occupancy state of site *i* and year *k* is:

$$z_{1,i} \sim Categorical(\phi_0)$$

$$\left(z_{k,i} \middle| z_{k-1,i} = m\right) \sim Categorical(\phi_{k-1})\ for\ k > 1$$

Transitions between states are a dynamic process through site colonization (γ) and extinction (ε) parameters. The probability of each community state is modeled with the multinomial logit-link for linear predictors of colonization and extinction in the transition probability matrix:

$$\phi_k = \begin{array}{c|cccc|} & U & A & B & AB \\ U & 1 & \exp\left(\beta_{ik}^{\varepsilon A|b}\right) & \exp\left(\beta_{ik}^{\varepsilon B|a}\right) & \exp\begin{pmatrix} \beta_{ik}^{\varepsilon A|b} + \beta_{ik}^{\varepsilon B|a} + \\ \beta_{ik}^{\varepsilon A|B} + \beta_{ik}^{\varepsilon B|A} \end{pmatrix} \\ A & \exp\left(\beta_{ik}^{\gamma A|b}\right) & 1 & \exp\begin{pmatrix} \beta_{ik}^{\gamma A} + \beta_{ik}^{\gamma A|B} + \\ \beta_{ik}^{\varepsilon B} \end{pmatrix} & \exp\left(\beta_{ik}^{\varepsilon B|a} + \beta_{ik}^{\varepsilon B|A}\right) \\ B & \exp\left(\beta_{ik}^{\gamma B|a}\right) & \exp\begin{pmatrix} \beta_{ik}^{\varepsilon A|b} + \beta_{ik}^{\gamma B|a} + \\ \beta_{ik}^{\gamma B|A} \end{pmatrix} & 1 & \exp\left(\beta_{ik}^{\varepsilon A|b} + \beta_{ik}^{\varepsilon A|B}\right) \\ AB & \exp\left(\beta_{ik}^{\gamma A|b} + \beta_{ik}^{\gamma B|a}\right) & \exp\left(\beta_{ik}^{yB|a} + \beta_{ik}^{yB|A}\right) & \exp\left(\beta_{ik}^{yA|b} + \beta_{ik}^{yA|B}\right) & 1 \end{array}$$

Columns of ϕ_k represent the occupancy states of sites in year *k* and rows denote the states of sites in year *k* + 1. Elements of each column sum to 1, as a site must transition to one of the four states. The logit-linear predictors for each parameter are:

$$\begin{array}{ll} \beta_{ik}^{\gamma A|b} = \boldsymbol{X_{ik}c_A} & \beta_{ik}^{\gamma A|B} = \boldsymbol{X_{ik}g_A} \\ \beta_{ik}^{\gamma B|a} = \boldsymbol{X_{ik}c_B} & \beta_{ik}^{\varepsilon A|B} = \boldsymbol{X_{ik}g_A} \\ \beta_{ik}^{\varepsilon A|b} = \boldsymbol{X_{ik}d_A} & \beta_{ik}^{yB|A} = \boldsymbol{X_{ik}h_A} \\ \beta_{ik}^{\varepsilon B|a} = \boldsymbol{X_{ik}d_A} & \beta_{ik}^{\varepsilon B|A} = \boldsymbol{X_{ik}h_A} \end{array}$$

Such that $\mathbf{X_{ik}}$ denotes a set of covariate values at site *i* in year *k*, which form a row vector of the values $[1 \quad x_{ik1} \quad x_{ik3} \quad x_{ik3}]$, where the initial '1' denotes a constant required for the inclusion of an intercept term in the resultant equation, x_{ik1} is the opportunistic removal covariate, x_{ik2} is the strategic removal covariate and x_{ik3} is the flow covariate (NAA). Each removal covariate is modeled as an indicator variable where '0' denotes no removal and '1' denotes opportunistic or strategic removal, respectively. The coefficients $\boldsymbol{c}$, $\boldsymbol{d}$, $\boldsymbol{g}$, and $\boldsymbol{h}$ describe each species' colonization and extinction rates in the presence ($\boldsymbol{g}$ and $\boldsymbol{h}$) and absence ($\boldsymbol{c}$ and $\boldsymbol{d}$) of one another. Altogether, this method produces the conditional occupancy probabilities (e.g., $\psi^{A|b}$ or $\psi^{A|B}$) directly from the logistic regression coefficients, therefore the unconditional (marginal) probability of species A occupying a site can be calculated as: $\psi^{A} = \psi^{A|b} + \psi^{A|B}$. A nearly identical process was used to model the first year of occupancy and detection probabilities following Fidino and colleagues (2019). Detection was estimated from the four repeat surveys of seasonal long-term monitoring data per year. However, in our model we assumed detection was not conditional on the presence or absence of other species in the community. Because stream surveys typically cover all habitats within a site (pool, riffle, run) and marginal areas like undercut banks or root wads where fish may be taking cover, we thought it would be unlikely for captures to be conditional on the presence of another species at the site.

4.3.5 *Modeling approach*

We evaluated model fit for each species pair using c-hat. In this case, c-hat was a goodness of fit test using the ratio of the chi-square statistics for observed and simulated model data, respectively (Kery and Royle 2016). We used c-hat to evaluate model fit for the predictions of each possible occupancy state of our multi-state model (i.e., U, A, B, AB). Values of the ratio larger than 1 indicate overdispersion and lack of model fit but are considered moderate up to a value of 4 or less (Kery and Royle 2016, MacKenzie et al. 2018). Then, we compared the posterior distributions of the two chi-square statistics by summarizing with a Bayesian *p*-value. The c-hat ratio has a value near to 1 when model fit is adequate. Bayesian *p*-values near 0.5 (away from 0 or 1) indicate observed data is consistent with model estimates. Values near 0 or 1 would indicate model estimates are more extreme or less extreme than the observed data, respectively (Gelman 2005). Occupancy probabilities were also used to assess the independence of the two species in each modeled pair using a species interaction factor (SIF) proposed by Richmond and colleagues (Richmond et al. 2010). Models were fit in JAGS v.4.3.0 (Plummer and Plummer 2003) with the runjags package (Denwood 2016) in program R v. 3.6.0 (R Core Team 2019). Each co-occurrence model ran with 8 chains, a 1000-step adaptation, 5,000 step burn-in, with posteriors sampled 10,000 times, thinned by 10. We checked for model convergence using visual inspection of chains and the Gelman-Rubin diagnostic, ensuring values were less than 1.05 (Gelman and Rubin 1992).

4.4 Results

The goodness of fit statistic indicated the model provided a good fit to the data (Appendix Table 1). All c-hat values were close to 1, indicating that the multi-state models were not over- or under-dispersed. Similarly, all Bayesian p-values were close to 0.5, indicating that the chance of observing a chi-square discrepancy from the simulated model fit more extreme than the one for the observed dataset was unlikely. Models suggested that native and nonnative species dynamics were most influenced by the conditional occurrence of other species. On average, native species tended to be more likely to colonize or go extinct where they co-occurred with nonnative species (Table 2, Fig. 3). This factor most strongly affected extinction probabilities and woundfin was the only native species whose extinction probability was not significantly influenced by pairwise interactions with a nonnative species. In contrast, on average nonnative centrarchids and red shiner tended to be less likely to colonize or go extinct where they co-occurred with native, though the interaction effect was only significant for red shiner (Table 2). The other factors in the model, related to removal efforts and annual flow conditions, had limited support because of high variability around parameter estimates (Table 2). However, model predictions derived from parameter estimates revealed that the influence of removal efforts and flow conditions resulted in meaningful differences in probabilities of native and nonnative species occupancy dynamics.

The effects of removal efforts on extinction probabilities did not differ based on the conditional occurrence of another species, so we focus on reporting predictions of removal efforts when native and nonnative species co-occur (Table 2, Fig. 3). Removal efforts tended to lower the extinction probabilities of native species and somewhat depended on whether efforts were opportunistic or strategic (Fig. 3a – d). Compared to no removal effort, extinction probabilities declined the most for chub following strategic removal efforts (Fig. 3a; mean diff = -0.10 [-0.15, -0.05]), for desert sucker following opportunistic removal efforts (Fig. 3b; mean diff = -0.16 [-0.21, -0.06]), and for speckled dace following strategic removal efforts (Fig. 3d; mean diff = -0.09 [-0.16, -0.01]), but the effects of removal on woundfin were equivocal. Nonnative species extinction probabilities tended to increase following removal efforts. The differences between strategic and no removal effort were meaningful for red shiner (mean diff = 0.11 [0.01, 0.30]), but equivocal for centrarchids.

The model also predicted that interactions between flow and nonnative species influenced native species extinction probabilities depending on the species pair (Fig. 3e - h). In the presence of nonnative species, chub, desert sucker, and woundfin extinction probabilities were highest in years with low flow anomalies and declined as flow anomalies became more positive (Fig. 3e - g). In the absence of nonnative species, extinction probabilities had the opposite trend, increasing with more positive flow anomalies. Speckled dace, was the only exception, with consistent extinction probabilities that remained higher in the presence of red shiner than in their absence (Fig. 3h). Unlike for native species, flow prediction probabilities were not informative of nonnative species extinction dynamics, as credible intervals spanned the full interval from 0 to 1 under all annual flow conditions.

Colonization probabilities were not strongly influenced by removal efforts. In general, model predictions were more uncertain for colonization probabilities than for extinction probabilities. As was true with extinction dynamics, the effects of removal efforts did not differ based on the conditional occurrence of another species (Table 2), so we focus on reporting predictions of removal efforts when native and nonnative species co-occur (Fig. 4). Opportunistic removal efforts had little to no effect on colonization rates of any native species (Fig. 4a – d). Colonization probabilities only significantly increased for native chub if removal efforts were strategically aimed at eradicating nonnative species (Fig. 4a; mean diff = 0.68 [0.13, 0.90]). Woundfin and speckled dace also had a tendency toward higher colonization probabilities under strategic removal efforts (Fig. 4c and 4d). However, strategic removal was predicted to lower the probability that desert sucker would colonize a site compared to no removal (Fig. 4b; mean diff = -0.30 [-0.37, -0.20]). Nonnative species colonization probabilities were unlikely to be affected by removal efforts (Table 2).

Colonization probabilities were influenced by annual flow conditions that were somewhat conditional on co-occurrence of the other species within a model set (Fig. 4e – h). Chub colonization probability tended to increase with higher annual flow conditions independent of the presence of centrarchids (Fig. 4e). However, the probability that desert sucker colonized a site with centrarchids declined with increasing flows such that during high flow years, desert sucker were more likely to colonize sites without centrarchids, whereas the opposite was true in years with low flow conditions (Fig. 4f). In the presence of red shiner, woundfin became more likely to colonize sites under higher annual flow conditions, but colonization probabilities were consistently low in low flow years (Fig. 4g). Speckled dace colonization probabilities were not much affected by the presence of red shiner (Fig. 4h). Again, flow was not a meaningful predictor of nonnative species colonization, as the credible intervals for probability estimates spanned the full interval from 0 to 1.

We found evidence that removal efforts and annual flow conditions affected native and nonnative species detection probabilities (Table 2, Appendix Fig. 1). Strategic removal efforts increased native chub and desert sucker detection probabilities as well as nonnative centrarchids but decreased the detection probability of red shiner in the model set with woundfin (Table 2). Native species detection increased to varying degrees with higher flow years, but only significantly influenced woundfin and, marginally, desert sucker detection probabilities (Table 2). Nonnative species detection probabilities tended to have the opposite trend as detection probabilities declined with higher flow years, with a significant trend for red shiner (Table 2).

Based on these varying dynamic patterns, the proportion of occupied sites for each species varied over time with estimates somewhat dependent on the species pair being modeled. Chub and woundfin occupancy declined and then stabilized or began recovering in 2004, two years after major removal efforts began to be implemented (Fig. 5). At the beginning of long-term monitoring, 60% (95% CI: 13-100) were occupied by chub, whereas by 2003, that number had fallen to 32% (CI: 19-43), a 28% decline. After 2003, the proportion of sites occupied by chub again increasing and by 2018, their occupancy had reached an estimate to 51% (CI: 35-69) occupancy probability. On average, the probability that chub occupied a site was 22% lower than centrarchid occupancy between 1993 and 2013. Likewise, woundfin occupancy probability was estimated to be 91% (CI: 46-100) and fell to 46% (CI: 24-67), a 45% decrease. Nonnative species tended to have the opposite trend, first increasing and then stabilizing, before declines began around 2012. Centrarchid occupancy increased at a low rate over the study period, reaching a peak of 77% (CI: 64-89) of occupied sites in 2012, when their occupancy began to decline. Model estimates of red shiner site occupancy exhibited different patterns and levels of uncertainty whether this nonnative was being compared to native woundfin or speckled dace. When compared to woundfin, red shiner initially increased the proportion of sites they occupied by 19% from 39% (CI: 13-67) in 1976 to 58% (CI: 36-80) by 1991, and then became relatively steady. In the model set with speckled dace, red shiner had fluctuating proportions of occupied sites, with average estimates at 39% (CI: 28-50) of sites. The proportion of sites occupied by desert sucker and speckled dace appeared to have an initial decline but then fluctuations in occupancy seemed to stabilize.

4.5 Discussion

Multi-state dynamic co-occurrence models provide valuable opportunities to investigate relationships among species and test hypotheses with the advantage of focusing on dynamic processes underlying occupancy patterns (Yackulic et al. 2014, MacKenzie et al. 2018, Fidino et al. 2019). Although it is common to evaluate co-occurrence dynamics of native and nonnative species across static environmental gradients (e.g., Yackulic et al. 2014, Lamothe et al. 2019), few studies have incorporated temporally varying factors that affect occupancy dynamics (but see[Miller et al. 2012]). Capturing dynamics of both native and nonnative fishes helped us understand the impacts of opportunistic and strategic invasive species removal efforts, and how these dynamics influence species occupancy through time. Here we show evidence for the positive influence of removal efforts for native species through the effect of decreasing native species' extinction probability and increasing their colonization probability. In general, strategic removal efforts had more consistent, predictable effects on native fish extinction and colonization probabilities, but importantly, opportunistic removal efforts were also influential, especially by lowering native fish probabilities of extinction.

Model predictions revealed that recovery efforts were strongly influential on native species occupancy dynamics. Even though recovery programs were implemented with the goal of conserving native chub and woundfin, they also influenced the dynamics of common native species like desert sucker and speckled dace. Strategic removal efforts had the greatest predicted impact on lowering extinction probabilities of native fishes, about 1.2 times more effective than opportunistic removal efforts. The predicted influence of removal efforts on native species colonization probabilities came with more uncertainty and depended on whether the effort was opportunistic or strategic and which species were being examined. Chub and woundfin colonization appeared to benefit most from recovery efforts. In addition to invasive species removal, woundfin, and chub colonization was bolstered by native fish repatriation efforts, which translocate fishes during chemical treatments and repatriate populations with hatchery stock in the Virgin River (Fridell and Bennion 2019). In the Gila River basin, strategic removal efforts are not supplemented by augmentation of roundtail chub, so natural recolonization is also likely to contribute to the increasing trend in chub occupancy since 2010 (Zaimes et al. 2019). Using a combination of management actions, including containment, eradication, and repatriation, most likely prevented or reversed further declines of native fishes. Optimal recovery programs balance invasive species eradication with active endangered species management taking into account the consequences of removing nonnative species (e.g., Lampert et al. 2014).

Species interactions had a significant influence on occupancy dynamics. Native species not only had higher extinction probabilities when nonnative species were present, but higher colonization probabilities as well. Mixed native and nonnative fish assemblages were common. For example, in the Verde River, only 7% of site, year combinations had an assemblage made up entirely of native species, whereas 18% of records had an assemblage made up entirely of nonnative species. Therefore, we hypothesize that native fishes were more likely to colonize a site with nonnative species because a high proportion of sites were consistently occupied nonnative species. The corollary is that nonnative species are unlikely to colonize a site where a native species is present, which we also observed, because sites only occupied by native species in the model pair were rare. An alternative, and not mutually exclusive hypothesis is that native and nonnative fishes are occupying the same sites because of suitable habitat availability. Unfortunately, we could not test this hypothesis because we did not have habitat data associated with surveys. This additional environmental information can be important to include when available as it may affect estimates of detection, colonization, and extinction probabilities of interacting species (e.g. Yackulic et al. 2014).

Flow regulation and nonnative species are both important factors for native species declines (Light and Marchetti 2007). We showed that interactions between flow and nonnative species may be particularly important factors of native species local extinction probabilities. Predicted extinction probabilities were highest during low flow conditions, particularly in model comparisons between native fishes and nonnative centrarchids. This result supports the work of other studies which have shown that native fish populations have an advantage over nonnative species during years with high flow, particularly in association with high spring runoff (Gido et al. 2013), and a disadvantage during low flow periods (Ruhí et al. 2015). Often other environmental factors in combination with flow determine habitat suitability for fishes, such as temperature, dissolved oxygen, and turbidity in association with run-off from the landscape (Shea et al. 2015, Whitney et al. 2016). As habitats contract with declining flows, temperatures increase and dissolved oxygen declines (Lake 2000), forcing vulnerable small-bodied and young-of-year fishes into remaining suitable habitat with higher predation risk (Labbe and Fausch 2000). Because of higher extinction risk at low flows in the presence of nonnative fishes, removal efforts may be most beneficial to local persistence of native fishes by conducting them during low flow periods. However, given the likelihood of physiological stressful environmental conditions, managers should consider the availability of nearby suitable refuge habitat, such as deep, well-oxygenated pools, where native fishes can be quickly translocated.

Nonnative species occupancy dynamics were most influenced by strategic removal efforts. These removal efforts resulted in higher predicted estimates of nonnative species extinction probability over opportunistic removal efforts or no removal effort. However, predicted differences in extinction between a strategic removal effort and no removal were only significant for red shiner. The period of time over which successful eradication was achieved may affect model estimates. For example, red shiner has been eradicated from the upper Virgin River since 2013 (Bennion and Fridell 2019), whereas centrarchids have only been eradicated from a few sites located in Bonita Creek, since 2017 (Blasius and Conn 2019). Estimates of nonnative species colonization probabilities, if not equivocal, also had a tendency to increase, especially under opportunistic removal efforts. There are two potential explanations for this result. First, species with high fecundity and short juvenile life stages with high survivorship, like centrarchids or red shiners, exhibit overcompensatory recruitment and population growth when control efforts remove less than 80% of populations (Zipkin et al. 2008, 2009). Second, low abundances may encourage intraspecific colonization through dispersal, known as a vacuum effect (*sensu* Gibson et al. 2002). Given these responses in population growth, considering the merits of different control strategies is important.

Occupancy alone may not be enough to establish species status or the success or failure of conservation and management activities. However, positive relationships between occupancy and abundance indicate that lower proportions of occupied sites may be conservative indicators of large population declines and vice versa (Miranda and Killgore 2019) Together, opportunistic and strategic removal strategies helped in recovery efforts of two species of conservation concern. In the lower Colorado River Basin, the proportion of sites occupied by chub increased, while woundfin distributions stabilized. For chub, a consistent decadal decline in occupancy began to be reversed around 2004, when the Virgin River recovery plan started to be strongly implemented with simultaneous invasive species removal, hatchery augmentation efforts and barrier construction. In the case of woundfin, 8 of 24 or 33% of sites in their current range are in the upper Virgin River where red shiner have been extirpated, and multiple barriers are in place.

Invasive species remain as one of the persistent conservation challenges for biodiversity (Early et al. 2016, Reid et al. 2019). Although both opportunistic and strategic removal efforts can affect colonization and extinction occupancy dynamics of native and nonnative species, strategic removal efforts are likely to be more effective in controlling nonnative species populations and recovering native species populations for a longer period of time. In the short term, opportunistic suppression may be more feasible than eradication, but dedicating resources to an intensive eradication up front is often less costly in long-term calculations (Panzacchi et al. 2007, Syslo et al. 2013). Similarly, "aggressive suppression," defined as greater than 90% of population reduction, can result in comparable positive outcomes as total eradication (Prior et al. 2018). The advantage of suppressing large proportions of target nonnative species populations is that it can leverage biological phenomenon such as Allee effects (Tobin et al. 2011). Thus, strategic efforts, which combine management actions such as containment and consistent removal will be most likely to result in eradicating invasive species while recovering native species. Containment is an integral part of strategic removal efforts because it can create a more manageable area to implement any recovery actions and limits setbacks by preventing recolonization. Barriers are a common part of native species restoration efforts in freshwater systems of the southwestern United States (Clarkson and Marsh 2010), but they enhance conservation success in many ecosystems (Hermoso et al. 2015). However, as more barriers are constructed it will be increasingly important to weigh potential benefits against the potential cost of additional fragmentation (Fausch et al. 2009, Milt et al. 2018, Rahel and McLaughlin 2018). Even in limited areas, consistent removal effort is likely to be important in order to keep populations suppressed to avoid overcompensatory growth. To increase effectiveness, sometimes particular life stages need to be targeted (Ellis and Elphick 2007, Zipkin et al. 2009).

Advances in ecological statistics and growing availability of long-term data facilitate our ability to quantify the patterns and processes underlying the data by accounting for uncertainty in imperfect detection and other factors that contribute to dynamic changes in species occurrence. Though we used rivers as our study system, the modeling approach and management programs highlighted here are applicable more broadly. We provide empirical estimates that highlight how opportunistic and strategic removal efforts can shift native and nonnative species occupancy dynamics. With these estimates we showed that management programs that combined multiple approaches were most successful in controlling nonnative species and increasing the persistence of threatened and endangered native species. Even over large areas with long established nonnative populations, recovery goals can be met through a combination of containment and consistent, progressive application of removal efforts. Evaluating the effectiveness of removal strategies is an integral component in the management decision process that together with consideration for economic and social context, supports ongoing and future management actions aimed at protecting native species diversity.

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4.8 Tables

Table 4.1. Summary of nonnative species control strategies and associated effort for three rivers within the Colorado River Basin.

River Basin Study area	Strategy	Method	Technique	Freq.	Duration per effort (days)	Number of personnel	nSite	Total length (river km)	Target species	Start yr	End yr	Citations
Verde River												
	Suppression (Fig. 1.b.iii.)	Mechanical removal	Backpack electrofishing , seining	biannual	1	5-7	2	3	smallmouth bass, green sunfish, yellow bullhead, red shiner, fathead minnow	1999	2004	Neary and Rinne 2012
	Suppression (Fig. 1.b.iii.)	Mechanical removal	Backpack electrofishing , seining	2 to 3 times per year	3	5 to 7	2	8	smallmouth bass, green sunfish, yellow bullhead, red shiner, fathead minnow	2006	2009	Neary and Rinne 2012
Gila River												
upper Gila River (NM)	Suppression (Fig. 1.b.ii.)	Mechanical removal	Backpack electrofishing	annually (Jun)	4-5	10 to 12	1	4.6	all nonnatives	2007	2018	Propst et al. 2015
Bonita Creek	Containment (Fig. 1.a.ii.)	Barrier construction	--	once	--	--	--	--	all nonnatives	2008	2008	Robinson et al. 2009
	Eradication (Fig. 1.c.i)	Chemical treatment	Rotenone	once	2	5 to 15	--	4.3	all nonnatives	2008	2008	Robinson et al. 2009

River Basin Study area	Strategy	Method	Technique	Freq.	Duration per effort (days)	Number of personnel	nSite	Total length (river km)	Target species	Start yr	End yr	Citations
	Eradication (Fig. 1.c.ii)	Mechanical removal	Backpack electrofishing, hoop nets, minnow traps, seining	1 to 3 times per year	3	4 to 6	3	4.3	green sunfish and yellow bullhead	2009	2018	Marsh and Associates report 2013, Blasius and Conn 2015
Aravaipa Creek	Containment (Fig. 1.a.i.)	Barrier construction	--	once	--	--	--	--	all nonnatives	2001	2001	Clarkson and Marsh 2010
San Pedro River	NA	None	--	--	--	--	--	--	--	--	--	Stefferud and Stefferud 2011
Virgin River												
upper Virgin (UT)	Eradication (Fig. 1.c.i)	Mechanical removal; chemical treatment	Seining, minnow traps, and Rotenone	at least annually	5	30+	5	64.4	green sunfish, rainbow trout, and red shiner	1996	2008	Miller et al. 2014, Fridell and Bennion 2019
	Eradication (Fig. 1.c.i)	Mechanical removal; chemical treatment	Seining, minnow traps, and Rotenone	at least annually	--	--	--	10.3	red shiner	1996	2004	Fridell and Bennion 2019 (Phase I - III)
	Eradication (Fig. 1.c.i)	Mechanical removal; chemical treatment	Seining, minnow traps, and Rotenone	at least annually	--	--	--	24.5	red shiner	2004	2011	Fridell and Bennion 2019 (Phase IV - V)
lower Virgin (AZ, NV)	Suppression (Fig. 1.b.iii.)	Mechanical removal	Seining	biannual	3	8 to 10	1	7.6	red shiner	1999	2001	Golden and Holden 2004
	Suppression (Fig. 1.b.iii.)	Mechanical removal; chemical treatment	Seining, hoop nets, backpack electrofishing; Rotenone	once			1	1.6	blue tilapia	2002	2002	Golden and Holden 2005
	Containment (Fig. 1.a.ii.)	Barrier construction (2)	--	--	--	--	--	--	red shiner	2008	2010	USFWS 2008
	Eradication (Fig. 1.c.)	Chemical treatment	Rotenone	once			1	34 - 50	red shiner	1988	1988	Minckley 1988

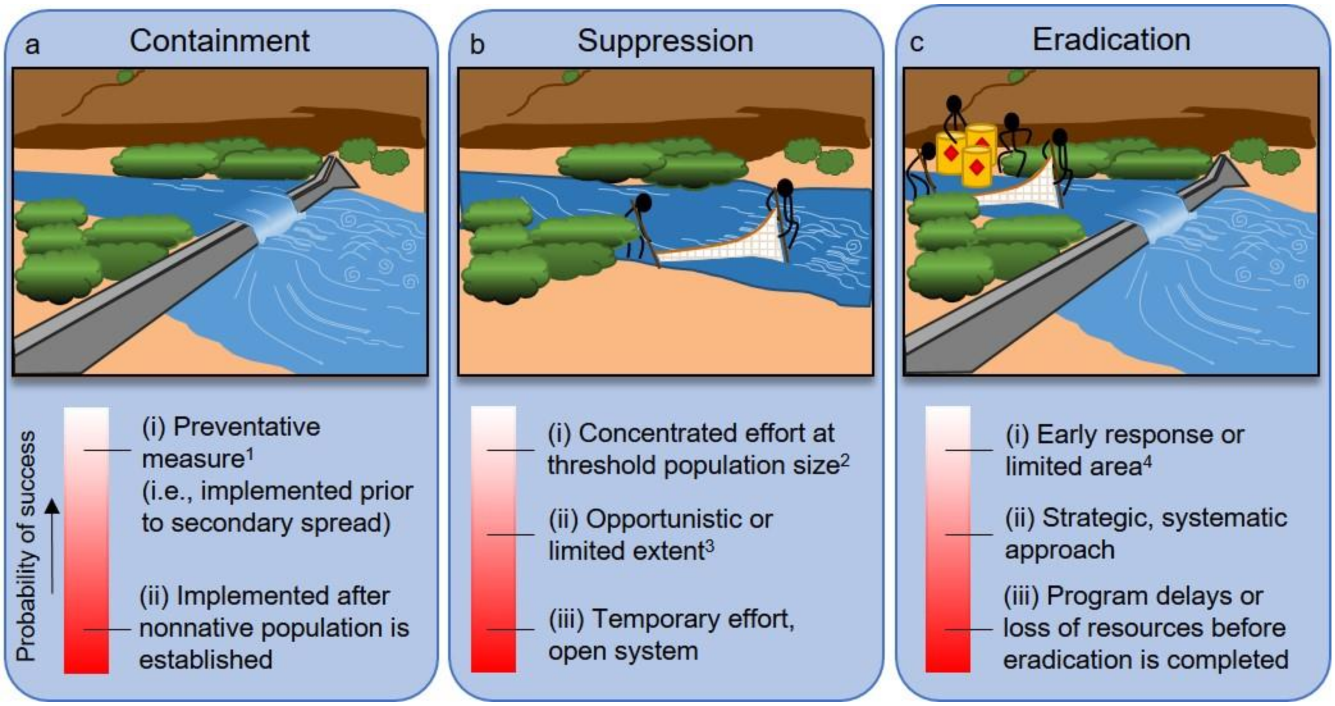
River Basin Study area	Strategy	Method	Technique	Freq.	Duration per effort (days)	Number of personnel	nSite	Total length (river km)	Target species	Start yr	End yr	Citations
	Eradication (Fig. 1.c.iii.)	Chemical treatment	Rotenone	once	7		1	27.4	red shiner	2014	2014	Fridell and Bennion 2019 (Phase VI), Kegerries et al. 2018
	Eradication (Fig. 1.c.iii.)	Mechanical removal	Seining	--	90		1	27.4	red shiner	2015	2016	Fridell and Bennion 2019 (Phase VI)
	Containment (Fig. 1.a.ii.)	Barrier modification	--	once						2017	2017	Fridell and Bennion 2019 (Phase VI)
	Eradication (Fig. 1.c.iii.)	Chemical treatment	Rotenone	once	--	--	1	27.4	red shiner	2018	2018	Fridell and Bennion 2019 (Phase VI)

Table 4.2. Colonization, extinction, and detection estimates from the model. Displayed are mean estimates and 95% credible intervals (CI) on the logit scale, with (*) indicating significant model parameters that do not encompass zero and (+) indicating marginally significant model parameters that are bounded by zero.

Process Species	Parameter	First order (**c**, **d**) Mean (CI)	Interaction influence (**g**, **h**) Mean (CI)
Extinction			
Chub	Intercept	-2.1 (-2.8, -1.5) *	-1.1 (-1.9, -0.3) *
	Opportunistic removal	-1.6 (-4.6, 1.5)	-0.5 (-3.4, 2.4)
	Strategic removal	-1.8 (-4.0, 0.3)	-0.2 (-2.8, 2.3)
	Flow NAA	0.2 (-0.3, 0.7)	-0.5 (-1.3, 0.2)
Desert sucker	Intercept	-3.0 (-3.7, -2.3) *	-0.8 (-1.6, 0.0) +
	Opportunistic removal	-1.5 (-4.9, 1.3)	-0.5 (-3.6, 2.3)
	Strategic removal	-1.0 (-3.1, 0.8)	0.9 (-1.9, 3.4)
	Flow NAA	0.1 (-0.3, 0.6)	-0.3 (-1.1, 0.5)
Woundfin	Intercept	-3.8 (-4.8, -2.9) *	-0.9 (-3.0, 1.4)
	Opportunistic removal	0.0 (-3.4, 3.8)	0.0 (-3.9, 3.5)
	Strategic removal	-0.3 (-2.7, 1.8)	1.0 (-1.5, 3.6)
	Flow NAA	-0.1 (-1.2, 0.9)	-1.2 (-2.8, 0.3)
Speckled dace	Intercept	-3.5 (-4.1, -3.0) *	-3.9 (-5.1, -2.6) *
	Opportunistic removal	-1.2 (-4.3, 1.9)	0.1 (-3.7, 4.0)
	Strategic removal	-0.5 (-3.2, 1.7)	1.8 (-0.8, 4.6)
	Flow NAA	0.0 (-0.4, 0.5)	0.1 (-0.9, 1.1)
Centrarchids	Intercept	-1.5 (-2.0, -1.0) *	0.2 (-0.5, 1.1)
(vs. roundtail chub)	Opportunistic removal	-0.6 (-3.7, 2.3)	-1.2 (-4.5, 1.7)
	Strategic removal	0.0 (-2.6, 2.6)	-0.8 (-4.0, 2.0)
	Flow NAA	0.1 (-0.4, 0.5)	-0.5 (-1.1, 0.1)
Red shiner	Intercept	-4.8 (-6.4, -4.7) *	2.4 (1.4, 3.5) *
(vs. woundfin)	Opportunistic removal	0.0 (-3.7, 3.7)	0.0 (-3.9, 3.6)
	Strategic removal	2.4 (0.2, 4.5) *	0.1 (-2.4, 2.4)
	Flow NAA	0.7 (-0.2, 1.7)	-0.1 (-1.2, 1.1)
Colonization			
Chub	Intercept	-2.8 (-3.4, -2.3) *	-0.3 (-1.1, 0.5)
	Opportunistic removal	0.3 (-3.5, 4.2)	0.8 (-2.5, 4.3)
	Strategic removal	3.4 (0.2, 6.7) *	-0.1 (-3.4, -0.1) *
	Flow NAA	0.4 (-0.4, 1.0)	0.3 (-0.6, 1.2)
Desert sucker	Intercept	-2.5 (-3.2, -1.8) *	-1.0 (-1.7, -0.4) *
	Opportunistic removal	0.4 (-3.2, 3.9)	0.9 (-2.6, 4.4)
	Strategic removal	-2.1 (-5.2, 0.8)	0.9 (-1.6, 3.7)
	Flow NAA	0.3 (-1.0, 1.5)	0.5 (-0.5, 1.6)

Process Species	Parameter	First order (**c**, **d**) Mean (CI)	Interaction influence (**g**, **h**) Mean (CI)
Woundfin	Intercept	-3.4 (-4.7, -2.3) *	0.2 (-1.8, 2.3)
	Opportunistic removal	0.0 (-3.6, 3.7)	0.0 (-3.6, 3.8)
	Strategic removal	0.5 (-2.1, 3.0)	0.1 (-3.3, 3.3)
	Flow NAA	-0.2 (-1.3, 0.8)	0.7 (-0.9, 2.2)
Speckled dace	Intercept	-4.1 (-4.7, -3.5) *	-3.5 (-4.8, -2.4) *
	Opportunistic removal	-1.2 (-4.3, 1.6)	0.9 (-3.0, 5.0)
	Strategic removal	0.8 (-1.3, 2.9)	-0.2 (-3.5, 3.2)
	Flow NAA	0.2 (-0.5, 0.8)	0.5 (-0.3, 1.3)
Centrarchids	Intercept	-1.1 (-1.5, -0.7) *	0.7 (-0.2, 1.5)
(vs. roundtail chub)	Opportunistic removal	0.9 (-2.4, 4.3)	0.3 (-3.5, 4.3)
	Strategic removal	-0.3 (-2.9, 2.1)	0.6 (-2.7, 3.9)
	Flow NAA	-0.3 (-0.7, 0.6)	0.0 (-0.9, 1.0)
Red shiner	Intercept	-4.6 (-6.4, -2.9) *	1.7 (0.5, 3.1) *
(vs. woundfin)	Opportunistic removal	0.0 (-3.5, 3.6)	0.0 (-3.7, 3.5)
	Strategic removal	0.5 (-3.2, 4.3)	0.2 (-2.4, 2.8)
	Flow NAA	0.5 (-0.8, 1.6)	0.5 (-0.5, 1.7)
Detection			
Chub	Intercept	0.2 (0.1, 0.3) *	--
	Opportunistic removal	-0.3 (-0.8, 0.2)	--
	Strategic removal	1.8 (1.2, 2.5) *	--
	Flow NAA	0.1 (-0.1, 0.2)	--
Desert sucker	Intercept	0.6 (0.5, 0.7) *	--
	Opportunistic removal	-0.2 (-0.7, 0.3)	--
	Strategic removal	1.0 (0.4, 1.7) *	--
	Flow NAA	0.1 (0.0, 0.2) *	--
Woundfin	Intercept	1.6 (1.4, 1.8) *	--
	Opportunistic removal	0.0 (-3.8, 3.5)	--
	Strategic removal	-0.6 (-1.3, 0.1)	--
	Flow NAA	0.5 (0.2, 0.7) *	--
Speckled dace	Intercept	1.4 (1.2, 1.5) *	--
	Opportunistic removal	2.1 (-0.3, 4.7)	--
	Strategic removal	0.5 (-0.2, 1.2)	--
	Flow NAA	0.0 (-0.1, 0.2)	--
Centrarchids	Intercept	-0.7 (-0.9, -0.6) *	--
(vs. roundtail chub)	Opportunistic removal	1.2 (0.7, 1.9) *	--
	Strategic removal	1.1 (0.5, 1.8) *	--
	Flow NAA	0.0 (-0.2, 0.1)	--
Red shiner	Intercept	3.1 (2.7, 3.5) *	--
(vs. woundfin)	Opportunistic removal	0.0 (-3.5, 3.7)	--
	Strategic removal	-1.6 (-2.5, -0.8) *	--
	Flow NAA	-0.4 (-0.7, -0.1) *	--

4.9 Figures



[1]Fausch et al. 2006, Clarkson and Marsh 2010
[2]Baxter et al. 2008
[3]Propst et al. 2015
[4]Knapp et al. 2007, Simberloff 2014, Messager and Olden 2018

Figure 4.1 Conceptual figure of management actions available to control nonnative species populations. Management actions are not mutually exclusive. The probability of success for a given control strategy resulting in a limited distribution, smaller population size or successful elimination of a nonnative species depends on when efforts are started and the duration, frequency, and magnitude of the effort (panel a, b, and c, conditions i – iii)

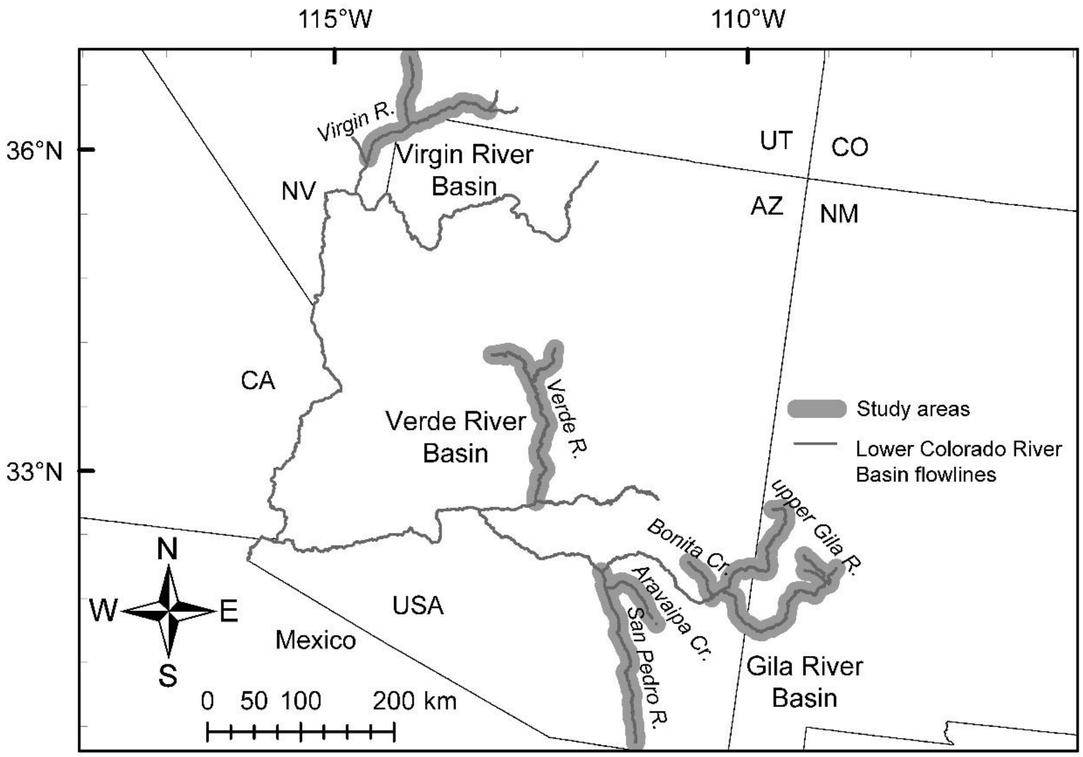


Figure 4.2. Study area map. Streams and rivers where long-term fish sampling took place are highlighted. Other creeks and rivers where nonnative control efforts took place are labeled to correspond with information presented in Table 1.

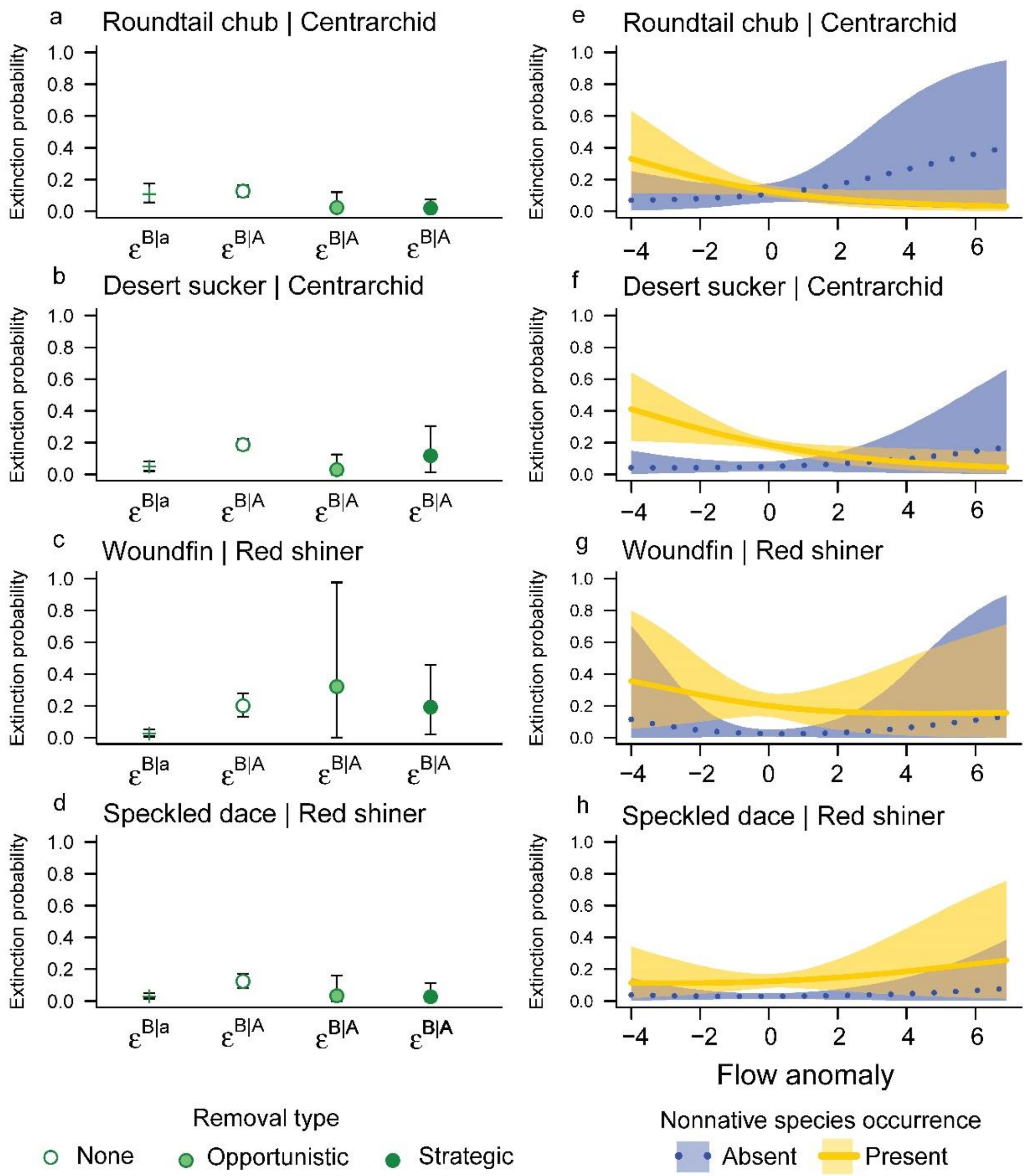


Figure 4.3. Predictions of native and nonnative fish extinction probabilities for lower Colorado River basin populations monitored between 1976 and 2018. We present derived mean estimates (points) and 95% credible intervals (error bars) for extinction probabilities (ε) conditional on the absence (B|a) or presence (B|A) of the nonnative species and predicted extinction probabilities of opportunistic and strategic removal efforts in the presence of nonnative species (panels a-d). We also present mean estimates (lines) and 95% credible intervals (shaded polygons) for the effects of flow net annual anomalies (panels e-h) from the four sets of multi-state co-occurrence models. Species pairs in each model set are indicated by labels over each plot.

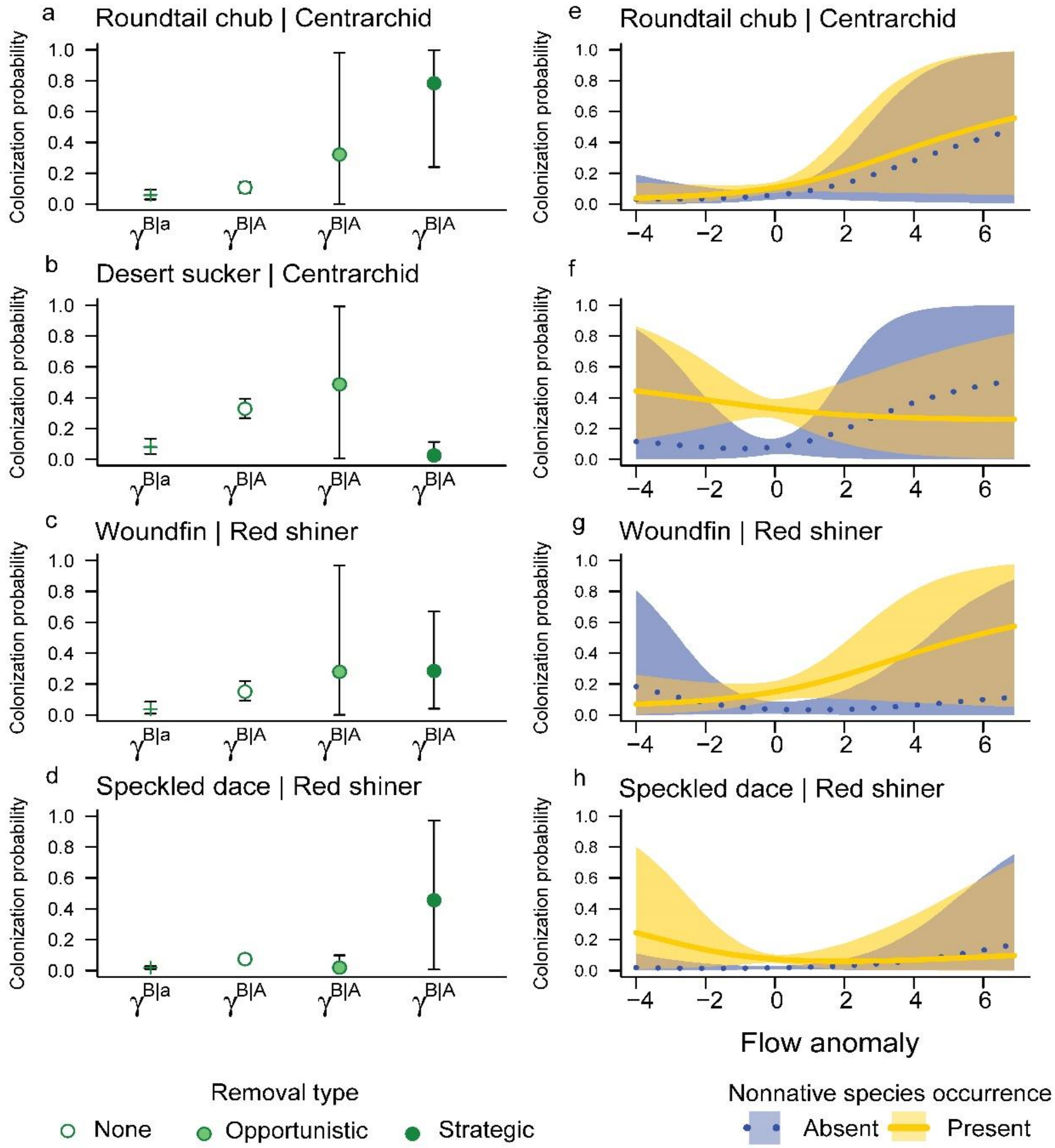


Figure 4.4. Predictions of native and nonnative fish colonization probabilities for lower Colorado River basin populations monitored between 1976 and 2018. We present derived mean estimates (points) and 95% credible intervals (error bars) for colonization probabilities (ε) conditional on the absence (B|a) or presence (B|A) of the nonnative species and predicted colonization probabilities of opportunistic and strategic removal efforts in the presence of nonnative species (panels a-d). We also present mean estimates (lines) and 95% credible intervals (shaded polygons) for the effects of flow net annual anomalies (panels e-h) from the four sets of multi-state co-occurrence models. Species pairs in each model set are indicated by labels over each plot.

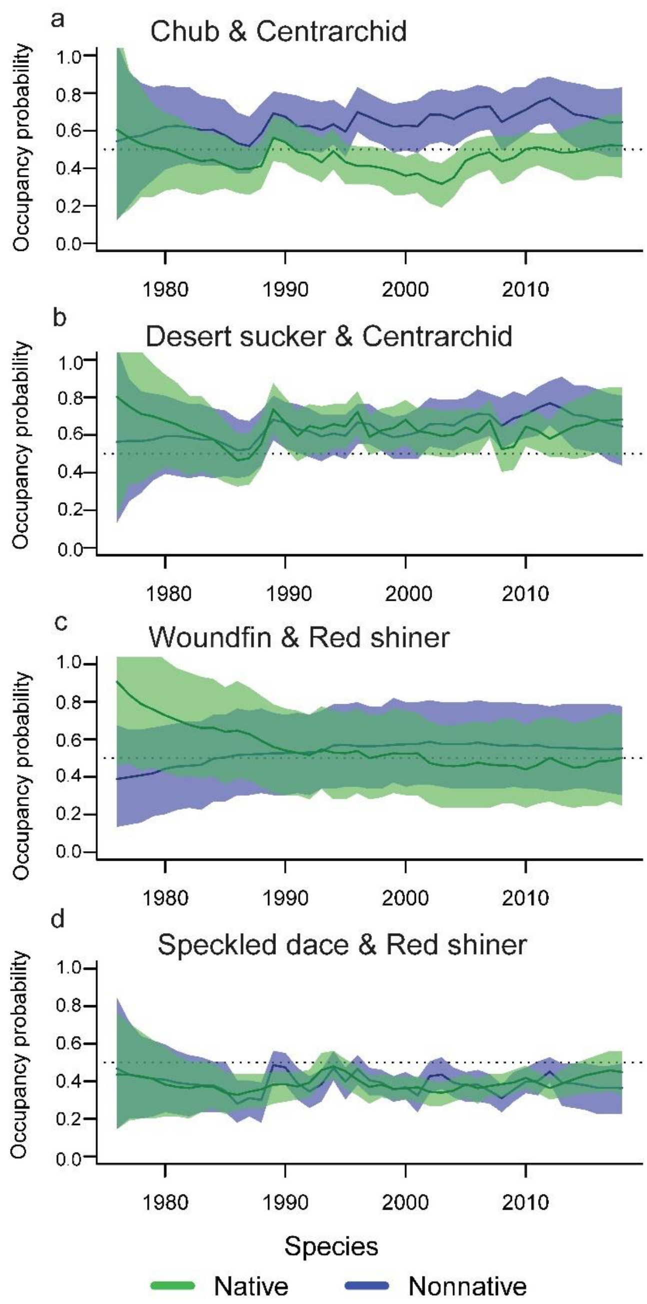


Figure 4.5. Model-averaged probability of species occurrence for four pairs of native and nonnative fish populations monitored in the lower Colorado River basin between 1976 and 2018. Unconditional (marginal) occupancy probabilities for each species are indicated by solid lines with shaded polygons representing 95% credible intervals

4.10 Chapter 4 Appendix 1.

Table S 4.1 Estimates of model fit using the overdispersion parameter (c-hat) and Bayesian p-values. Mean parameter estimates and 95% credible intervals of c-hat are presented for all four states of the multi-state model (unoccupied [U], occupied by nonnative species [A], occupied by nonnative species [B], and occupied by both species [AB]) along with mean estimates of Bayesian p-values (bpv).

Model	State	c-hat Mean (CI)	bpv Mean
Chub vs. Centrarchids	U	1.4 (0.5, 3.1)	0.3
	A	1.3 (0.5, 2.9)	0.4
	B	1.6 (0.9, 3.1)	0.1
	AB	1.6 (0.6, 4.2)	0.3
Desert sucker vs. Centrarchids	U	0.8 (0.5, 1.2)	0.9
	A	1.2 (0.6, 2.2)	0.3
	B	1.7 (0.4, 4.4)	0.3
	AB	1.5 (0.8, 2.8)	0.1
Woundfin vs. red shiner	U	1.1 (0.3, 2.9)	0.6
	A	1.2 (0.4, 2.8)	0.4
	B	1.1 (0.3, 3.2)	0.6
	AB	1.1 (0.3, 2.8)	0.6
Speckled dace vs. red shiner	U	1.7 (0.6, 4.8)	0.2
	A	1.2 (0.5, 2.4)	0.4
	B	0.5 (0.0, 2.0)	0.9
	AB	0.8 (0.4, 1.9)	0.8

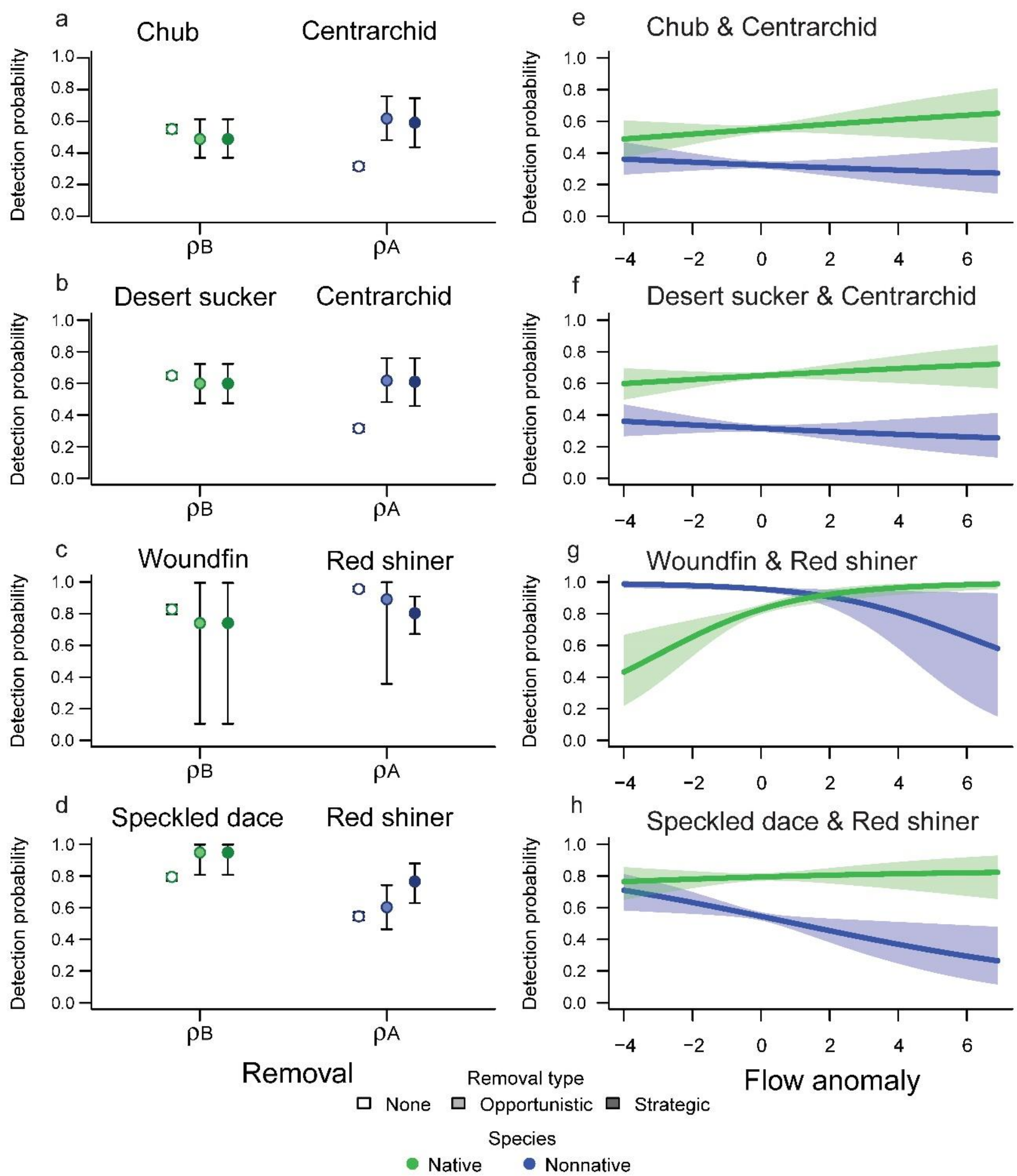


Figure S 4.1 Effects of removal and flow on detection probability for native and nonnative species or lower Colorado River basin populations monitored between 1976 and 2018. Estimates are mean probabilities of detection with 95% credible intervals as arrows or shaded polygons. Detection probability was more strongly related to removal efforts for nonnative species (ρ^A) than native species (ρ^B) (panels a – d). Flow conditions generally affected native and nonnative species detection with opposite trends (panels e – h) that was strongest for the woundfin and red shiner co-occurrence pair (g).

VITA

Jane Sarah Rogosch was born to two Czech parents and grew up in New Mexico, where she fell in awe of the diversity of organisms living in the muddy waters of the Rio Grande. She graduated with a Bachelor of Science from the University of New Mexico in 2009. For two years she worked on research related to native fish conservation in the clear and turquoise waters of Arizona before pursuing graduate degrees. She received her Master of Science from Kansas State University in 2015, where she studied the impact of low-head dams on fishes and river geomorphology. Her dissertation research concerns the ecology and management of desert fishes.