SPATIOTEMPORAL RESPONSE OF AQUATIC NATIVE AND NONNATIVE TAXA TO
WILDFIRE DISTURBANCE IN A DESERT STREAM NETWORK

by

JAMES E. WHITNEY

B.S., Emporia State University, 2007
M.S., Kansas State University, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

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Abstract

Many native freshwater animals are imperiled as a result of habitat alteration, species introductions and climate-moderated changes in disturbance regimes. Native conservation and nonnative species management could benefit from greater understanding of critical factors promoting or inhibiting native and nonnative success in the absence of human-caused ecosystem change. The objectives of this dissertation were to (1) explain spatiotemporal patterns of native and nonnative success, (2) describe native and nonnative response to uncharacteristic wildfire disturbance, and (3) test the hypothesis that wildfire disturbance has differential effects on native and nonnative species. This research was conducted across six sites in three reaches (tributary, canyon, and valley) of the unfragmented and largely-unmodified upper Gila River Basin of southwestern New Mexico. Secondary production was measured to quantify success of native and nonnative fishes prior to wildfires during 2008-2011. Native fish production was greater than nonnatives across a range of environmental conditions, although nonnative fish, tadpole, and crayfish production could approach or exceed that of native macroinvertebrates and fishes in canyon habitats, a warmwater tributary, or in valley sites, respectively. The second objective was accomplished by measuring biomass changes of a warmwater native and nonnative community during 2010-2013 before and after consecutive, uncharacteristic wildfires. Several native insect and fish taxa decreased after both wildfires, whereas nonnative decreases were most pronounced for salmonids and more limited for other taxa. Finally, effects of uncharacteristic wildfires followed by extreme flooding on metapopulations of native and nonnative fishes were contrasted during 2008-2013. Wildfire and flood disturbances increased extinction probabilities of all native fishes while leaving many nonnative fishes unaffected. These findings revealed a swinging pendulum of native and nonnative success, wherein wildfire disturbance resulted in a pendulum swing in favor of nonnatives. Ensuring the pendulum swings back in favor of natives will be facilitated by management activities that decrease wildfire size and intensity and maintain inherent ecosystem resilience.

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Preface

The contents of this dissertation represent original research developed with my major adviser, Keith Gido, as well numerous other coauthors. As such, Chapters 2, 3, and 4 are presented in the first-person plural and/or third-person for the purpose of publication in peer-reviewed journals with multiple authors. Chapter 2 has been accepted for publication in the *Canadian Journal of Fisheries and Aquatic Sciences* with Keith Gido and David Propst as coauthors. Chapter 3 is formatted for *Freshwater Science* with Keith Gido, Tyler Pilger, David Propst, and Thomas Turner as coauthors. Chapter 4 is formatted for *Forest Ecology and Management* with Keith Gido, Tyler Pilger, David Propst, and Thomas Turner as coauthors.

Chapter 1 - Native fishes, nonnative introductions, and uncharacteristic wildfire: conserving native fishes in a period of global change

Native Fish Imperilment

Native fish populations are experiencing increasing extinction risk in North American freshwaters. Approximately 700 (39%) North American fish taxa are vulnerable to extinction, with 61 taxa already presumed extinct (Jelks et al. 2008). The extinction rate of freshwater fish is predicted to increase in the decades to come, exceeding rates of many terrestrial taxa (Ricciardi and Rasmussen 1999). Regional estimates of extinction risk reveal even more-alarming prospects, as up to 78% of fish species are at-risk of extinction in the depauperate but highly-endemic river basins of western North America (Olden and Poff 2005). Causes for increased extinction risk of freshwater fishes include the elimination of habitats necessary to the completion of life histories (Bunn and Arthington 2002), prevention of rescue effects (*sensu* Brown and Kodric-Brown 1977), and creation of harsh water conditions (Richter et al. 1997). Activities that lead to these sources of imperilment include impoundment construction, surface and groundwater withdrawals, eutrophication and other forms of pollution, and watershed alteration through agriculture, industrialization, and urbanization (Dudgeon et al. 2006; Strayer and Dudgeon 2010). Furthermore, nonnative species have been widely-introduced throughout freshwaters and cause native imperilment via competition, predation, and disease (Moyle and Light 1996; Rahel 2002). Successful conservation of native fishes could benefit from a greater understanding of factors that promote native persistence or limit nonnative establishment and spread under varying degrees of anthropogenic alteration.

In addition to being a cause of native imperilment, anthropogenic habitat alteration is also believed to facilitate the establishment and spread of nonnative species (Kolar and Lodge 2001; Bunn and Arthington 2002; Koehn 2004). For instance, man-made impoundments are much more likely to have nonnative species compared to natural lakes, and can facilitate nonnative invasion into surrounding areas (Johnson et al. 2008). In contrast, natural habitat conditions are thought to inhibit nonnative species and promote native success even when nonnative species are

present (Poff et al. 1997; Bunn and Arthington 2002). Although there is a plethora of evidence to support the idea that anthropogenic habitat alterations promote nonnative success (Shea and Chesson 2002; Havel et al. 2005), data suggesting that native species can outperform nonnatives when natural conditions remain is less abundant. The major reason for this is that so few rivers remain that lack anthropogenic habitat alteration (Carpenter et al. 2011). Determining levels of success of co-occurring native and nonnative assemblages could help inform current conservation practices, wherein a common goal is to restore natural conditions to tip the balance towards greater native success (Propst and Gido 2004; Souchon et al. 2008; Cross et al. 2011). For example, recreating the natural disturbance regime of a system (e.g., through prescribed flows or watershed management), to which native species have an evolutionary history (Lytle and Poff 2004), might favor natives and limit nonnatives.

The research for this dissertation was conducted in the upper Gila River Basin of southwestern New Mexico, USA. Similar to other southwestern river basins this system contains an imperiled fish fauna, with four of eight native fish species protected under state or federal law (Propst et al. 2008). Protected species include the federally-endangered spikedace *Meda fulgida* and loach minnow *Tiaroga cobitis*, the federally-threatened Gila trout *Oncorhynchus gilae*, and the state threatened headwater chub *Gila nigra*. Unlike other southwestern river systems the upper Gila River maintains a natural flow regime (*sensu* Poff et al. 1997), is unfragmented, and has a largely-unmodified catchment (Propst et al. 2008). However, the native fauna of the upper Gila River are threatened by numerous nonnative taxa, which feed on and compete with natives (Pilger et al. 2010; Stefferud et al. 2011). The upper Gila River thus presents an opportunity to study patterns of native and nonnative success in a river basin lacking anthropogenic alteration, which could help inform ecosystem management and native fish conservation. As such, the objectives of Chapter 2 of this dissertation were to document and explain spatiotemporal patterns of native fish and nonnative fish, crayfish, and tadpole success in an unfragmented and largely unmodified river system in the desert southwest.

Wildfire Disturbance and Stream Biota

Although the upper Gila River Basin lacks major anthropogenic development, forested portions of the catchment have been altered by 100+ years of fire suppression (Swetnam 1990; Hurteau et al. 2013). Fire suppression results in elevated fuel loads with a greater continuity,

which coupled with a warming climate, can lead to larger, more frequent, and more intense wildfire (Westerling et al. 2006). These factors coupled with severe drought culminated in a series of large and intense wildfires in the upper Gila River Basin during 2011-2013. Wildfire's alteration of vegetation and soil can impact stream biota by altering resource availability and increasing temperature, sedimentation, and discharge (Gresswell 1999; Rieman et al. 2012), and can have severe impacts when ash flows result from rainfall on a recently burned landscape (Bozek and Young 1994; Lyon and O'Connor 2008). Ash flows can be hypoxic and may contain elevated levels of toxic compounds such as ammonium, trace metals, and ferrocyanides (Rinne 1996; Lyon and O'Connor 2008). However, much of the information we have concerning the response of stream biota to wildfire and ash flows has come from coldwater systems (Rieman et al. 2003), which contain their own community of macroinvertebrates and fishes (e.g. salmonids) that may respond differently compared with warmwater communities. For example, salmonids' low tolerance for hypoxia (Doudoroff and Shumway 1970) could increase the effects of wildfire and ash flows. Greater study of biotic responses to wildfire in warmwater systems will help predict the impacts of climate change on stream biota, which in the coming decades is forecasted to result in more frequent wildfires of a larger size and greater intensity (Brown et al. 2004; McKenzie et al. 2004; Moritz et al. 2012). Thus, the objective of the 2nd chapter of this dissertation was to quantify the responses of macroinvertebrates and macro-consumers to consecutive wildfires in the upper Gila River Basin.

An organism's response to wildfire is partially dictated by their traits, including life history, physiological tolerance, habitat preference, trophic guild, and movement capabilities. Many of the nonnative taxa that have been introduced into the upper Gila River and elsewhere in the Colorado River Basin have highly-divergent traits compared to native fauna (Olden et al. 2006; Pilger et al. 2010). For example, many nonnative fishes prefer low-velocity habitats (limnophilic), silt substrate, and feed at higher trophic levels, whereas many native fishes prefer flowing water habitats (rheophilic), rubble substrate, and feed at lower trophic levels. Because wildfire affects many environmental factors (discharge, substrate, resource availability) that influence the success of these traits, it could be predicted that native and nonnative taxa could exhibit differential responses to wildfire (Dunham et al. 2003; Young 2012). This hypothesis has received some attention for native and nonnative salmonids (Sestrich et al. 2011), but empirical data from warmwater native and nonnative species are lacking. As such the objectives of

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Chapter 4 of this dissertation were to compare the response of native and nonnative fishes to wildfire in the upper Gila River.

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Chapter 2 - Factors associated with the success of native and nonnative species in an unfragmented arid-land riverscape

Abstract

Native fish persistence is threatened by the establishment and spread of nonnatives. Identifying environmental and biotic factors associated with the success of co-occurring native fishes and nonnative taxa is central to identifying mechanisms responsible for native declines and nonnative expansion. We related physicochemical variables, food resources, and community composition to the success (secondary production) of native and nonnative fishes, tadpoles, and crayfish across six sites in three reaches (tributary, canyon, and valley) during 2008-2011 in the Gila River, NM. Native fish success was greater than nonnative success across a range of physicochemical conditions, basal resource supply rates, and nonnative communities, although nonnative fish, tadpole, and crayfish success could approach or exceed that of native fishes in canyon habitats, a warmwater tributary, or in downstream valley sites, respectively. Native fish success was lowest in canyon reaches, when Flathead Catfish (*Pylodictis olivaris*) and Common Carp (*Cyprinus carpio*) were highly productive. These results demonstrate the potential for native fish persistence in the presence of nonnatives in physically-unmodified streams, highlighting the importance of habitat preservation for native conservation.

Introduction

Throughout rivers worldwide native fish populations are experiencing precipitous declines (Dudgeon et al. 2006; Jelks et al. 2008). Implicated in these declines are the widespread introductions of nonnative species, which pose a substantial threat to persistence of native freshwater fauna (Lodge et al. 2000; Dudgeon et al. 2006; Gozlan et al. 2010). Indeed, nonnative species generally rank second only to habitat alteration as threats to native population persistence (Vitousek et al. 1996; Ricciardi 2004; Jelks et al. 2008). Nonnative species introductions are not ubiquitously deleterious, however, and it is acknowledged that many native populations remain unchanged following nonnative introductions (Lodge 1993; Moyle and Light 1996). The contrasting reality that nonnative species can simultaneously be a serious malignancy in some aquatic ecosystems and a benign presence in others points to the context-dependency of invader impacts (Lodge 1993; Moyle and Light 1996; McIntosh 2000).

Identifying biotic and abiotic circumstances associated with the success of native and nonnative species in co-occurring habitats is thus a central challenge for conservation and invasion biology (Kolar and Lodge 2001).

The establishment and effect of alien species in aquatic environments are governed by a combination of invader traits, environmental characteristics, and recipient community composition (Williamson and Fitter 1996; Marchetti et al. 2004). Among fishes, piscivores are often successful invaders and, once established, can lead to drastic decreases in native populations (Goldschmidt et al. 1993; Moyle and Light 1996; Mitchell and Knouft 2009). Species that have rapid life cycles or possess unique functional characteristics relative to the recipient ecosystem may also be successful invaders and create serious problems (Ricciardi et al. 1998; Cross et al. 2010; Martinez 2012). Invasion success is limited by the compatibility of physiological and life-history requirements of the invader and the invaded environment (Minckley and Meffe 1987; Baltz and Moyle 1993). Anthropogenic habitat alterations often compromise abiotic filters (Olden et al. 2006) and can promote nonnative establishment (Moyle and Light 1996). Native community composition can also influence establishment and integration of invaders, with communities that contain many native predators or high native richness thought to be most resistant to invasion (Lodge 1993). Native community richness may also help predict invasion impact, with depauperate native communities generally exhibiting the greatest declines following invasion (Moyle and Light 1996).

Understanding factors associated with native persistence in the presence of nonnatives is crucial to native conservation given the paucity of habitats that lack invaders (Moyle 2013). We evaluated factors associated with native fish and nonnative taxa success in the upper Gila River, NM, USA. Long-term (19-26 years) monitoring of population dynamics in the Gila River basin revealed that native and nonnative success (density and richness) exhibited contrasting responses to flow regime variation, with natives increasing during high flow periods (Propst et al. 2008; Stefferud et al. 2011). These responses were not consistent across locations however, as native density and richness were inversely associated with nonnative abundance at some sites while remaining relatively constant at others. This pattern suggested that differences in environmental characteristics and community composition among sites were interacting to influence relative success of native and nonnative populations. Thus, our main objectives were to 1) describe spatiotemporal patterns in environmental conditions and fish community composition; 2)

compare success between native fishes and nonnative fishes, tadpoles, and crayfish; and 3) identify environmental correlates of native fish and nonnative taxa success. We used secondary production to quantify the success of native and nonnative taxa. Productivity incorporates information on functional processes such as population dynamics, growth rates, and life history, thus providing one of "the most comprehensive representations of success" (Benke 1993). Further, evaluating the associations of primary and invertebrate secondary productivity with success of fishes allows for quantification of consumptive demand and potential resource limitation, providing greater information about biotic interactions. Identifying associations among functional properties of this ecosystem allowed us to identify potential mechanisms that can inform conservation of native fauna threatened by nonnatives and predict environmental conditions that may promote native persistence or curtail nonnative spread.

Materials and methods

Study Sites

The upper Gila River system in New Mexico is not fragmented by dams, has a relatively pristine watershed, and retains a natural flow regime (Propst et al. 2008). To investigate the influence of landscape characteristics and network position on native and nonnative success we adopted a natural experimental framework by *a priori* selecting two study sites each in tributary, canyon, and valley reaches positioned along a 105-river kilometer gradient (Fig. 2.1). We predicted that differences in catchment and riverscape characteristics among reaches would lead to variation in physicochemical characteristics, basal resource supplies, community structure, and secondary production that could then be used to identify factors associated with native and nonnative success. The most upstream reach (1726-1737m above sea level [a.s.l]) occurred in the Gila National Forest (much of it within the Gila Wilderness) and consisted of sites located on the West Fork (mean baseflow discharge $\approx$ 0.09 m^3 s^{-1}) and Middle Fork (mean baseflow discharge $\approx$ 0.17 m^3 s^{-1}) Gila River tributaries that flowed through a mountainous landscape dominated by coniferous forest. The middle reach (1410-1690m a.s.l.), also in the Gila National Forest, was positioned on the Gila mainstem in a high-gradient canyon-bound section (mean discharge at baseflow $\approx$ 0.76 m^3 s^{-1}) that bisected similar terrain as tributary reaches. The downstream reach (1328-1362m a.s.l.) began where the canyon-bound Gila River debouches onto the low-gradient Cliff-Gila Valley. Within this sparsely-settled reach, water is diverted

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onto cultivated fields and pasture; consequently discharge is diminished somewhat (mean discharge at baseflow ≈ 0.63 m^3 s^{-1}).

Environmental Characteristics

We selected a suite of measurements that characterize the potential constraints in habitat and energy availability that were thought to influence fish populations across the 6 sites. Abiotic physicochemical habitat variables were not measured continuously during the study, but were measured at the study's beginning and end to assess their temporal variability within sites relative to spatial variability among sites. Annual mean and maximum water temperatures were measured using HOBO temperature loggers that recorded water temperature every two hours during July 2008-2009 and again during July 2011-2012. Total nitrogen (TN) and total phosphorus (TP) concentrations were measured during October of 2008 and 2012 using the persulfate oxidation method of Ameel et al. (1993). Mean values of depth and velocity (Marsh-McBirney flow meter) were calculated at base flow from measurements taken at 5 points each along 6-11 transects in June 2008 and 2011 at each of the 6 sites. Among-year differences in the flow regime were quantified with mean daily discharge data from the United States Geological Survey (USGS) Gila River near Gila gauge (#09430500). Annual flow regime attributes that represent the dominant drivers of southwestern discharge patterns (winter precipitation, spring snowmelt, summer monsoons) were characterized with variables found to influence native and nonnative fishes in unaltered streams of the desert southwest (Gido et al. 2013). These variables included mean spring discharge (mean daily discharge during 01 March to 30 June), summer coefficient of variation (CV) of mean daily discharge (standard deviation divided by the mean of daily discharge during 01 July to 30 September), and base flow index (smallest values of mean daily discharge computed over any 7-consecutive days during the annual period divided by mean annual flow; larger values representative of more consistent flows). Smallest values of mean daily discharge over 7 consecutive days typically occur from late May until the monsoon season commences in the middle of July (Stefferud et al. 2011).

Mean annual biomass and productivity of primary producers and macroinvertebrates were used to measure availability of basal energy sources for native and nonnative species. Mean annual biomass and productivity were estimated for three years (each sample year = 01 June through 01 June). For each sample year, 5 samples were taken seasonally from riffle and

pool habitats at each site (June, August, October, February, and June the following year) to estimate mean annual habitat-weighted biomass of primary producers and macroinvertebrates. Primary producer biomass was measured as the concentration of chlorophyll *a*. Chlorophyll *a* samples were taken by collecting three rocks from each of six transects. Chlorophyll *a* was extracted from whole rocks using 95% ethanol, analyzed spectrophotometrically, and then corrected for rock surface area (Sartory and Grobbelarr 1984; Steinman et al. 2006). Primary production was measured using the one-station dissolved oxygen change technique corrected for the reaeration flux (Owens et al. 1964; Bott 2006). Dissolved oxygen and temperature were recorded every ten minutes over a twenty-four hour period using sondes, and daily changes in these values were used to calculate gross primary production. Primary production was corrected for the reaeration flux using the surface renewal model (Owens et al. 1964). Macroinvertebrates were taken from pools with a core sampler (0.018 m^2; n=6), large woody debris (LWD; average surface area= 0.035 m^2; n=3), and riffles with a Surber sampler (0.093 m^2, 250-µm mesh, n=6), for a total of 15 replicates per site per sample period. Macroinvertebrates were identified to family for insect taxa and order or class for non-insect taxa. Specimen length was measured and biomass estimated using published length-mass relationships (Burgherr and Meyer 1997; Benke et al. 1999; Sabo et al. 2002). Secondary production for Chironomidae and Simuliidae was calculated using the instantaneous growth rate method, with daily growth rates estimated from temperature and size specific models developed by Walther et al. (2006) for Chironomidae and Hauer and Benke (1987) for Simuliidae. The range of sizes and temperatures for our sites and their models was similar. For all other taxa, mean annual habitat-weighted biomass was converted to production (Waters 1977; Benke and Huryn 2006) using published P/B ratios for similar taxa from geographically proximal locations (Fisher and Gray 1983; Thorp & Covich 2001; Merritt et al. 2008, and references therein).

Native Fish and Nonnative Taxa

Collection of fish, tadpoles, and crayfish was accomplished by a two-pass closed population mark-recapture effort in four to six riffle or pool macrohabitats at each site. Block nets (4 cm mesh) were deployed up and downstream of the study site to inhibit movement of larger, more mobile fishes. Individuals were collected during the first pass with a combination of backpack electrofishing and seining (4.6 x 1.2m, 3.2mm mesh), measured for total length and

marked by clipping the caudal fin (fishes and tadpoles) or telson (crayfish), and then returned to their respective macrohabitat. The site was re-sampled using identical methods during a second pass 12-24 hours later. A representative subset of individuals was weighed to generate length-mass relationships for each species, so that mass of all captured individuals could be estimated. The Chapman mark-recapture population estimator was used to calculate population size, with population estimates multiplied by the average weight of individuals to estimate biomass (Seber 1982; Hayes et al. 2007). Population size and biomass were estimated separately for riffles and pools, with site level estimates calculated from habitat area-weighted averages. Population size and biomass were quantified every June, August, and October beginning in June 2008 and ending in June 2011 with annual estimates calculated from the mean and standard error of these temporal samples; August 2010 was excluded when high flows precluded sampling. Secondary production for abundant taxa was quantified using the size-frequency method corrected for the cohort production interval (CPI) (Hynes 1961; Hamilton 1969; Benke 1979) or by multiplying mean annual biomass by taxon-specific production to biomass (P/B) ratios for rare taxa (Hayes et al. 2007). Cohort production intervals (average maximum age of an individual in the population) were determined from length-frequency histograms, whereas P/B ratios were obtained from Waters (1977).

Analysis

All analyses were conducted in R version 2.13.0 (R Development Core Team 2011). To assess the temporal constancy of physicochemical variables we correlated values from year 1 with values from year 3. Spatiotemporal variation in physical characteristics, basal food resources, and annual flow regime variation was described using three separate principal component analyses (PCAs). Because each of these datasets contains variables measured on different scales, correlation rather than covariance matrices were used as PCA input. To fulfill the PCA assumption of linear relationships among variables, natural log transformations were performed on primary producer and macroinvertebrate biomass and production. Native and nonnative fish composition was described with two separate PCAs based on natural log (x+1) transformed secondary production, with covariance matrices used for PCA input. Species that comprised <1% of annual secondary production were removed prior to analysis so as to not unduly influence results. Singular value decomposition was used to calculate eigenvalues for all

five PCAs. The number of principal component (PC) axes retained in each analysis was determined using the brokenstick eigenvalue method from the vegan package (Oksanen et al. 2011). This method takes a "stick" of unit length and randomly breaks it into pieces of different length, with the number of pieces equal to the number PCA input variables. Each axis that has an eigenvalue greater than the length of its corresponding broken stick element was then retained and used as a correlate of native or nonnative success (Legendre and Legendre 1983; Jackson 1993).

Success of native fishes and nonnative fishes, tadpoles, and crayfish was estimated using total secondary production. To examine factors associated with spatiotemporal variation in success of these four taxonomic groups, a modeling approach using multiple linear regression coupled with Akaike's Information Criterion corrected for small sample size (AIC_c) in the MuMIn package (Barton 2012) was used (Burnham and Anderson 2002).   Significant axes from the physical characteristics PCA, basal food resources PCA and the flow regime PCA were included as correlates to evaluate the association between environmental characteristics and success of our four taxonomic groups. Because we lacked information on physicochemical parameters during the middle year of our study, principal component axis scores from the first and third year were averaged to generate scores for the second year. Further, because we only had mean daily discharge from a single location, the same principal component axis scores were used as correlates of success for each site within a sample year, thus representing among-year variation in regional precipitation patterns (Stefferud et al. 2011). Correlates of success representing the effect of nonnative taxa on native success included significant PCs from the nonnative fish community composition PCA, and total nonnative fish, crayfish, and tadpole production. Significant native fish community PCs, and total native fish, nonnative tadpole and crayfish production were used to test associations with nonnative fish success. Native and nonnative fish community composition PCs and total production were examined for associations with success of nonnative tadpole and crayfish production. Our modeling approach examined the unique and joint associations of environmental characteristics, community productivity and composition with success using subsets of success correlates for each response. Model averaging was then conducted on models with $\Delta AIC_c < 2$ to determine the model-averaged slope and relative importance of each success correlate (Burnham and Anderson 2002). Relative

importance of a success correlate was the sum of the Akaike weights across all models that contained a particular correlate.

Results

Environmental Characteristics

Among-site differences in physicochemical parameters remained relatively constant from the beginning of the study to the end as indicated by moderate to high correlations (r= 0.55-0.96) between variables measured during year 1 and 3, excluding total phosphorus (r=0.15). Spatial patterns were represented in the PCA (Fig. 2.2a), with the first axis representing a longitudinal gradient from tributary 1 (negative scores), to tributary 2 and canyon sites (scores near zero), to valley sites (positive scores). Physicochemical changes associated with this PC included high mean annual water temperature, total nitrogen, and velocity at valley sites, high depth in the canyon sites, and cold water temperatures in tributary 1 compared to other sites (Table 2.1). The first PC represented the only significant PCA axis, and explained 39% of the variation in physicochemical parameters. The only major temporal changes in these spatial patterns occurred at tributary 2, where depth and temperature increased while velocity decreased throughout the study, potentially a result of beaver dam construction in the middle of the site during the second year of the study.

The annual mean and variability of mean daily discharge was relatively similar among sample years 1 and 3 (mean of year 1= 2.89 m^3 s^{-1}, standard deviation (SD) = 1.74; mean of year 3= 2.16 m^3 s^{-1}, SD= 1.55) but was much greater in year 2 (mean of year 2= 5.48 m^3 s^{-1}, SD= 8.61; Fig. 2.2b). High spring flows were responsible for year 2 having the highest mean flows, which coupled with its low base flow index resulting from diminished flows at the beginning of the sample year, helped distinguish year 2 from years 1 and 3 along the first axis of the flow regime PCA (Fig 2.2c). Only the first axis of the flow regime PCA was significant, explaining 83% of the variability in flow regime attributes.

Primary producer and macroinvertebrate biomass and productivity were generally similar among tributary and canyon sites, but were much greater at valley locations (Table 2.2). These attributes were consistent across years, although magnitude of difference was lower during year 2. Also, primary producer and macroinvertebrate biomass and productivity at Tributary 1 increased greatly during year 3. This productivity gradient was represented in the PCA along the

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first axis, with valley sites having positive scores and tributary (except Tributary 1 in year 3) and canyon sites having negative scores (Fig. 2.2d). Only the first principal component was significant, and it explained 83% of the variability in basal food resources.

Native and Nonnative Community Composition

Native fish community composition represented by the first PCA axis illustrated a transition from the low production native fish community in canyon 2 (positive scores), to the moderate production community in canyon 1 and the valley (scores near zero), to highly-productive communities in the tributaries (negative scores; Table 2.2; Fig. 2.3a). Species that accounted for this productivity gradient were Longfin Dace (*Agosia chrysogaster*), Spikedace (*Meda fulgida*), and juvenile suckers (*Catostomus* spp.), characterizing valley sites; Speckled Dace (*Rhinichthys osculus*) characterizing tributary sites; and Desert Sucker (*Catostomus clarkii*) and Sonora Sucker (*Catostomus insignis*) exhibiting high abundance across all sites excluding canyon 2 (Table 2.3; Fig. 2.3a). Although neither species were very productive compared to other native fishes, Headwater Chub (*Gila nigra*) was most productive in the tributary sites, whereas greatest productivity of Loach Minnow (*Tiaroga cobitis*) was at valley sites. The second axis of the native fish community PCA separated the valley reach from tributary sites (Fig. 2.3a). PC1 and PC2 were the only significant axes, and explained 73% of the variation in community structure.

The first axis of the nonnative fish community composition PCA separated the canyon 2 community during year 3, which had highly-negative scores and was characterized by high production of Flathead Catfish (*Pylodictis olivaris*) and Common Carp (*Cyprinus carpio*), from the rest of the sites and sample periods (Table 2.3; Fig. 2.3b). Other canyon samples also had negative scores on the first PC, but were less negative than those of canyon 2 in year 3. The second axis of this PCA separated the coldwater nonnative community (Rainbow Trout [*Oncorhynchus mykiss*] and Brown Trout [*Salmo trutta*]) found at tributary 1 from the warmwater nonnative community characteristic of tributary 2 (Smallmouth Bass [*Micropterus dolomieu*] and Yellow Bullhead [*Ameiurus natalis*]). Because nonnative fishes exhibited low production in the valley sites, their scores were near zero for both principal components. The first two PCs represented the only significant axes, and explained a combined 83% of the variability in nonnative fish community structure.

Native Fish and Nonnative Taxa Production

Native fish biomass and production were generally greatest at tributary sites, low to intermediate at canyon sites, and intermediate to high in the valley reach (Table 2.2). These patterns were consistent across years, although native fish production declined precipitously at Canyon 2 after year 1. Canyon 2 was also the only site where native fish production was less than that of nonnative fishes, whereas native fish production was generally much greater (≥ 7 times) than nonnative fishes at other sites. Nonnative fish productivity was generally greatest at Canyon 2, lowest at the two valley sites, and intermediate at the tributary and upper canyon sites. Biomass and production of nonnative American Bullfrog (*Lithobates catesbeianus*) tadpoles was low at all sites except Tributary 2, which had peak bullfrog productivity during year 2, when it equaled 53% of native fish production (Table 2.2; Fig. 2.3c). Nonnative Virile Crayfish (*Orconectes virilis*) biomass and productivity approached or exceeded that of native fish production at the three most-downstream sites, and attained its highest levels at Valley 2 during year 2 (Table 2.2; Fig. 2.3d).

Correlates of Success

The association of environmental factors and community composition with variation in native or nonnative success differed with taxonomic group of interest. For instance, five models that contained six correlates of success were found to be equally parsimonious in explaining native fish production, with these models explaining 37 to 57% of the variation in native fish production (Table 2.4). Of the six correlates included in these models, four had significant model-averaged slope coefficients, including nonnative fish community PC1 and PC2, physicochemical characteristics PC1, and flow regime PC1. Model-averaged slopes suggested that native fish production increased as the nonnative community became less like that of the canyon (Flathead Catfish and Common Carp) and more like that of Tributary 1 (Rainbow and Brown Trout) or Tributary 2 (Yellow Bullhead and Smallmouth Bass), and as mean spring discharge increased. Native fish production tended to decrease as water temperature, depth, velocity, and total nitrogen increased. Nonnative fish production had four parsimonious models that could explain its variation, which contained the success correlates of physical characteristics PC1, flow regime PC1, native fish community PC2, and resource availability PC1. These models explained 37 to 53% of the variation in nonnative fish production. In contrast to native

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fish production, nonnative fish production increased along the first PCs of the physical characteristics and flow regime PCAs, suggesting contrasting associations of native versus nonnative fishes to the same environmental gradients. Nonnative fish production also decreased as the native fish community became more like that of the valley (Longfin Dace, Spikedace, Juvenile suckers) and as basal resource supply increased. Only two models containing two success correlates were necessary to explain 36 to 61% of the variation in American Bullfrog tadpole production, with only one of these success correlates (nonnative fish community PC2) exhibiting a significant model-averaged slope. This relationship suggested that American Bullfrog tadpole production increased as the nonnative fish community became increasingly characterized by Yellow Bullhead and Smallmouth Bass. Nonnative Virile Crayfish production was best explained by a single model that contained two success correlates; physical characteristics PC1 and nonnative fish community PC2. This model explained 52% of the variation in Virile Crayfish production, and indicated production increased as water temperature, depth, velocity, and total nitrogen increased and as the nonnative fish community became less like that of Tributary 2 (Yellow Bullhead and Smallmouth Bass).

Discussion

By measuring production across multiple trophic levels we were able to provide an evaluation of factors associated with the success of native fishes in the presence of nonnative taxa that incorporated community composition, energy availability, and physicochemical characteristics among years with highly-divergent flow regimes. Our results demonstrated that our *a priori* selected sites encompassed high variation in native and nonnative success, which coupled with highly-variable environmental characteristics and community composition among sites, created the opportunity to identify factors associated with variation in success. We found that native fish production was generally greater than that of nonnatives throughout a range of conditions, whereas nonnative success was more idiosyncratic among species. Our ability to identify factors associated with the success of native fishes and nonnative taxa helped generate hypothesized factors enabling native persistence in the presence of nonnatives, as well as those that promote or enhance nonnative establishment and spread.

Native fish production was high in tributary and valley reaches, which differed in a number of physicochemical characteristics, energy availability, and community composition. In

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contrast, native fish production was lower in the canyon reach and especially at Canyon 2, where native fish went from being moderately-productive during the first year of the study to nearly absent during the final study year. This 91% decrease in native productivity corresponded to large increases in nonnative fish production, which increased by 7 times at this site during the same time period. These increases in nonnative productivity were driven by Flathead Catfish and Common Carp, and were strongly associated with decreased native fish productivity (NNPC1; Fig. 2.3b). Although our data are correlative, evidence suggested that nonnative Flathead Catfish and Common Carp were the primary driver of decreased native productivity at Canyon 2, as there were no other substantial changes in physicochemical characteristics, resource availability, or productivity of other nonnative taxa at this location through time. Further evidence came from Canyon 1, where less dramatic decreases in native fish production occurred as productivity of Flathead Catfish and Common Carp increased. The sheer productivity of Flathead Catfish and Common Carp could be one potential reason for their negative association with native fishes, as total nonnative fish production at Canyon 2 was on average 2.7 times greater than the next most productive site for nonnative fishes (Tributary 2). High productivity of nonnatives could lead to significant competition with and predation on native fishes via high consumptive demand, although we would have predicted that total nonnative fish production rather than Flathead Catfish and Common Carp production should have been a more important correlate of success if this was the case. Ecological traits may also help explain the negative associations of Flathead Catfish with native fish production, as Flathead Catfish have been documented to be the most piscivorous fish species in the upper Gila River (Pilger et al. 2010). The trophic ecology of Flathead Catfish (piscivore) and Common Carp (omnivore/detritivore) may also help explain their invasion success, as these trophic groups are predicted to be the most successful invaders in minimally-altered systems (Moyle and Light 1996).

The success of nonnative fishes tended to increase with depth and temperature and as base flow and variation in summer discharge increased. Native fishes exhibited contrasting responses to these same environmental gradients, preferring shallower habitats in the tributary and valley sites and greater mean spring discharge. Although our results are based on only three years of data, these years' flow regimes (year 1= 2.89 m^3 s^{-1}; year 2= 5.48 m^3 s^{-1}; year 3= 2.18 m^3 s^{-1}; 1927-2009= 4.3 m^3 s^{-1}) were quite different relative to the long-term mean, which allowed

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us to investigate broad responses to habitat and flow regime variation. Further, our short-term findings of contrasting responses by native and nonnative fishes to habitat characteristics and flow regime variation are consistent with more long-term findings in the upper Gila River (Propst et al. 2008; Stefferud et al. 2011), and in other southwestern streams (Gido et al. 2013). These other studies came to similar conclusions, wherein nonnative fishes preferred deep pools and low flow conditions while native fishes preferred shallower habitats and high discharge periods, especially when high discharge events came with spring snowmelt rather than monsoonal storms. Differential responses of nonnatives may be a result of them lacking necessary life-history and behavioral adaptations for survival in highly variable flow regimes characteristic of southwestern North American streams (Moyle and Light 1996; Fausch et al. 2001) or being morphologically maladapted to these systems (Olden et al. 2006).

The primary correlate of American Bullfrog tadpole success was the production of Yellow Bullhead and Smallmouth Bass. This result might be related to similar habitat preferences of these species, which are provided at the location where these species were most productive (Tributary 2). However, the patchy distribution and abundance of American Bullfrog tadpoles is also consistent with potentially complex food web dynamics in which nonnative fish facilitate American Bullfrog invasions (Adams et al. 2003). Nonnative fishes can promote American Bullfrog invasion by consuming dragonfly nymphs (Werner and McPeek 1994) that prey upon American Bullfrog larvae, thus releasing them from predation because the fish themselves do not consume unpalatable American Bullfrog tadpoles (Kruse and Francis 1977). Diet of Smallmouth Bass and Yellow Bullhead in the Gila River reported by Pilger et al. (2010) was consistent with these other studies in that they consumed predaceous macroinvertebrates such as dragonfly nymphs, while native fishes did not consume these taxa.

The success of nonnative Virile Crayfish was greater in downstream valley sites, where water temperature was higher and nonnative fishes less common than in upstream reaches. Water temperature has been identified as an important predictor of Virile Crayfish abundance in other systems, as this species increases its consumption rates and activity levels once mean daily water temperature exceeds >16° C (Richards et al. 1996; Whitledge and Rabeni 2003). Because water temperatures at all sites, excluding Tributary 1, were as warm or warmer than those of other streams where Virile Crayfish have spread (Martinez 2012; Moody and Taylor 2012) it seems likely other factors limited their upstream distribution in the upper Gila River. Regardless

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of the mechanism(s) responsible for crayfish establishment, they may be having large ecosystem effects in the upper Gila River, as their biomass in downstream locations approached or exceeded that of other macroinvertebrates and fishes combined during our study. Nonnative Virile Crayfish biomass also equaled the combined biomass of macroinvertebrates and fishes in the Yampa River of Colorado during a drought (Martinez 2012). This high biomass of crayfish was hypothesized to subsidize large populations of nonnative smallmouth bass, which opportunistically preyed on native fishes. Other potential consequences of high production of Virile Crayfish in the upper Gila River include alteration of organic matter dynamics and macroinvertebrate community structure (Moody and Sabo 2013), as well as increasing predation risk for native fishes (Light 2005).

A commonly held perception in aquatic ecology is that native species will outperform nonnative taxa where habitats remain largely unmodified (Moyle and Light 1996; Poff et al. 1997). The paucity of unaltered rivers in which to investigate this perception certainly has contributed to it being an apparently unexamined dynamic. The comparatively unmodified upper Gila River, however, provided an opportunity to test the validity of this perception. Encouragingly for conservation, we found that native success was relatively high across a broad range of environmental conditions, and, with some exceptions, was greater than that of nonnative fishes, crayfish, or tadpoles. In addition, high levels of native success were temporally-stable among years with highly-divergent flow regimes, thus highlighting the resilience of the native fish community in this physically-unmodified river. Although comparatively pristine, the upper Gila River is under continual threat of degradation owing to the scarcity of water in the region. Uncertainty regarding the direct and indirect interactions among nonnative fishes, crayfish, and tadpoles makes prediction of native responses to anthropogenic change difficult, but this study provides additional evidence for the importance of preserving natural flow regimes and pristine watersheds to ensure successful native fish conservation in the presence of nonnative species (Poff et al. 1997). For those instances when natural abiotic conditions are not adequate to ensure high levels of native success, targeted removal of especially problematic nonnatives may be necessary to ensure persistence of native fish assemblages.

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Figure 2.1 Map of study area describing position of tributary, canyon, and valley sites in the upper Gila River, NM, USA. Tributary 1 was located on the West Fork and Tributary 2 was located on the Middle Fork. Canyon 1 and Valley 1 are the more upstream sites in their respective reach.
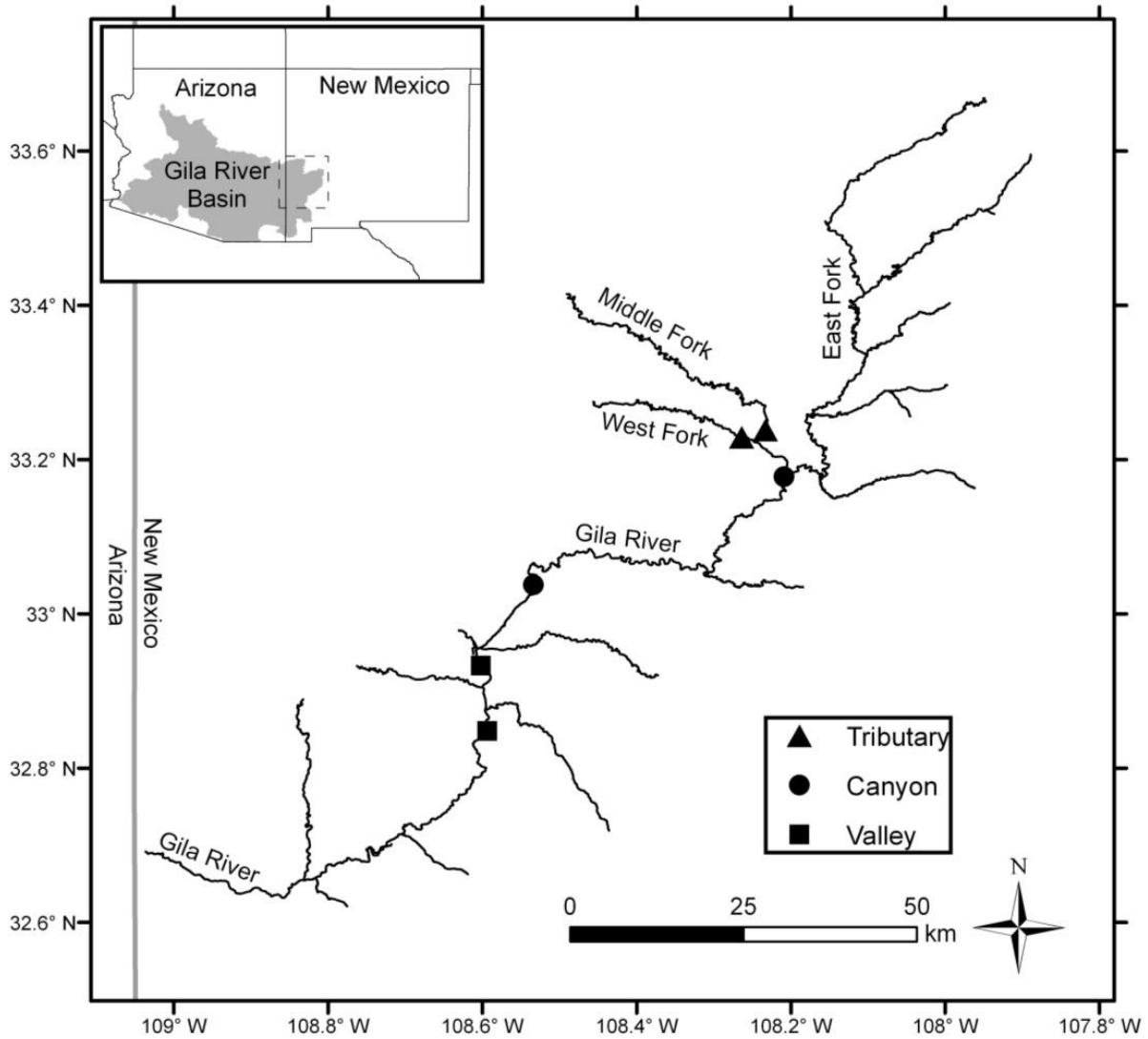
Figure 2.2 Spatiotemporal variation in (a) physicochemical parameters, (b) mean daily discharge at USGS gauge #09403500, (c) flow regime metrics calculated from the USGS gauge, and (d) basal resource availability in the upper Gila River, NM, USA. Timing of sampling at the six localities is also indicated on panel (b). Site codes are reach/site number-year (e.g. T1-1= Tributary 01 in year 1). T=tributary; C= canyon; V=valley. Panel (a) abbreviations are: Vel= mean site velocity; TN= total nitrogen concentration; TP= total phosphorus concentration; MeanTemp= mean annual water temperature; MaxTemp= maximum annual water temperature; Depth= mean site depth. Panel 2 abbreviations are: SummerCV= summer coefficient of variation calculated during 01 July – 30 Sept; MeanSpring= mean daily discharge during 01 March – 30 June; BaseFlow= base flow index (minimum 7-day mean daily discharge divided by mean annual flow). Abbreviations for panel (d) are: Chla= chlorophyll *a* concentration; GPP= gross primary production; MacPro= macroinvertebrate secondary production; MacBio= macroinvertebrate biomass.
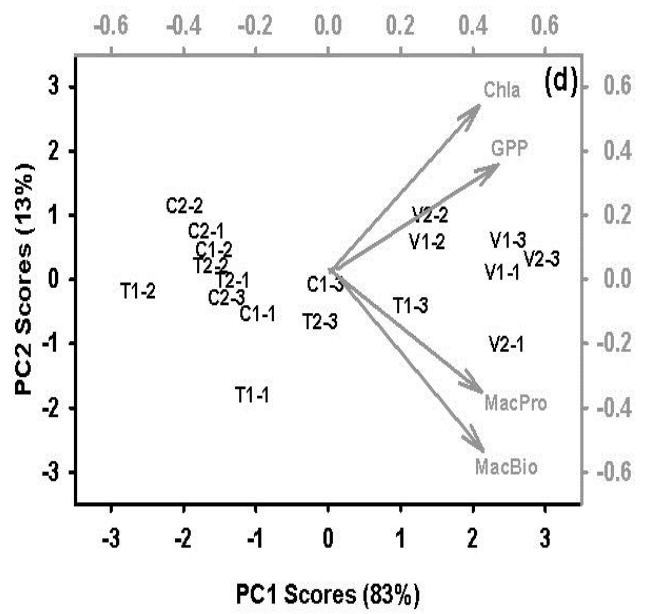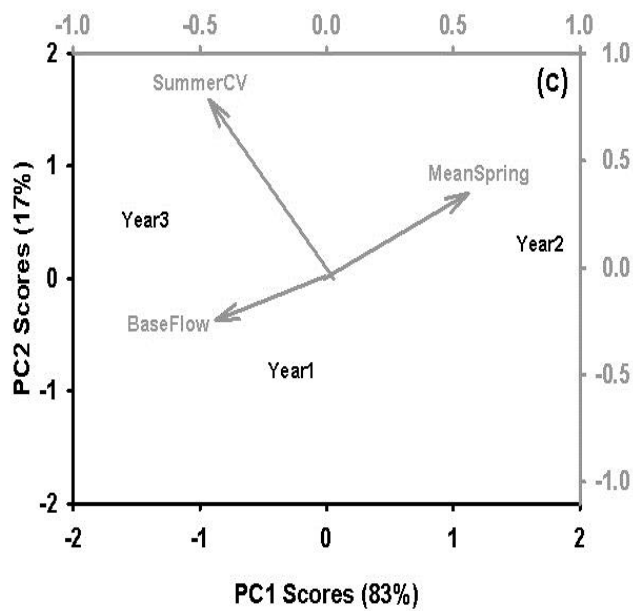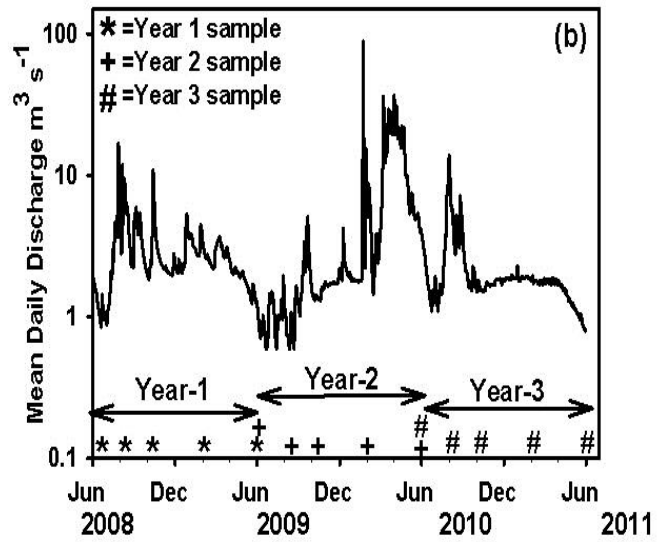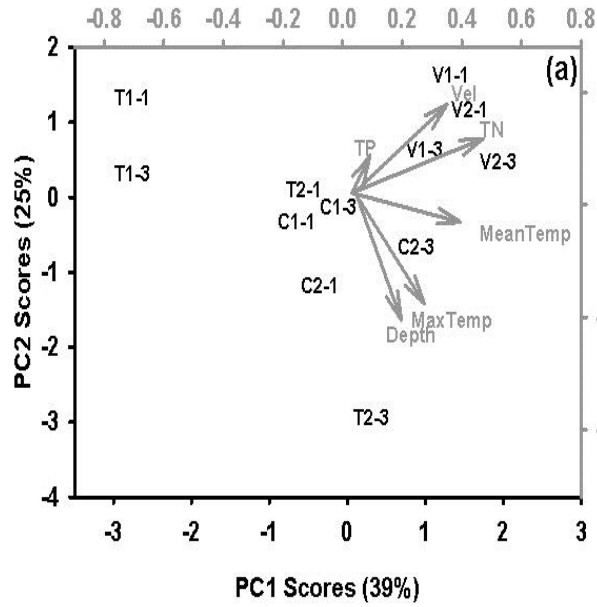
Figure 2.3 Spatiotemporal variation in production of (a) native fishes, (b) nonnative fishes, (c) American Bullfrog tadpoles (*Lithobates catesbeianus* [LITCAT]), and (d) Virile Crayfish (*Orconectes virilis* [ORCVIR]) in the upper Gila River, NM, USA. Site codes are reach/site number-year (e.g. T1-1= Tributary 01 in year 1. T=tributary; C= canyon; V=valley. Species codes in panels (a) and (b) are as follows: MEDFUL= Spikedace (*Meda fulgida*) CATSPP= unidentifiable juveniles of the genus *Catostomus*; TIACOB= Loach Minnow (*Tiaroga cobitis*); AGOCHR= Longfin Dace (*Agosia chrysogaster*) CATCLA= Desert Sucker *(Catostomus clarkii)* CATINS= Sonora Sucker (*Catostomus insignis*) RHIOSC= Speckled Dace (*Rhinichthys osculus*) GILNIG= Headwater Chub (*Gila nigra*) PYLOLI= Flathead Catfish (*Pylodictis olivaris*) CYPCAR= Common Carp (*Cyprinus carpio*) MICDOL= Smallmouth Bass (*Micropterus dolomieu*) AMENAT= Yellow Bullhead (*Ameiurus natalis*) SALTRU= Brown Trout (*Salmo trutta*) and ONCMYK= Rainbow Trout (*Oncorhynchus mykiss*).
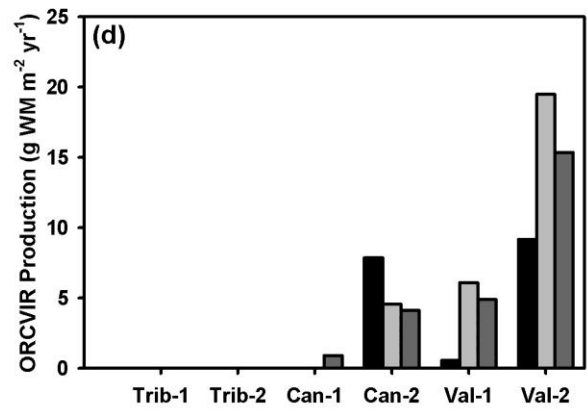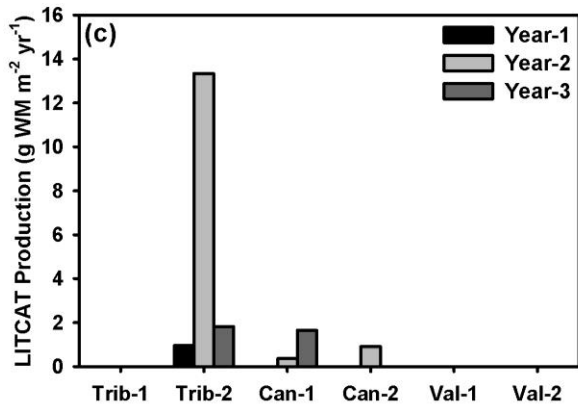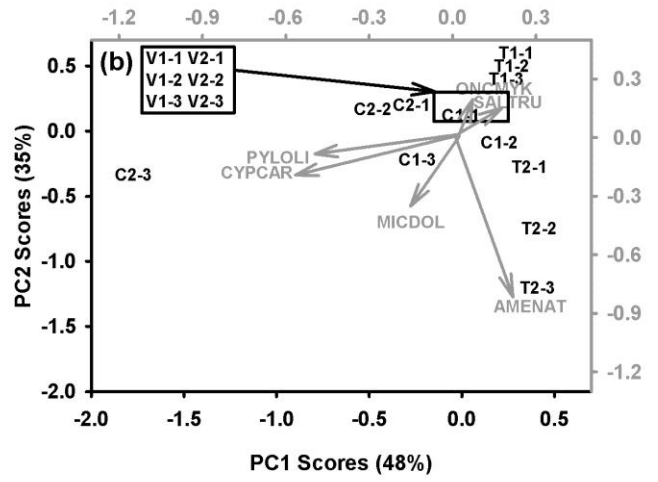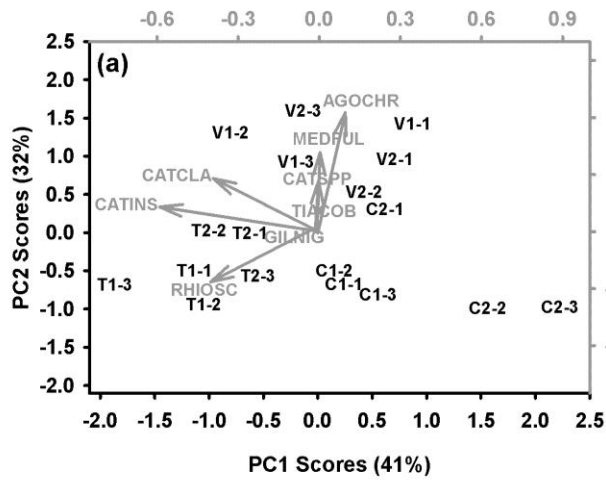
Table 2.1 Physicochemical characteristics of study sites in the upper Gila River, NM. Mean and maximum annual water temperature (°C) was recorded during July 2008-2009 and July 2011-2012; total nitrogen (TN) and total phosphorus (TP) were recorded in October 2008 and 2012; depth (meters) and velocity (meters/second) were measured at baseflow in June 2008 and 2011. Trib= tributary; Can= canyon; Val= valley.

Study Period	Locality	Mean Temperature °C	Max Temperature °C	TN ppb	TP ppb	Depth m	Velocity m/s
Beginning	Trib 1	12.0	25.6	107	83	0.17	0.14
(2008-2009)	Trib 2	14.6	29.9	101	58	0.16	0.19
	Can 1	15.0	27.1	127	36	0.31	0.19
	Can 2	15.1	28.3	105	55	0.40	0.16
	Val 1	15.7	28.3	335	62	0.20	0.28
	Val 2	16.2	28.8	288	83	0.28	0.26
End	Trib 1	11.6	27.9	143	29	0.13	0.12
(2011-2012)	Trib 2	15.6	32.4	139	37	0.37	0.10
	Can 1	14.8	28.3	131	19	0.31	0.26
	Can 2	14.9	29.5	282	89	0.42	0.17
	Val 1	15.7	29.5	343	35	0.17	0.22
	Val 2	16.2	30.0	421	57	0.25	0.22

Table 2.2 Biomass and production of primary producers, macroinvertebrates, native fishes, and nonnative taxa across six sites in the upper Gila River, NM over three years. T=tributary; C= canyon; V= valley. Biomass of primary producers is in units of micrograms (µg) chlorophyll *a* cm^{-2}; units of macroinvertebrate biomass are grams (g) of dry mass (DM) m^{-2}; units of native fish and nonnative taxa biomass are g of wet mass (WM) m^{-2}. Units of gross primary production are in grams of O$_2$ m^{-2} year^{-1}; units of macroinvertebrate secondary production are g DM m^{-2} year^{-1}; units of native fish and nonnative taxa production are g WM m^{-2} year^{-1}. LITCAT= *Lithobates catesbeianus*, American Bullfrog tadpole and ORCVIR= *Orconectes virilis*, Virile Crayfish.

Taxonomic Group	Site	Biomass				Production			
		Year-1	Year-2	Year-3	Mean	Year-1	Year-2	Year-3	Mean
Primary Producer	T1	13.0	14.9	38.1	**22.0**	1176	1019	2550	**1582**
	T2	24.7	19.7	22.8	**22.4**	1174	1764	1877	**1605**
	C1	20.4	23.2	28.7	**24.1**	1511	1576	2272	**1786**
	C2	27.4	27.1	24.0	**26.2**	1263	1468	1260	**1330**
	V1	50.5	36.0	60.4	**49.0**	5674	6476	4885	**5678**
	V2	39.4	41.3	66.4	**49.0**	3771	6527	5885	**5394**
Mean		**29.2**	**27.0**	**40.1**		**2428**	**3138**	**3122**	
Macroinvertebrate	T1	1.12	0.59	1.76	**1.16**	47.7	18.2	72.1	**46.0**
	T2	0.70	0.60	1.14	**0.81**	26.9	23.0	40.3	**30.1**
	C1	0.94	0.61	1.08	**0.88**	28.1	19.4	33.4	**27.0**
	C2	0.62	0.45	0.88	**0.65**	28.0	14.8	30.4	**24.4**
	V1	1.43	1.06	1.59	**1.36**	92.8	54.6	119.9	**89.1**
	V2	2.13	1.08	2.02	**1.74**	120.3	43.5	102.2	**88.7**
Mean		**1.16**	**0.73**	**1.41**		**57.3**	**28.9**	**66.4**	
Native Fish	T1	9.27	7.82	8.69	**8.59**	23.7	20.5	33.4	**25.9**
	T2	9.57	10.03	8.76	**9.45**	21.2	24.7	18.4	**21.4**
	C1	4.31	4.37	2.58	**3.75**	11.4	13.5	6.45	**10.5**
	C2	2.53	0.92	0.32	**1.26**	10.6	1.86	0.98	**4.5**
	V1	5.27	5.99	4.00	**5.09**	16.6	32.8	19.8	**23.1**
	V2	4.00	3.25	5.43	**4.23**	14.0	11.9	25.2	**17.0**
Mean		**5.83**	**5.40**	**4.96**		**16.3**	**17.5**	**17.4**	
Nonnative Fish	T1	3.25	2.89	1.33	**2.49**	1.38	0.84	0.36	**0.86**
	T2	1.11	2.58	4.37	**2.69**	0.91	2.18	4.01	**2.36**
	C1	1.34	0.97	3.13	**1.81**	0.64	0.69	1.96	**1.10**
	C2	3.30	3.29	15.0	**7.20**	0.98	1.24	7.23	**3.15**
	V1	0.28	0.44	0.58	**0.43**	0.13	0.23	0.49	**0.28**
	V2	0.59	0.52	1.12	**0.74**	0.27	0.20	0.53	**0.33**

Taxonomic Group	Site	Biomass				Production			
		Year-1	Year-2	Year-3	Mean	Year-1	Year-2	Year-3	Mean
Mean		**1.65**	**1.78**	**4.26**		**0.72**	**0.90**	**2.43**	
LITCAT	T1	0.00	0.00	0.05	**0.02**	0.00	0.00	0.05	**0.02**
	T2	2.30	10.2	4.80	**5.77**	0.96	13.3	1.82	**5.37**
	C1	0.04	0.19	0.65	**0.29**	0.04	0.36	1.65	**0.68**
	C2	0.02	0.58	0.11	**0.24**	0.01	0.91	0.05	**0.32**
	V1	0.01	0.09	0.11	**0.07**	0.00	0.03	0.02	**0.02**
	V2	0.00	0.00	0.00	**0.00**	0.00	0.00	0.00	**0.00**
Mean		**0.40**	**1.84**	**0.95**		**0.17**	**2.44**	**0.60**	
ORCVIR	T1	0.00	0.00	0.00	**0.00**	0.00	0.00	0.00	**0.00**
	T2	0.00	0.00	0.00	**0.00**	0.00	0.00	0.00	**0.00**
	C1	0.01	0.03	0.52	**0.19**	0.02	0.05	0.92	**0.33**
	C2	6.55	3.19	2.62	**4.12**	7.87	4.56	4.12	**5.52**
	V1	0.35	4.33	2.50	**2.39**	0.55	6.09	4.91	**3.85**
	V2	6.26	12.9	8.67	**9.27**	9.16	19.5	15.4	**14.7**
Mean		**2.20**	**3.41**	**2.39**		**2.93**	**5.03**	**4.22**	

Table 2.3 Mean and standard error of annual density (number per m^2) and biomass (grams of wet mass per m^2) of native and nonnative fishes, American Bullfrog tadpoles, and Virile Crayfish across six sites over three years in the upper Gila River, NM USA. Sample year 1= June 2008-2009; sample year 2= June 2009-2010; sample year 3= June 2010-2011. Trib= tributary; Can= canyon; Val= valley.

| | | | Density (# m^{-2}) | | | | | | Biomass (g WM m^{-2}) | | | | | |
| | | | Mean (Year) | | | Standard Error (Year) | | | Mean (Year) | | | Standard Error (Year) | | |
Origin	Species	Site	1	2	3	1	2	3	1	2	3	1	2	3
Native	Longfin Dace	Trib 1	0.08	0.07	0.17	0.04	0.03	0.14	0.03	0.07	0.11	0.01	0.02	0.08
	(*Agosia chrysogaster*)	Trib 2	0.36	0.61	0.07	0.17	0.23	0.02	0.82	1.55	0.16	0.45	0.61	0.08
		Can 1	0.06	0.33	0.10	0.02	0.17	0.08	0.09	0.53	0.12	0.05	0.33	0.08
		Can 2	3.36	0.35	0.55	2.53	0.13	0.02	3.38	0.45	0.60	2.38	0.21	0.21
		Val 1	4.79	1.54	1.48	3.71	0.68	0.75	1.90	1.45	1.73	0.96	0.61	1.12
		Val 2	1.31	1.56	1.55	0.41	0.71	1.08	1.86	2.69	0.91	0.97	1.19	0.38
	Desert Sucker	Trib 1	0.25	0.28	1.17	0.11	0.12	0.61	3.81	2.44	5.04	1.52	0.73	2.50
	(*Catostomus clarkii*)	Trib 2	0.62	0.57	0.60	0.31	0.30	0.43	4.27	5.26	3.59	2.13	2.41	2.25
		Can 1	0.16	0.13	0.10	0.04	0.03	0.05	0.93	0.80	0.53	0.24	0.10	0.22
		Can 2	0.43	0.09	0.05	0.35	0.04	0.02	1.96	1.14	0.28	0.83	0.44	0.07
		Val 1	0.69	1.46	0.79	0.40	1.21	0.32	3.57	4.03	2.64	1.27	2.87	0.37
		Val 2	0.23	0.32	0.46	0.13	0.15	0.18	1.72	3.55	2.49	0.60	0.81	0.35
	Sonora Sucker	Trib 1	0.76	0.41	0.32	0.49	0.13	0.19	13.36	11.14	8.06	2.90	4.59	2.97
	(*Catostomus insignis*)	Trib 2	0.42	0.36	0.14	0.16	0.13	0.03	11.96	11.26	12.89	3.54	3.80	4.26
		Can 1	0.46	0.29	0.09	0.18	0.10	0.01	5.34	6.41	3.90	1.77	1.60	0.51
		Can 2	0.35	0.02	0.01	0.31	0.01	0.00	1.50	0.44	0.09	0.83	0.28	0.03
		Val 1	0.34	1.83	0.30	0.17	1.61	0.12	1.71	3.15	3.42	0.31	2.19	1.59
		Val 2	0.33	0.14	0.17	0.13	0.02	0.04	2.06	2.11	3.27	0.21	0.46	0.92
	Catostomus spp.	Trib 1	1.90	0.00	0.00	1.32	0.00	0.00	0.67	0.00	0.00	0.40	0.00	0.00
		Trib 2	2.58	0.45	0.59	2.12	0.44	0.59	0.81	0.14	0.19	0.54	0.14	0.19
		Can 1	2.47	0.65	0.30	1.30	0.39	0.30	0.47	0.18	0.05	0.21	0.12	0.05

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			Density (# m^{-2})						Biomass (g WM m^{-2})					
			Mean (Year)			Standard Error (Year)			Mean (Year)			Standard Error (Year)		
Origin	**Species**	**Site**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Native	*Catostomus* spp.	Can 2	0.14	0.09	0.12	0.14	0.09	0.12	0.04	0.01	0.02	0.04	0.01	0.02
		Val 1	7.50	3.05	0.51	4.68	2.56	0.51	2.21	1.19	0.15	1.27	1.05	0.15
		Val 2	1.78	0.32	0.28	1.53	0.23	0.28	0.72	0.19	0.21	0.59	0.15	0.21
	Headwater Chub	Trib 1	0.00	0.01	0.01	0.00	0.00	0.01	0.07	0.09	0.07	0.04	0.21	0.03
	(Gila nigra)	Trib 2	0.19	0.13	0.11	0.10	0.09	0.09	0.38	1.71	0.67	0.05	1.32	0.27
		Can 1	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spikedace	Trib 1	0.25	0.18	0.17	0.16	0.09	0.08	0.08	0.14	0.08	0.03	0.04	0.04
	(Meda fulgida)	Trib 2	0.05	0.00	0.06	0.04	0.00	0.05	0.05	0.00	0.07	0.03	0.00	0.05
		Can 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	7.99	2.36	0.24	6.83	1.63	0.06	2.28	1.47	0.24	1.23	1.06	0.04
		Val 2	1.55	0.44	1.56	0.69	0.17	0.96	0.54	0.62	1.43	0.20	0.22	0.96
	Speckled Dace	Trib 1	0.95	2.10	3.70	0.18	0.49	2.34	0.92	2.76	4.16	0.22	0.62	1.97
	(Rhinichthys osculus)	Trib 2	0.04	0.09	0.83	0.02	0.05	0.73	0.08	0.20	1.20	0.04	0.10	1.04
		Can 1	0.01	0.02	0.09	0.00	0.00	0.04	0.01	0.05	0.12	0.00	0.01	0.06
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Loach Minnow	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(Tiaroga cobitis)	Trib 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Can 1	0.03	0.04	0.31	0.01	0.01	0.14	0.05	0.07	0.40	0.02	0.01	0.17
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
		Val 1	0.86	2.31	0.70	0.25	1.01	0.20	1.10	2.02	1.10	0.30	0.46	0.29

			Density (# m^{-2})						Biomass (g WM m^{-2})					
			Mean (Year)			Standard Error (Year)			Mean (Year)			Standard Error (Year)		
Origin	Species	Site	1	2	3	1	2	3	1	2	3	1	2	3
Native	Loach Minnow	Val 2	0.22	0.44	0.66	0.11	0.26	0.05	0.25	0.47	0.84	0.07	0.24	0.11
Nonnative	Yellow Bullhead	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
	(Ameiurus natalis)	Trib 2	0.06	0.07	0.07	0.02	0.02	0.02	0.70	1.84	3.08	0.03	0.63	0.80
		Can 1	0.00	0.01	0.02	0.00	0.00	0.00	0.06	0.24	0.20	0.05	0.07	0.04
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.01
	Common Carp	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00
	(Cyprinus carpio)	Trib 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Can 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.81	9.08	0.00	0.81	4.04
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.41	0.00	0.31	0.41
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.01	0.16	0.00	0.01
	Smallmouth Bass	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01
	(Micropterus dolomieu)	Trib 2	0.01	0.03	0.04	0.01	0.02	0.03	0.24	0.57	0.84	0.13	0.04	0.37
		Can 1	0.01	0.00	0.01	0.01	0.00	0.01	0.11	0.14	0.18	0.07	0.12	0.17
		Can 2	0.02	0.00	0.02	0.02	0.00	0.01	0.99	0.03	0.56	0.99	0.03	0.31
		Val 1	0.01	0.00	0.01	0.00	0.00	0.01	0.13	0.03	0.15	0.09	0.03	0.09
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.01	0.00	0.08	0.01
	Rainbow Trout	Trib 1	0.04	0.06	0.01	0.01	0.04	0.00	1.30	0.84	0.69	0.39	0.40	0.34
	(Oncorhynchus mykiss)	Trib 2	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.02	0.07	0.00
		Can 1	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.20	0.00	0.20	0.20	0.00
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Flathead Catfish	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

			Density (# m^{-2})						Biomass (g WM m^{-2})					
			Mean (Year)			Standard Error (Year)			Mean (Year)			Standard Error (Year)		
Origin	**Species**	**Site**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Nonnative	(*Pylodictis olivaris*)	Trib 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.41
		Can 1	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.38	2.75	0.55	0.26	2.16
		Can 2	0.00	0.01	0.00	0.00	0.00	0.00	2.31	2.44	5.39	1.37	0.55	0.74
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.10	0.02	0.08	0.09	0.02
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.44	1.08	0.43	0.32	0.54
	Brown Trout	Trib 1	0.09	0.13	0.04	0.08	0.07	0.02	1.95	2.05	0.64	0.90	1.11	0.16
	(*Salmo trutta*)	Trib 2	0.00	0.01	0.01	0.00	0.01	0.00	0.07	0.07	0.03	0.03	0.05	0.01
		Can 1	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.01	0.01	0.00
		Can 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	American Bullfrog tadpole	Trib 1	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.03	0.04
	(*Lithobates catesbeianus*)	Trib 2	0.19	0.82	0.26	0.15	0.27	0.15	2.30	10.19	4.82	2.14	4.81	3.21
		Can 1	0.00	0.02	0.04	0.00	0.01	0.03	0.04	0.19	0.65	0.03	0.06	0.59
		Can 2	0.00	0.11	0.01	0.00	0.08	0.01	0.02	0.58	0.11	0.02	0.38	0.08
		Val 1	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.09	0.11	0.01	0.07	0.10
		Val 2	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.03	0.03	0.00
	Virile Crayfish	Trib 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(*Orconectes virilis*)	Trib 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Can 1	0.00	0.00	0.03	0.00	0.00	0.02	0.01	0.03	0.52	0.01	0.01	0.49
		Can 2	0.99	0.43	0.50	0.83	0.13	0.21	6.55	3.19	2.62	5.37	1.03	1.48
		Val 1	0.07	0.70	0.38	0.05	0.46	0.11	0.35	4.33	2.50	0.20	3.66	1.67
		Val 2	1.26	2.95	2.38	0.99	1.04	1.13	6.26	12.85	8.67	4.12	6.10	6.32

Table 2.4 Models with ΔAIC$_c$ <2 (Akaike's Information Criterion corrected for small sample size) examining spatiotemporal variation in the success (secondary production) of native and nonnative fishes, nonnative American Bullfrog tadpoles (*Lithobates catesbeianus*; LITCAT), and nonnative Virile Crayfish (*Orconectes virilis*; ORCVIR). Degrees of freedom (df), Akaike weight (w_i = relative model likelihood), and adjusted coefficient of determination (Adj. R^2) are reported for each model. Relative importance (sum of Akaike weights across all models with ΔAIC$_c$ <2 that contain that success correlate), slope (β), and statistics determining slope significance (z-statistic and p-value) of the success correlate were averaged across models with ΔAIC$_c$ <2. Bold success correlates indicate a statistically-significant (p<0.05) model-averaged slope coefficient. Success correlate abbreviations are: NNPC1= the first principal component (PC) from the nonnative fish community principal component analysis (PCA; Fig. 2.3b); ResPC1= the first PC of the basal resources PCA (Fig. 2.2d); AbiPC1= the first PC of the abiotic physicochemical characteristics PCA (Fig. 2.2a); FlowPC1= the first PC of the flow regime PCA (Fig. 2.2c); NNPC2= the second PC of the nonnative fish community PCA (Fig. 2.3b); LITCAT= secondary production of American Bullfrog tadpoles (Fig. 2.3c); and NatPC2= the second PC of the native fish community PCA (Fig. 2.3a).

Success Metric	Top Models	df	ΔAIC$_c$	w_i	Adj. R^2	Success Correlate	Relative Importance	β	z-statistic	p-value
Native Fish Production	NNPC1	3	0.00	0.30	0.37	**NNPC1**	**0.70**	**10.5**	**2.52**	**0.01**
	AbiPC1+ResPC1+NNPC1	5	0.43	0.24	0.51	ResPC1	0.70	3.66	1.59	0.11
	ResPC1+NNPC1	4	1.08	0.17	0.41	**AbiPC1**	**0.53**	**-4.47**	**2.03**	**0.04**
	AbiPC1+FlowPC1+ResPC1+NNPC2	6	1.21	0.16	0.57	**FlowPC1**	**0.16**	**3.78**	**2.51**	**0.01**
	AbiPC1+ResPC1+LITCAT	5	1.58	0.13	0.48	**NNPC2**	**0.16**	**-10.5**	**2.21**	**0.03**
						LITCAT	0.13	1.13	1.90	0.06
Nonnative Fish Production	AbiPC1+FlowPC1+ResPC1	5	0.00	0.40	0.49	**AbiPC1**	**1.00**	**0.70**	**2.36**	**0.02**
	AbiPC1+NatPC2	4	1.15	0.22	0.37	**FlowPC1**	**0.78**	**-0.72**	**2.14**	**0.03**
	AbiPC1+FlowPC1+NatPC2	5	1.20	0.22	0.46	**NatPC2**	**0.60**	**-1.48**	**2.25**	**0.02**
	AbiPC1+FlowPC1+ResPC1+NatPC2	6	1.82	0.16	0.53	**ResPC1**	**0.56**	**-0.82**	**2.54**	**0.01**
LITCAT Production	FlowPC1+NNPC2	4	0.00	0.61	0.39	**NNPC2**	**1.00**	**-4.48**	**2.80**	**0.005**
	NNPC2	3	0.92	0.39	0.28	FlowPC1	0.61	0.91	1.85	0.07
ORCVIR Production	AbiPC1+NNPC2	4	0.00	1.00	0.52	**AbiPC1**	**1.00**	**2.67**	**4.11**	**0.0009**
						NNPC2	**1.00**	**5.69**	**4.70**	**0.03**

Chapter 3 - Biotic response to consecutive wildfires in a warmwater dryland river network

Abstract

The size, frequency, and intensity of wildfires in western North America have increased in recent decades. Responses of stream biota to wildfire have been mostly studied in coldwater systems with little know about the responses of warmwater communities; including both native and nonnative taxa. We measured changes in physical habitat and resource availability as well as biomass changes of a warmwater community of native and nonnative macroinvertebrates and macro-consumers following consecutive, large wildfires in the upper Gila River, NM, USA. Changes in habitat and resource availability were related to fire size and post-wildfire precipitation, as larger fire size and moderate discharge were associated with greater post-wildfire changes. Several insect taxa responded to these changes with reduced biomass. Native fish biomass decreased for six of seven species after both wildfires, and decreases were associated with site proximity to fire. Nonnative decreases following wildfire were most pronounced for salmonids, with other taxa exhibiting more limited responses. More pronounced responses of native fishes to wildfires suggest that changing wildfire regimes represent an additional threat to the persistence of native fauna in southwestern streams, and suggest management activities promoting ecosystem resilience might help ameliorate wildfire effects.

Introduction

Wildfires are a natural agent of ecological change in rivers draining forested biomes of western North America, and are important in maintaining their heterogeneity (Covington et al. 1994; Hessburg and Agee 2003; Hurteau et al. 2013). However, the frequency, size, and intensity of wildfires in the western United States have increased in recent decades (Westerling et al. 2006). This phenomenon is attributed to the higher temperatures and earlier snowmelt associated with climate change coupled with elevated fuel loads from 100+ years of fire suppression (Westerling et al. 2006; Hurteau et al. 2013). This trend of greater fire frequency, size, and intensity is predicted to accelerate and intensify as a result of climate change in the decades to come (Brown et al. 2004; McKenzie et al. 2004; Moritz et al. 2012). Recent and

future changes in wildfire regimes will have numerous and potentially severe consequences for stream biota.

The effects of wildfires on stream communities can be partitioned into those that are direct and immediate versus those that are indirect and delayed (Gresswell 1999; Rieman et al. 2012). Direct effects occur when a wildfire burns a stream's riparian corridor, increasing water temperature from heat dissipation (Hall and Lantz 1969; Hitt 2003), alkalinity (Cushing and Olson 1963), and phosphorus and nitrogen concentrations from ash deposition and smoke diffusion (Spencer and Hauer 1991). Direct effects are most pronounced in smaller streams, as greater water volume buffers larger streams against such changes. These effects are short-lived however, and are considered pulse disturbances (Niemi et al. 1990; Gresswell 1999). Indirect effects result from wildfire's alteration of watershed vegetation and soil characteristics, and include increased water yield (Legleiter et al. 2002) and sedimentation (Benda et al. 2003), decreased inputs of large woody debris (May and Gresswell 2003), increased temperature from a loss of canopy cover (Dunham et al. 2007; Sestrich et al. 2011), and altered quantity and quality of resource inputs (Mihuc and Minshall 1995; Malison and Baxter 2010). Indirect effects also attenuate with stream size, but are press disturbances that have their greatest influence during the first ten years of the wildfire but can last for several hundred years until the forest regenerates to pre-wildfire levels (Minshall et al. 1989).

The magnitude of wildfire effects on streams are related to the characteristics of the wildfire, the characteristics of the focal stream, and post-fire precipitation events (Gresswell 1999; Rieman et al. 2012). Wildfire characteristics include size, severity (influence on soil), intensity (impacts on vegetation), and timing (Brown 1990). Stream features that dictate wildfire impacts include volume, distance from the fire, and catchment characteristics (geology, topography, vegetation, soil, geomorphology). Major precipitation effects associated with wildfire occur when rain falls on a recently burned catchment, producing ash flows. Ash flows may result in hypoxic water conditions (Lyon and O'Connor 2008), high suspended sediment loads (Bozek and Young 1994), and extreme flooding (Rinne 1996; Viera et al. 2004; Howell 2006). Given this context-dependency it is important to document stream characteristics, fire characteristics, and post-fire precipitation in assessing the effects of wildfire on riverine communities.

Given the numerous physical effects wildfires have on rivers, wildfires can impact stream biota in multiple ways. For instance, wildfire induced changes in channel stability, sedimentation, and resource availability can decrease macroinvertebrate abundance (Gresswell 1999). Furthermore, habitat changes can result in altered macroinvertebrate community composition with the post-wildfire environment selecting for taxa with shorter turnover times, high dispersal abilities, or autochthonous resource preferences (Mihuc and Minshall 1995; Viera et al. 2004; Verkaik et al. 2013). Macroinvertebrate abundance and community structure can also be severely altered by wildfire-induced flooding (Rinne 1996; Earl and Blinn 2003; Viera et al. 2004). Fish are also susceptible to post-wildfire hydrologic events, but may be less affected by habitat changes (Gresswell 1999). Ash flows can have the greatest impact on fish communities, as these post-wildfire hydrologic events can result in mass mortality and extirpation of fishes (Propst et al. 1992; Bozek and Young 1994; Rinne 1996).

Complex life histories (i.e. require movement among multiple habitats for feeding, spawning, rearing, and refuge), high dispersal abilities and connectivity can confer high resilience and rapid recolonization (Rieman and Dunham 2000; Burton 2005). The majority of post-fire studies on fish response to wildfire has occurred in coldwater systems and has been conducted on salmonids (Rieman et al. 1995; Rieman and Clayton 1997; Rieman et al 2003). The low physiologic tolerance of salmonids to hypoxia explains their limited resistance to wildfire induced ash flows (Doudoroff and Shumway 1970), and their complex life histories confer their high resilience and rapid recovery (Rieman and Dunham 2000). The response of communities in warmwater systems containing fishes with different life histories, physiological tolerances, and movement capabilities are less well investigated and thus poorly understood.

In addition to wildfire, the introduction of nonnative species represents another agent of global change affecting streams in western North America. Many of nonnatives documented in the Colorado River Basin have divergent life-histories, morphologies, habitat preferences, physiologies, and trophic guilds relative to native species (Olden et al. 2006; Pilger et al. 2010), and thus may possess different susceptibilities to wildfire effects (Dunham et al. 2003; Young 2012). Furthermore, other lineages of vertebrates (e.g., American Bullfrog *Lithobates catesbeianus*) and invertebrates (Order Decapoda: Family Cambaridae) have been added to the Colorado River Basin (Clarkson and DeVos 1986; Moody and Taylor 2012). Conserving native and managing nonnative biota under a changing fire regime would benefit from a greater

understanding of their responses to wildfire of different size and intensity, as well as in streams of different characteristics. As such, the objectives of this manuscript were to compare the immediate effects and responses of native and nonnative biota to consecutive wildfires in the upper Gila River across streams with different catchment characteristics. We also quantified the effects of wildfire on habitat and resource availability to identify potential drivers of biotic change.

Methods

Study Area

This study was conducted across three longitudinal zones in the upper Gila River of southwest New Mexico, USA, with two sites positioned in each of the three zones (Fig. 3.1). Longitudinal zones were defined by stream size, surrounding geology, and elevation, and were labeled tributary, canyon, and valley (Table 3.1). The two sites in the tributary region were located on the West and Middle Forks of the Gila River, whereas the four sites in the canyon and valley region were located on the Gila River mainstem. Mean stream width and water temperature were lowest in the West Fork and increased downstream across longitudinal zones, although mean depth was generally greatest in the canyon (Table 3.1). Tributary and canyon catchments were composed primarily of mixed-conifer forest, including ponderosa pine *Pinus ponderosa*, piñon pine *Pinus* spp., Douglas-fir *Pseudotsuga menziessi*, and *Juniperus* spp., whereas valley sites occurred in the Cliff-Gila Valley and had greater anthropogenic modification from agriculture (mainly irrigated pasture) and scattered human settlement. Riparian areas were composed of willow *Salix* spp., Cottonwood *Populus* spp., and sycamore, *Plantanus* spp. regardless of longitudinal zone.

Wildfire Characteristics

All study sites were affected by consecutive wildfires in 2011 and 2012. From 17 April through 6 June 2011, the Miller Fire burned 35,950 hectares (ha) (Fig. 3.1). This fire burned the riparian areas of both tributary sites, with distance from fire perimeter increasing downstream for other study sites (Table 3.1). The following year the Whitewater-Baldy Fire burned an additional 120,535 ha during 9 May through 23 July. Study site distance from the Whitewater-Baldy perimeter was generally greater relative to the Miller Fire, and canyon 2 had the most

proximal position to fire perimeter. These wildfires were both unusually large, as fires larger than 1,000 ha were historically a rare component of the southwestern fire regime (Dietrich 1983; Swetnam 1990). Fire-generated ash washed through study sites during the monsoon seasons following each fire. The Miller Fire was followed by a moderately strong monsoon season (mean daily discharge [MDD] during 01 July- 30 Sept= 2.72 m^3 s^{-1}; maximum MDD= 31.7 m^3 s^{-1}; USGS gage #09430500), whereas a weaker monsoon followed the Whitewater-Baldy Fire (MDD=1.81 m^3 s^{-1}; max MDD= 5.24 m^3 s^{-1}).

Flow Regime Comparison

In addition to wildfire, flow regime represents another potential driver of changes in habitat quality, resource availability, and fish abundance in the upper Gila River (Propst et al. 2008; Stefferud et al. 2011; Gido et al. 2013). To evaluate the possibility that temporal differences in flow regime that may or may not be related to wildfire accounted for observed changes in response variables we calculated annual mean daily discharge (MDD), mean spring discharge (MDD during 01 March to 30 June), coefficient of variation (CV) of summer MDD (standard deviation divided by the mean of daily discharge during 01 July to 30 September), and base flow index (smallest values of MDD computed over any 7-consecutive days during the annual period divided by mean annual flow; larger values representative of more consistent flows) for the year prior to the fires (1 July 2010 – 30 June 2011) and the years following the Miller Fire (1 July 2011 – 30 June 2012) and the Whitewater-Baldy Fire (1 July 2012 – 30 June 2013), and as long-term values (1927-2013) using data from United States Geological Survey (USGS) Gila River near Gila gage (#09430500). These three metrics were chosen because they have been previously associated with interannual differences in fish abundance in the upper Gila River (Gido et al. 2013). Changes in response variables following wildfire without large differences in flow regime metrics provided greater evidence for a wildfire effect than stream discharge.

General Sampling Design

All sampling was conducted during March, June and October. Sampling prior to the wildfires occurred during 2010 (October) and 2011 (March and June), samples following the Miller Fire were collected in 2011 (October) and 2012 (March and June), and sampling following the Whitewater-Baldy Fire occurred in 2012 (October) and 2013 (March and June).

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Habitat was not measured in October 2010 (pre-fire) for any site, and habitat and stream macro-consumers (i.e. crayfish, tadpoles, and fish) were not sampled in March 2011 (pre-fire) at canyon 2, valley 1, and valley 2 (Table 3.2).

Sampling was conducted at the mesohabitat scale (pool or riffle), with six mesohabitats (three pools and three riffles) in tributary sites and four mesohabitats (two pools and two riffles) occurring in mainstem sites. Mesohabitat area was calculated by multiplying mean width (two to three widths per mesohabitat) by length of each mesohabitat. Grand site means were calculated from values of mesohabitat response variables by area-weighted averaging.

Habitat

Habitat quality was assessed by calculating percent silt and percent woody debris. At each site the occurrence of silt (<62 to >4 μm; Wood and Armitage 1997) was determined at five points along two (tributary) to three (mainstem) transects in each mesohabitat. The number of silt points per mesohabitat were then divided by the total number of points and then multiplied by 100 to determine percent silt. The length and width of large woody debris (i.e., ≥ 0.05 m circumference and a length ≥ 0.3 m) was measured in each mesohabitat, divided by total mesohabitat area, and then multiplied by 100 to determine percent large woody debris.

Resource Availability

Chlorophyll *a* concentration was used to quantify autochthonous resource availability. Chlorophyll *a* was sampled by collecting and pooling three rocks along six transects from an equal number of pool and riffle mesohabitats. The rock samples were kept in the dark and frozen until chlorophyll *a* was extracted with 95% ethanol and analyzed spectrophotometrically following the methods of Steinman et al. (2006). Chlorophyll *a* concentrations were then corrected for rock surface area and expressed as μg chlorophyll *a* cm^{-2}.

Benthic Macroinvertebrates

Benthic macroinvertebrates were sampled from pool mesohabitats using a stovepipe core (0.018 m^2), from riffle mesohabitats using a Surber sampler (0.093 m^2; mesh = 250 μm), and from large woody debris by scrubbing and removing individuals from pieces of large woody debris (average surface area = 0.035 m^2). Two (tributary) to three (mainstem) replicates were taken for each sample type, with replicates pooled into a single sample for each sample type and

preserved in 10% formalin. Individuals were separated from inorganic debris and organic detritus and measured for total length. Insects were identified to family using Merritt et al. (2008), whereas non-insects were identified to phylum or class using Thorp and Covich (2001). Biomass was calculated using published length-mass relationships of the lowest identified taxonomic unit (Burgherr and Meyer 1997; Benke et al. 1999; Sabo et al. 2002), and is expressed as mg dry mass (DM) m^{-2}.

Stream Macro-consumers

Stream macro-consumers (i.e. crayfish, tadpoles, fishes) were sampled during a single pass that included a combination of backpack electrofishing with one or two dipnetters and seining (4.6 x 1.2m, 3.2mm mesh). Captured individuals were identified to species, measured for total length and then returned alive to their respective mesohabitat. Species biomass was calculated using previously-quantified length-mass relationships specific to the upper Gila River (Whitney et al. 2014), and expressed as g wet mass (WM) per m^{-2}.

Analysis

All analyses were conducted in R version 3.1.0 (R Core Team 2014). Biomass was $\log_{10}(x)$ (chlorophyll *a*) or $\log_{10}(x+1)$ (macroinvertebrates and macro-consumers) transformed prior to analyses to satisfy assumptions of normally distributed errors and homoscedasticity. Changes in habitat quality, resource availability, and the biomass of taxonomic groups following the Miller and Whitewater-Baldy fires was accomplished using a two-way repeated-measures analysis of variance (rm-ANOVA). This analysis included interactive effects of site and time period (pre-fire, after Miller, after Whitewater-Baldy), and included sample month as the repeated factor. Site was treated as a fixed effect because we were interested in the response at each site, with site location chosen *a priori* to create a natural experimental framework allowing investigation of the effects of catchment characteristics and fire proximity on site wildfire responses. We did not incorporate spatial autocorrelation into the structure of this analysis, as an earlier study revealed large differences in abiotic and biotic properties over small spatial distances (Whitney et al. 2014). Results were considered significant at $p \leq 0.05$ and marginally significant at $p \leq 0.10$. If a significant or marginally-significant site by time period interaction occurred, pairwise Bonferroni-adjusted t-tests comparing time periods within sites were conducted. The main effect of site was not of interest in this study, and was only investigated to

determine spatially variable changes following wildfires (i.e. a site by time interaction). Therefore, post-hoc differences among sites were not examined unless there was a significant interaction of site with time period. Responses of rare macroinvertebrates (i.e. non-insects on average comprised < 10% of total macroinvertebrate biomass; insect families that on average comprised < 10% of total insect biomass) and stream macro-consumers (i.e. % occurrence < 10%) were not analyzed.

Results

Flow Regime Comparison

Our three study periods were similar in having low annual MDD and spring MDD relative to long-term values (Table 3.3). The year following the Miller Fire had high CV of summer discharge, which contrasted this year from other study years and from the long-term value. The base flow index was similar among study periods and the long-term value. Given that all study years were generally similar in having low discharge from drought conditions, we reasoned that any observed changes in habitat quality, resource availability, and biotic responses would be resultant from the effects of wildfire, but acknowledge that consecutive years of drought conditions might also result in cumulative effects on stream biota.

Habitat Quality

The main effects of time period ($F_{2,4}$ = 4.73; P = 0.088) and site ($F_{5,22}$ = 9.45; P < 0.001) had marginally significant and significant effects on percent silt, respectively, but these factors did not interact ($F_{10,22}$ = 1.63; P = 0.164; Table 3.4). Mean percent silt across sites went from 9% in the pre-fire period to 21% in the period following the Whitewater-Baldy fire (P = 0.024), but was only 12% during the period following the Miller Fire, which did not differ from the pre-fire period (P = 0.857; Fig. 3.2). Percent large woody debris was influenced by a time period by site interaction ($F_{10,22}$ = 3.24; P = 0.010). Percent wood relative to Miller Fire conditions decreased following the Whitewater-Baldy Fire by 70% at tributary 2, 57% at canyon 1, 56% at valley 1, and 69% at valley 2. Percent wood also decreased by 28% relative to pre-fire conditions following the Miller Fire, but only at canyon 1 (Fig. 3.2). However, the amount of wood habitat was small relative to total mesohabitat area, and generally comprised <10% of total mesohabitat area (Fig. 3.2).

Resource Availability

Chlorophyll *a* concentration was affected by an interaction between time period and site ($F_{10,30}$ = 2.53; P = 0.024; Table 3.4). Relative to pre-fire conditions (mean = 49.8 µg cm^{-2}) chlorophyll *a* concentration decreased following the Whitewater-Baldy Fire (mean = 11.3 µg cm^{-2}) across all sites (mean decrease = 38%; range = 24-58%), and decreased relative to the Miller period by 35-48% at the three lowermost sites (canyon 2, valley 1 and 2). Chlorophyll *a* concentration was unaffected by the Miller Fire, with mean concentration after the Miller Fire = 43.7 µg cm^{-2} (Table 3.4; Fig. 3.2).

Benthic Macroinvertebrates

Eleven classes of macroinvertebrates were encountered during sampling, including Turbellaria (flatworms), Oligochaeta (segmented worms) Clitellata (leeches), Gastropoda (snails and limpets), Bivalvia (nonnative Asian clam *Corbicula fluminea*), Arachnida (water mites), Insecta (insects), Branchiopoda (cladocerans), Maxillopoda (copepods), Ostracoda (seed shrimp), and Malacostraca (scuds) (Table 3.5). Members of the phyla Nematomorpha, Nematoda, and Nemertea were also collected, but were not identified beyond phylum. Oligochaeta and Insecta comprised the major portion of macroinvertebrate biomass and on average accounted for 95% (range = 73.0 – 99.9%) of total sample biomass. Because of this dominance and the rarity of other groups, segmented worms and insects were the only macroinvertebrates statistically examined. Within the class Insecta we collected nine orders represented by 62 families. Coleoptera and Diptera had the greatest number of families with 13 each, whereas Megaloptera (Corydalidae) and Lepidoptera (Crambidae) were comprised of a single family. Among these 62 families 26 were common enough to warrant investigation into their spatiotemporal changes in biomass, and on average represented 88% (range = 29.5 – 99.9%) of total Insecta biomass.

Oligochaeta biomass was influenced by site ($F_{5,30}$ = 6.64; P < 0.001), but was unaffected by the main effect of time period ($F_{2,6}$ = 0.12; P = 0.890) or by an interaction with time period ($F_{10,30}$ = 0.87; P = 0.568; Table 3.4). Several insect families were affected by a significant time period effect that did not interact with site (Table 3.4; Fig. 3.3). These included decreases by Corixidae (85%), Hydropsychidae (25%), and Crambidae (60%) following the Miller Fire relative to the pre-fire period, and Gomphidae (82%), Leptohyphidae (64%), and Tabanidae

(54%) following the Whitewater-Baldy Fire relative to the pre-fire period. Hydropsychidae and Crambidae also decreased again following the Whitewater-Baldy Fire, as their biomass during this time period was 35% and 89% lower, respectively, than the Miller Fire period. This resulted in a cumulative decrease of 51% for Hydropsychidae and 96% for Crambidae following both wildfires. Biomass decreases were most pronounced for Hydropsychidae, Leptohyphidae, and Tabanidae, which in the before period had mean untransformed biomass values of 210, 60, and 54 mg DM m^{-2}, respectively, and ended in the Whitewater-Baldy period with mean biomass values of 13, 3, and 5 mg DM m^{-2}, respectively. Pre-fire period biomass of other taxa was less than 17 mg DM m^{-2}, but always ended in the Whitewater-Baldy period less than 1 mg DM m^{-2}. More spatially limited wildfire-associated decreases occurred for two insect families, with Libellulidae decreasing from 17 to 0 mg DM m^{-2} at tributary 1 following the Miller Fire, and decreases of 8 to 0 for Libellulidae and 69 to 11 mg DM m^{-2} for Chironomidae at canyon 2 following the Whitewater Baldy Fire.

Stream Macro-consumers

The virile crayfish *Orconectes virilis* was the only species of nonnative crayfish collected, and the American bullfrog was the only species of nonnative tadpole collected. A total of eight native and twelve nonnative fish species was collected (Table 3.5). Native fish species were represented by two orders and three families, whereas nonnative fishes were composed of five orders with one family each. Responses of seven of eight native fishes and eleven of twelve nonnative fishes were examined. The responses of native Gila trout *Oncorhynchus gilae* and nonnative largemouth bass *Micropterus salmoides* were not investigated because of limited occurrences at our study sites.

Six of the seven native fishes exhibited significant changes following one or both wildfires. These changes were spatially-dependent however, as upper sites (tributary 1 and 2, canyon 1), generally experienced decreases following the Miller Fire, whereas lower sites (canyon 2, valley 1 and 2) exhibited decreases following the Whitewater-Baldy Fire. Native fish decreases following wildfire were spatially patchy within regions (upper or lower), as tributary 2 experienced more native decreases relative to other upper sites following the Miller Fire, and valley 2 experienced more decreases compared to other lower sites following the Whitewater-Baldy Fire. For instance, native longfin dace *Agosia chrysogaster* (81%), headwater chub *Gila*

nigra (100%), spikedace *Meda fulgida* (100%), and Sonora sucker *Catostomus insignis* (9%) all exhibited significant decreases in biomass at tributary 2 following the Miller Fire (Table 3.4; Fig. 3.4). Of these species Sonora sucker had the greatest biomass (3.8 g WM m^{-2}) at tributary 2 prior to the Miller Fire, with other species having biomass in the pre-fire period of less than 0.07 g WM m^{-2}. Speckled dace *Rhinichthys osculus* and loach minnow *Tiaroga cobitis* exhibited decreases of 93% and 84%, respectively, at canyon 1 following the Miller Fire, with speckled dace also decreasing by 62% at tributary 1. However, loach minnow (0.03 g WM m^{-2}) and speckled dace (0.008 g WM m^{-2}) had low biomass at canyon 1 prior to the Miller Fire, although the biomass of speckled dace at tributary 1 (0.45 g WM m^{-2}) was relatively high during the pre-fire period. Canyon 2 was the only lower site to exhibit changes in native biomass following the Miller Fire, with longfin dace biomass decreasing by an order of magnitude from 0.05 g WM m^{-2} to 0.005 g WM m^{-2}. Following the Whitewater-Baldy Fire longfin dace and Sonora sucker decreased by 87% (0.10 to 0.02 g WM m^{-2}) and 93% (0.68 to 0.04 g WM m^{-2}), respectively, at valley 2, and spikedace decreased from 0.006 to <0.0001 g WM m^{-2} valley 1. The only upper site to exhibit changes in native biomass following the Whitewater-Baldy Fire was a 74% decrease of 3.15 to 0.45 g WM m^{-2} in Sonora sucker at tributary 2 relative to the Miller Fire period. Desert sucker *Pantosteus clarkii* was the only native fish apparently unaffected by wildfire (Table 3.4).

Of the eleven nonnative macro-consumer species encountered, nine experienced significant changes in biomass following one or both wildfires. These changes were most pronounced following the Miller Fire at tributary 1 and canyon 2. Changes at tributary 1 following the Miller Fire resulted from the extirpation of rainbow trout *Oncorhynchus mykiss* (pre-fire = 0.18 g WM m^{-2}) and brown trout *Salmo trutta* (pre-fire = 0.64 g WM m^{-2}) (Table 3.4; Fig. 3.5), which were the only nonnative macro-consumers to occur at this site. Significant biomass decreases at canyon 2 following the Miller Fire occurred for channel catfish *Ictalurus punctatus* (99%; 0.12 to 0.0007 g WM m^{-2}), flathead catfish *Pylodictis olivaris* (67%; 5.19 to 0.81 g WM m^{-2}), and smallmouth bass *Micropterus dolomieu* (85%; 0.34 to 0.05 g WM m^{-2}). Red shiner *Cyprinella lutrensis* biomass also changed at canyon 2 following the Miller Fire, but this species only increased from 0.0004 to 0.007 g WM m^{-2} (Fig. 3.5). The only other site to exhibit changes following the Miller Fire was tributary 2, which had a 94% decrease in biomass of fathead minnow *Pimephales promelas* from 0.002 to 0.0001 g WM m^{-2}. Changes in nonnative

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macro-consumer biomass were fewer following the Whitewater-Baldy Fire, with common carp (pre-fire = 5.78 g WM m^{-2}) and green sunfish (pre-fire = 0.02 g WM m^{-2}) decreasing by 99% and 100%, respectively, at canyon 2, and green sunfish decreasing by 100% at valley 1 (pre-fire = 0.008 g WM m^{-2}). Biomass of virile crayfish, American bullfrog tadpoles, yellow bullhead *Ameiurus natalis*, and western mosquitofish *Gambusia affinis* did not change at any site following either wildfire.

Discussion

By measuring animal biomass across multiple locations through time we quantified effects of and responses to large, consecutive wildfires by multiple native and nonnative taxa, many of which (warmwater fishes, nonnative crayfish and tadpoles) have not been considered in other efforts to characterize impacts of wildfire on aquatic biota. Our findings revealed differential responses by taxa examined, and potentially differential mechanisms driving those responses.

Changes in habitat and basal resource availability were quite pronounced following the Whitewater-Baldy Fire, but were minimal following the Miller Fire. These habitat changes occurred despite most sites having a greater proximity to the Miller Fire compared to the perimeter of the Whitewater-Baldy Fire. The much greater size of the Whitewater-Baldy Fire (3.4 times larger) as well as post-fire hydrological events may explain these habitat changes. Relative to the Miller Fire the monsoon season following the Whitewater-Baldy Fire was much weaker and produced lower magnitude flows. Low-velocity flows that resulted from this monsoon would allow for much greater silt deposition from runoff originating from the burned area, and explain the increase in silt observed across all sites following this wildfire (Beschta and Jackson 1979; Wood and Armitage 1997). This increase in silt may also explain the decrease in chlorophyll *a* concentration observed following the Whitewater-Baldy Fire, as silt deposition has been demonstrated to decrease algal biomass both experimentally and in rivers (Yamada and Nakamura 2002; Izagirre et al. 2009).

Increases in silt and lower algal biomass following the Whitewater-Baldy Fire may also explain the more pronounced decrease in insect biomass following this fire. Infiltration of silt into the interstitial spaces of substrate decreases habitat suitability for many insects that prefer to

live on the undersurface of rocks (Erman and Ligon 1988; Richards and Bacon 1994), as well as interfere with their respiration (Lemly 1982). The insect taxa (Hydropsychidae and Crambidae) that exhibited the largest declines following wildfires both reside on the undersurface of rocks, thus siltation was a likely cause of their declines. In contrast, silt habitats are preferred by many Oligochaetes, thus explaining their lack of response to these habitat changes. Also, algal and macroinvertebrate biomass are positively correlated in the upper Gila River (Whitney et al. 2014), thus perturbations that decrease algal biomass would also be expected to decrease insect biomass. In addition to lower autochthonous resource supplies, insects may be responding to decreased quantity and quality of allochthonous inputs, which wildfires affect via alteration of terrestrial vegetation (Mihuc and Minshall 1995). Lower insect biomass associated with changes in habitat and resource availability are consistent with the findings from Gresswell (1999), wherein wildfire-induced decreases in habitat quality and basal resource availability were suggested to have the most pronounced effects on macroinvertebrate abundance.

Of the taxonomic groups examined native fishes were the most severely impacted by wildfires, with all species, excluding desert sucker, exhibiting marked decreased biomass following wildfires. These decreases were not necessarily related to wildfire-induced habitat changes, as decreases occurred following the Miller Fire despite no changes in habitat. These decreases were spatially-dependent, as upper sites generally exhibited greater decreases following the Miller Fire, whereas lower sites exhibited greater decreases following the Whitewater-Baldy Fire. These results suggested site proximity influences wildfire effects on native fishes. Similarly, Lyon and O'Connor (2008) determined that the impacts of a wildfire on fishes in the Buckland River, Australia decreased with increasing distance from the fire. Hypoxia resulting from ash flows was ascribed as the major reason for fish declines in the Buckland River, the effects of which attenuated downstream as they became diluted from increasing stream size and tributary inputs. Although dissolved oxygen was not measured during the ash flows that followed the Miller and Whitewater-Baldy fires, dead native fishes were found following ash flows from each fire. These fish kills may have resulted from hypoxia, or may have been related to other causes of toxic water chemistry (e.g., ammonium, trace metals, or ferrocyanides) generated by wildfires, which attenuated downstream. These spatial effects were patchy for both wildfires, however, as few decreases were observed in tributary 1 and valley 1 despite other nearby sites (tributary 2, valley 2) exhibiting large decreases. Patchiness of

wildfire effects is a common occurrence (Gresswell 1999), and may allow for rapid recolonization of impacted sites given the Gila River is unfragmented and refuge sites are proximal to severely-impacted sites.

Despite subjection to consecutive wildfires, the biomass of nonnative virile crayfish and American bullfrog tadpoles remained stable throughout the study. These responses contradicted those observed for crayfish and tadpoles of different species occurring in their native range following wildfire. For example, the abundance of Murray crayfish *Euastacus armatus* was severely reduced (81% decrease) following a hypoxic blackwater event in the Murray River of Australia (McCarthy et al. 2014). Although this blackwater event was not caused by a wildfire, the hypoxic conditions it produced were similar to those observed during a wildfire-induced ash flow on the Buckland River Australia that caused freshwater crayfish to exit the stream (Lyon and O'Connor 2008). Furthermore, densities of Rocky Mountain tailed frogs *Ascaphus montanus* in streams subjected to wildfire were only half of those in streams left unaffected (Hossack et al. 2006). These decreases in tadpole density were attributed to elevated temperature and ammonium concentrations caused by the wildfires. These contrasting responses to wildfire of crayfish and tadpoles in their native versus introduced ranges hint that some nonnatives may be more tolerant of harsh environmental conditions imposed by wildfires compared to native species, thus allowing for their successful invasion and persistence (Kolar and Lodge 2001; Marchetti et al. 2004). However, these contrasting responses are for members of the same order belonging to different families, and thus might be related to phylogenetic differences. The limited effect on American bullfrog might be due to the ability of terrestrial adults to withstand poor water quality and rapidly re-invade once conditions improved.   Similarly, the resistance of nonnative virile crayfish to ash flows may be related to the ability of crayfish to exit streams during harsh physicochemical conditions (Lyon and O'Connor 2008). Once outside of the stream crayfish can effectively move to refuge aquatic habitats with less severe abiotic conditions (Grote 1981; Claussen et al. 2000), and could also live terrestrially for several days (Pond 1975) and then re-enter the water once conditions improve. The lack of flushing flows during monsoons following either wildfire makes amphibious capabilities a viable mechanism promoting persistence. Had higher discharge occurred crayfish and bullfrogs persisting terrestrially or in the water may have been displaced.

Nonnative fishes showed their sharpest decreases following the Miller Fire, which was driven by the extirpation of nonnative salmonids in tributary 1. Drastic decreases and extirpations of native and nonnative salmonids following wildfires are well-documented (Propst et al. 1992; Rinne 1996; Rieman et al. 2012), especially when ash flows occur (Bozek and Young 1994). Salmonid extirpation following wildfire is not surprising if hypoxic blackwater conditions occur, as salmonids have among the lowest tolerances of hypoxic conditions of any freshwater fish (Doudoroff and Shumway 1970; Gee et al. 1978). Warmwater nonnative fishes were less impacted by wildfires, and maintained high biomass following wildfire at locations (tributary 2, canyon 1) where native fishes were greatly reduced. Limited nonnative response to wildfires suggests that the traits of successful invaders (habitat generalists; high environmental tolerance; Olden et al. 2006) that allow them to invade habitats may also promote persistence in the presence of severe disturbance (Moyle and Light 1996). Increased monitoring of post-wildfire water quality (concentrations of dissolved oxygen, ammonium, trace metals, total suspended solids, and ferrocyanides), coupled with experimental testing of among-species water quality tolerances are needed to identify mechanisms conferring differential native and nonnative resistance to wildfire.

Wildfire appears to be a plausible explanation for the temporal changes we observed in macroinvertebrate and macro-consumer biomass, as there were minimal differences in flow regime among years. However, we also acknowledge that the cumulative effects of successive years of drought may also be responsible for some changes. For instance, native fish richness and abundance has declined in response to consecutive years of drought in the upper Gila River, a pattern attributed to lower spawning success and greater predation pressure by nonnative piscivores (Propst et al. 2008). Drought might explain declines in native fishes we observed, but drought and wildfire are inextricably linked (Schullery 1989; Swetnam and Betancourt 1998) and thus require a before- after- control impact (BACI) design to fully disentangle their effects. The large size and position of wildfires during our study eliminated this option, however, as no suitable control sites within the Gila River catchment in New Mexico were left unaffected by wildfire. Regardless, several lines of evidence point to wildfire impacts on stream biota, including: the spatial pattern of native fish declines (upper sites decreased following Miller Fire, lower sites decreased following Whitewater-Baldy Fire), the punctuated rather than gradual nature of macroinvertebrate and fish declines, habitat-associated decreases in macroinvertebrate

biomass, and native fishes decreases at locations (tributary 1, valley 1 and 2) where nonnative piscivores were rare (Whitney et al. 2014).

Conclusion

Climate change in southwestern United States is predicted to increase intensity and severity of wildfires (Brown et al. 2004; McKenzie et al. 2004; Moritz et al. 2012) as a result of higher temperatures and longer fire seasons from reduced snowpack (Seager and Vecchi 2010). The effects of climate change will be compounded by decades of fire suppression in the region, which has resulted in elevated fuel loads (Covington and Moore 1994; Hurteau et al. 2013). Results from this study suggest these changes in fire regime will have pronounced negative consequences for native fishes, nonnative salmonids, and some native insects, while leaving native oligochaetes, nonnative crayfish, tadpoles, and many non-salmonid nonnative fishes less affected. Wildfire, at least at the increased extent and scale caused by historical fire suppression and ongoing climate change, thus represents an additional threat to persistence of native fauna in the American Southwest, which are already highly imperiled as a result of dewatering, nonnative species, and range fragmentation (Miller 1961; Minckley and Deacon 1991; Olden and Poff 2005). Native fauna would benefit from management activities that decrease fire size and severity (forest thinning and prescribed burning), but these activities carry their own set of concerns regarding forest management (Bisson et al. 2003; Rieman et al. 2010) and consequences for native fauna (Rieman and Clayton 1997). Activities that maintain the inherent resilience of ecosystems, such as nonnative removal (Propst et al. 2014) and maintenance or restoration of connectivity (Fagan 2002) may be more viable options for ensuring native fauna persistence under a changing fire regime.

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Figure 3.1 Study site locations and wildfire perimeters. Tributary 1 is located on the West Fork and tributary 2 is located on the Middle Fork; canyon 1 and valley 1 are the more upstream sites in their respective regions.
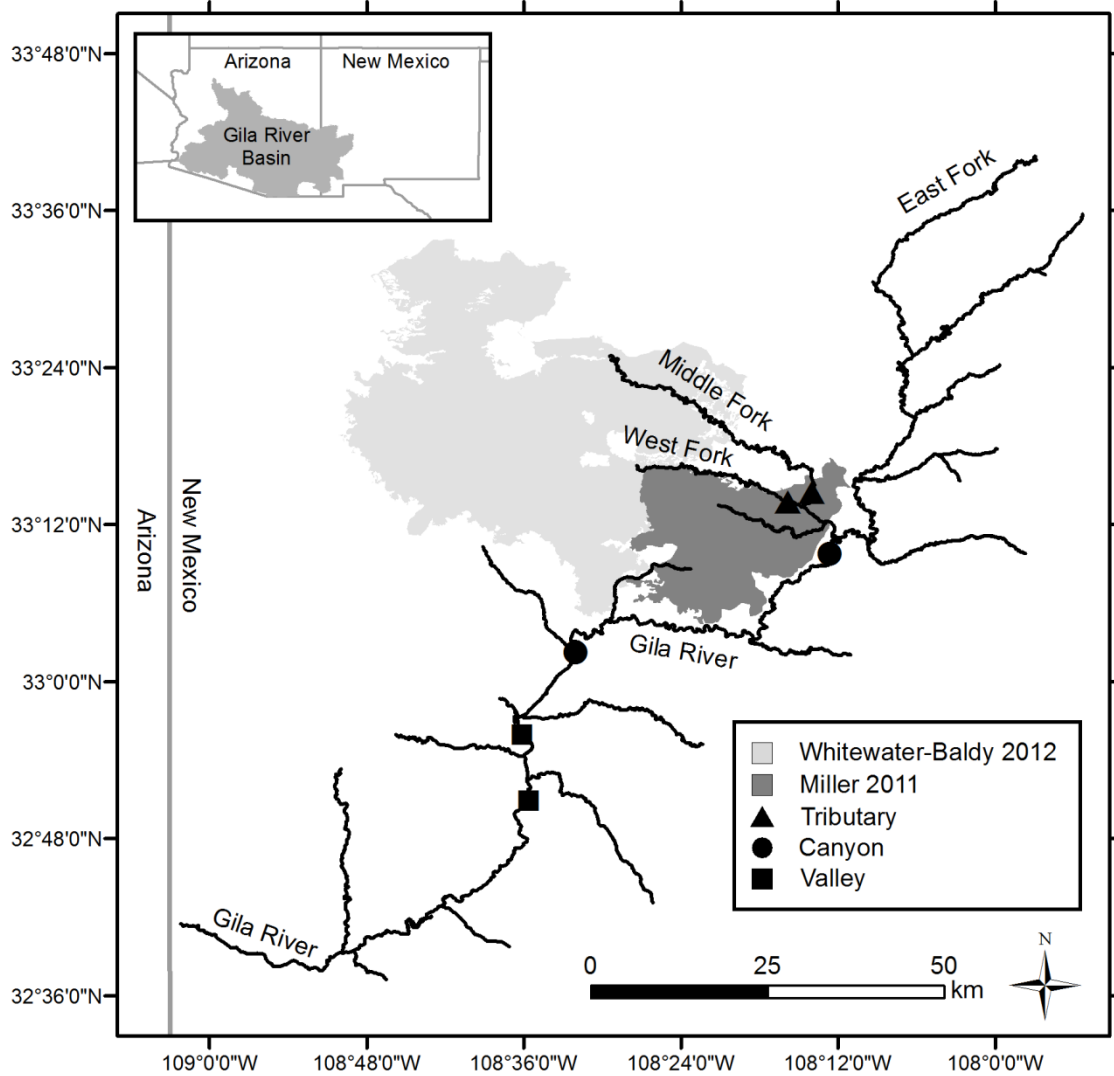
Figure 3.2 Differences in mean percent silt, percent large woody debris (LWD), and chlorophyll *a* concentration across six sites before and after consecutive wildfires in the upper Gila River Basin, NM, USA. See Table 3.3 for statistical results. When only time period is presented then all sites responded similarly. Letters denote differences among time periods within sites, not among sites. Error bars represent one standard deviation (SD). Chlorophyll *a* was $\log_{10}$ transformed. Tri = tributary; Can = canyon; Val = valley.
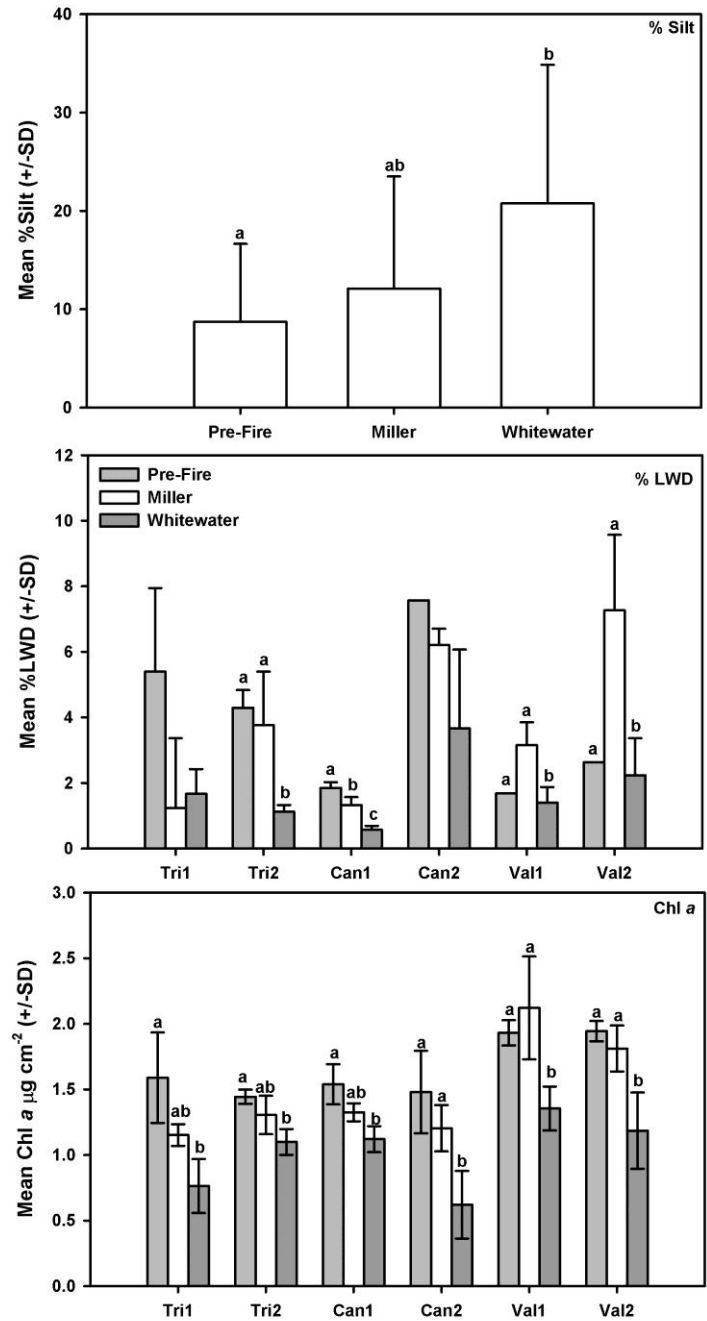
Figure 3.3 Insect families demonstrating significant time period or site by time period responses to consecutive wildfires in the upper Gila River Basin, NM, USA. See Table 3.3 for statistical results. When only time period is presented then all sites responded similarly. Letters denote differences among time periods within sites, not among sites. Error bars represent one standard deviation (SD). All values were $\log_{10}$ transformed. Tri = tributary; Can = canyon; Val = valley. DM = dry mass.
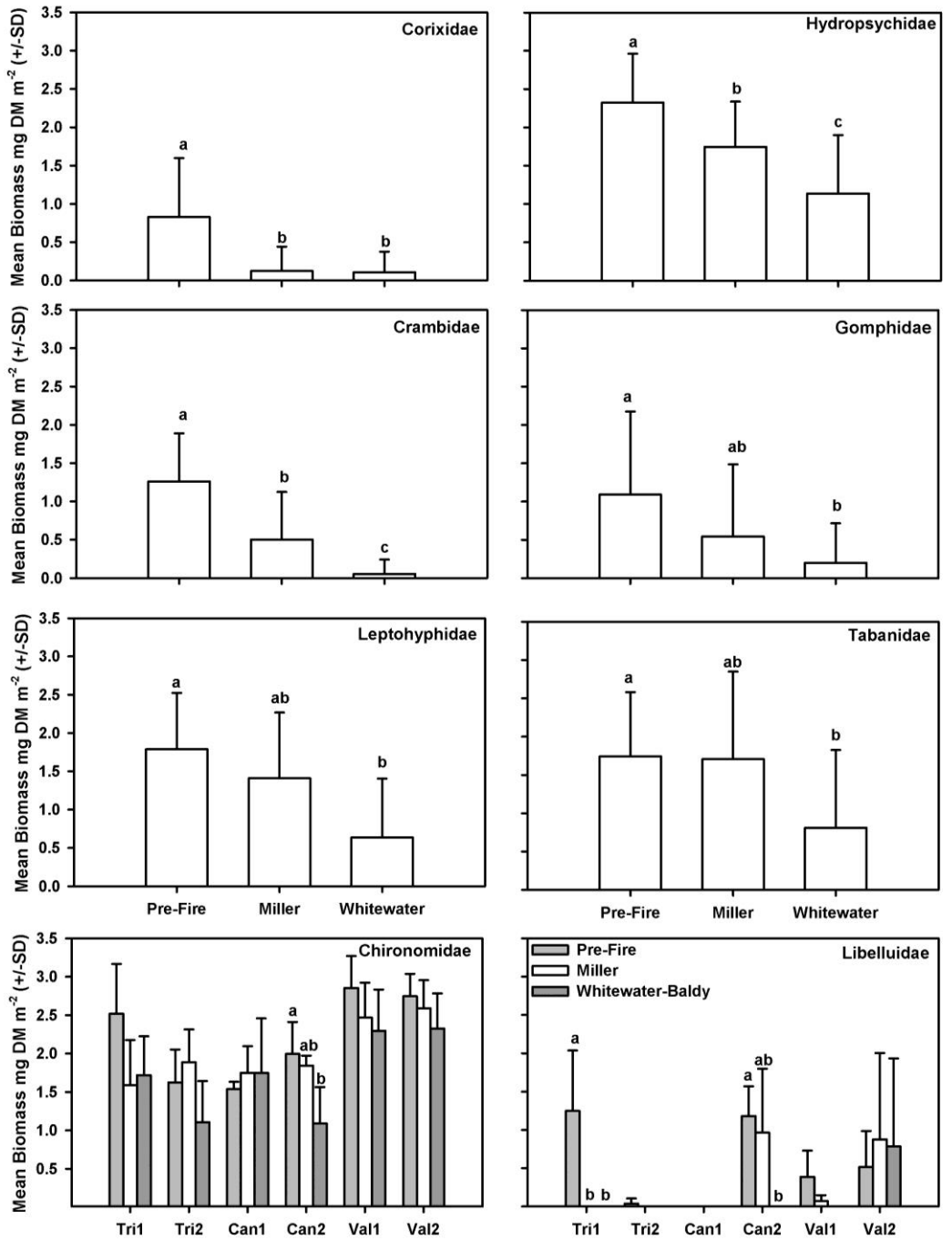
Figure 3.4 Native fishes demonstrating significant site by time period responses to consecutive wildfires in the upper Gila River Basin, NM, USA. See Table 3.3 for statistical results. Letters denote differences among time periods within sites, not among sites. Error bars represent one standard deviation (SD). All values were log_{10} transformed. Tri = tributary; Can = canyon; Val = valley. WM = wet mass.
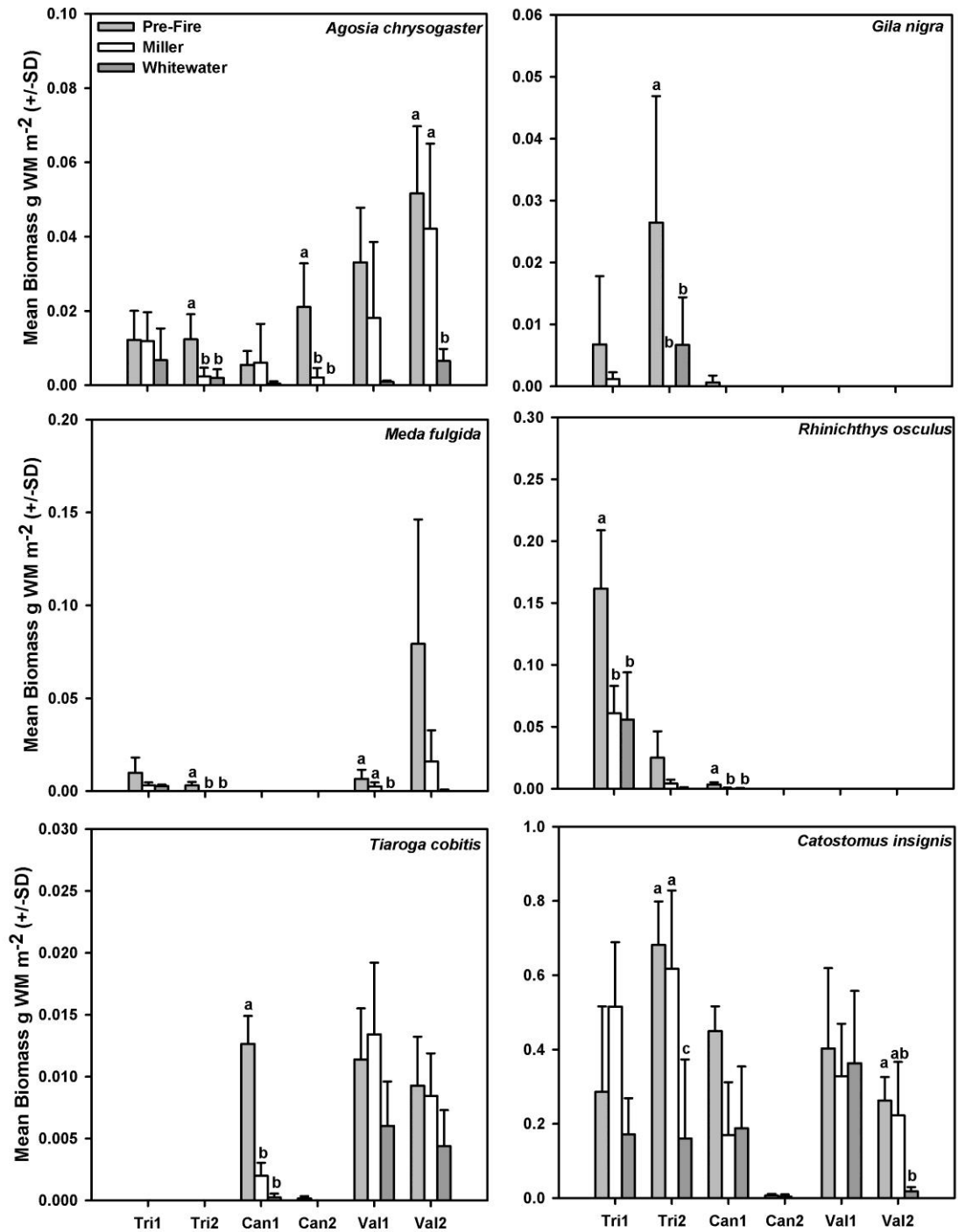
Figure 3.5 Nonnative fishes demonstrating significant site by time period responses to consecutive wildfires in the upper Gila River Basin, NM, USA. See Table 3.3 for statistical results. Letters denote differences among time periods within sites, not among sites. Error bars represent standard deviation (SD). All values were $\log_{10}$ transformed. Tri = tributary; Can = canyon; Val = valley. WM = wet mass.
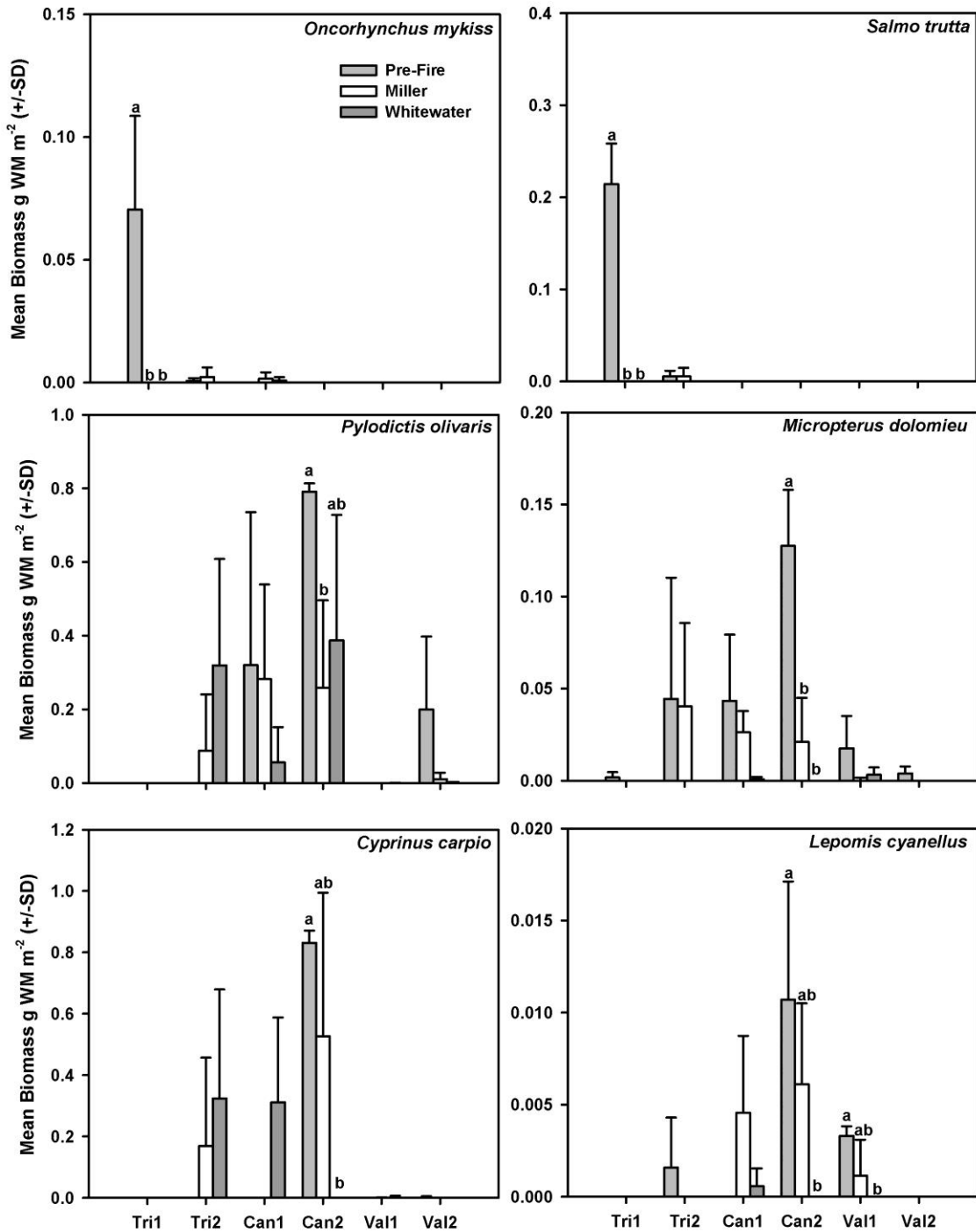
Table 3.1 Study site characteristics. Mean width, and depth were calculated during March, June, and October of 2011-2013, whereas mean annual water temperature was recorded during July 2011-2012 (see Whitney et al. 2014 for detailed methods). Miller and Whitewater Distance are the shortest watercourse distance from a study site to the perimeter of each fire.

Region	Site	Waterbody	Mean Width (m)	Mean Depth (m)	Mean Annual Temperature (°C)	Miller Distance (km)	Whitewater Distance (km)
Tributary	1	West Fork	5.1	0.18	11.6	0.0	21
	2	Middle Fork	8.1	0.35	15.6	0.0	24
Canyon	1	Mainstem	10.6	0.36	14.8	1.3	32
	2	Mainstem	11.5	0.43	14.9	19	10
Valley	1	Mainstem	12.9	0.27	15.7	35	25
	2	Mainstem	12.1	0.32	16.2	46	38

Table 3.2 Study sampling design with timing of sampling for each response variable. An "—" indicates a variable was not sampled at any site, an "X" indicates a variable was sampled across all sites, and "Upper" indicates a variable was only sampled at the three upper sites (tributary 1 and 2 and canyon 1).

Response Variable	Pre-Fire			After Miller			After Whitewater-Baldy		
	October 2010	March 2011	June 2011	October 2011	March 2012	June 2012	October 2012	March 2013	June 2013
% Silt	—	—	X	X	X	X	X	X	X
% Large Wood	—	—	X	X	X	X	X	X	X
Chlorophyll *a*	X	X	X	X	X	X	X	X	X
Macroinvertebrates	X	X	X	X	X	X	X	X	X
Macro-consumers	X	Upper	X	X	X	X	X	X	X

Table 3.3 Flow regime characteristics for the three study periods as well as for the period of record. MDD= mean daily discharge. Spring was defined as 1 March – 30 June; summer was defined as 1 July – 30 September.

Time Period	Dates	Annual MDD $m^3 \, s^{-1}$	Mean Spring MDD $m^3 \, s^{-1}$	Summer CV	Base Flow
Pre-Fire	July 2010-June 2011	2.04	1.24	0.74	0.26
Miller	June 2011-May 2012	2.56	2.12	1.49	0.21
Whitewater	June 2012-May 2013	2.07	2.35	0.48	0.18
Long-Term	June 1928-May 2013	4.43	5.02	0.46	0.27

Table 3.4 P-values from repeated measures analysis of variance (rm-ANOVA) investigating the interactive effects of site and time period. Significant (P ≤ 0.05) or marginally-significant (P ≤ 0.10) time period or site by time period interactions are in bold. Post-hoc analyses for significant site effects were not examined. LWD = large woody debris; WW = Whitewater-Baldy Fire; Tri = tributary; Can = canyon; Val = valley. Fish species codes are first three letters of the genus and first three letters of the specific epithet; see Table 3.4 for complete names.

Response Variable	Site	Time	Site X Time	Time Response	Sites Affected
% Silt	<0.001	**0.088**	0.164	WW>Before	All
% LWD	<0.001	**0.023**	0.010	Miller<Before	Can1
				WW<Miller	Tri2,Can1,Val1,Val2
Chlorophyll *a*	<0.001	**0.003**	**0.024**	WW<Before	All Sites
				WW<Miller	Can2,Val1,Val2
Oligochaeta	<0.001	0.890	0.568		
Gomphidae	0.250	**0.033**	0.572	WW<Before	All
Libellulidae	0.004	0.153	**0.093**	Miller<Before	Tri1
				WW<Before	Can2
Calopterygidae	0.637	0.360	0.568		
Coenagrionidae	0.275	0.678	0.520		
Baetidae	0.016	0.775	0.820		
Ephemerellidae	0.246	0.753	0.949		
Leptohyphidae	0.002	**0.047**	0.272	WW<Before	All
Nemouridae	0.338	0.440	0.540		
Perlodidae	0.472	0.458	0.451		
Taeniopterygidae	0.355	0.475	0.578		
Corixidae	0.023	**0.044**	0.413	Miller<Before	All
Hebridae	0.044	0.574	0.777		
Naucoridae	0.337	0.205	0.420		
Veliidae	0.670	0.926	0.359		
Corydalidae	0.077	0.278	0.996		
Glossosomatidae	0.004	0.154	0.248		
Helicopsychidae	<0.001	0.261	0.452		
Hydropsychidae	0.160	**0.034**	0.160	Miller<Before	All
				WW<Miller	All
Hydroptilidae	0.213	0.440	0.744		
Crambidae	0.117	**0.004**	0.212	Miller<Before	All
				WW<Miller	All
Dryopidae	0.062	0.169	0.810		
Elmidae	<0.001	0.590	0.262		
Psephenidae	0.098	0.573	0.417		
Chironomidae	<0.001	0.268	**0.056**	WW<Before	Can2
Simuliidae	0.796	0.121	0.546		

Response Variable	Site	Time	Site X Time	Time Response	Sites Affected
Tabanidae	0.002	**0.003**	0.264	WW<Before	All
AGOCHR	<0.001	0.020	**0.015**	Miller<Before	Tri2,Can2
				WW<Before	Val2
GILNIG	0.003	0.002	**0.034**	Miller<Before	Tri2
MEDFUL	0.001	0.092	**0.007**	Miller<Before	Tri2
				WW<Before	Val1
RHIOSC	<0.001	0.022	**<0.001**	Miller<Before	Tri1,Can1
TIACOB	<0.001	0.007	**<0.001**	Miller<Before	Can1,
CATINS	<0.001	0.032	**0.014**	WW<Miller	Tri2,
				WW<Before	Tri2,Val2
PANCLA	<0.001	0.520	0.294		
ORCIVR	<0.001	0.868	0.999		
LITCAT	0.044	0.691	0.561		
CYPCAR	<0.001	0.837	**<0.001**	WW<Before	Can2
CYPLUT	0.014	0.010	**0.019**	Miller>Before	Can2
				WW<Miller	Can2
PIMPRO	0.025	0.836	**0.083**	Miller<Before	Tri2
AMENAT	<0.001	0.384	0.450		
ICTPUN	0.036	0.056	**0.026**	Miller<Before	Can2
PYLOLI	<0.001	0.420	**0.015**	Miller<Before	Can2
ONCMYK	<0.001	0.015	**<0.001**	Miller<Before	Tri1
SALTRU	<0.001	<0.001	**<0.001**	Miller<Before	Tri1
GAMAFF	0.458	0.408	0.448		
LEPCYA	<0.001	0.020	**0.006**	WW<Before	Can2,Val1
MICDOL	<0.001	0.009	**0.002**	Miller<Before	Can2

Table 3.5 List of taxa encountered during the study and indication whether their response was statistically analyzed.

Phylum	Class	Order	Family	Scientific Name	Common Name	Statistically Analyzed
Platyhelminthes	**Turbellaria**				flatworm	No
Nematoda					roundworm	No
Nematomorpha					horsehair worm	No
Nemertea					ribbon worm	No
Annelida	**Oligochaeta**				segmented worm	Yes
	Clitellata				leeches	No
Mollusca	**Gastropoda**				snails, limpets	No
	Bivalvia			*Corbicula fluminea*	Asian clam	No
Arthropoda	**Arachnida**				water mites	No
	Branchiopoda				cladocerans	No
	Maxillopoda				copepods	No
	Ostracoda				seed shrimp	No
	Malacostraca				scuds	No
		Decapoda	Cambaridae	*Orconectes virilis*	virile crayfish	Yes
	Insecta	**Odonata**	Calopterygidae		damselfly nymph	Yes
			Coenagrionidae		damselfly nymph	Yes
			Gomphidae		dragonfly nymph	Yes
			Libellulidae		dragonfly nymph	Yes
		Ephemeroptera	Baetidae		mayfly nymph	Yes
			Ephemerellidae		mayfly nymph	Yes
			Heptageniidae		mayfly nymph	No
			Isonychiidae		mayfly nymph	No
			Leptohyphidae		mayfly nymph	Yes
			Leptophlebiidae		mayfly nymph	No
			Siphlonuridae		mayfly nymph	No
		Plecoptera	Leuctridae		stonefly nymph	No
			Nemouridae		stonefly nymph	Yes
			Perlodidae		stonefly nymph	Yes
			Taeniopterygidae		stonefly nymph	Yes
		Hemiptera	Belostomatidae		giant water bug	No
			Corixidae		water boatmen	Yes
			Gerridae		water strider	No
			Hebridae		velvet water bug	Yes
			Macroveliidae		shore bug	No
			Naucoridae		creeping water bug	Yes
			Notonectidae		backswimmer	No
			Veliidae		riffle bug	Yes

Phylum	Class	Order	Family	Scientific Name	Common Name	Statistically Analyzed
Arthropoda	Insecta	Megaloptera	Corydalidae		hellgrammite	Yes
		Trichoptera	Apataniidae		caddisfly larvae	No
			Glossosomatidae		caddisfly larvae	Yes
			Helicopsychidae		caddisfly larvae	Yes
			Hydropsychidae		caddisfly larvae	Yes
			Hydroptilidae		caddisfly larvae	Yes
			Lepidostomatidae		caddisfly larvae	No
			Leptoceridae		caddisfly larvae	No
			Limnephilidae		caddisfly larvae	No
			Philopotamidae		caddisfly larvae	No
			Polycentropodidae		caddisfly larvae	No
			Psychomyiidae		caddisfly larvae	No
		Lepidoptera	Crambidae		moth larvae	Yes
		Coleoptera	Carabidae		beetle larvae	No
			Curculionidae		beetle larvae	No
			Dryopidae		beetle larvae	Yes
			Dytiscidae		beetle larvae	No
			Elmidae		beetle larvae	Yes
			Gyrinidae		beetle larvae	No
			Heteroceridae		beetle larvae	No
			Hydrophilidae		beetle larvae	No
			Psephenidae		beetle larvae	Yes
			Ptilidae		beetle larvae	No
			Scirtidae		beetle larvae	No
			Staphylinidae		beetle larvae	No
			Tenebrionidae		beetle larvae	No
		Diptera	Athericidae		fly larvae	No
			Ceratopogonidae		fly larvae	Yes
			Chironomidae		fly larvae	Yes
			Dixidae		fly larvae	No
			Dolichopodidae		fly larvae	No
			Empididae		fly larvae	No
			Ephydridae		fly larvae	No
			Psychodidae		fly larvae	No
			Simuliidae		fly larvae	Yes
			Stratiomyidae		fly larvae	No
			Tabanidae		fly larvae	Yes
			Tanyderidae		fly larvae	No
			Tipulidae		fly larvae	No

Phylum	Class	Order	Family	Scientific Name	Common Name	Statistically Analyzed
Chordata	**Amphibia**	**Anura**	Ranidae	*Lithobates catesbeianus*	American bullfrog	Yes
	Native	**Cypriniformes**	Cyprinidae	*Agosia chrysogaster*	longfin dace	Yes
	Actinopterygii			*Gila nigra*	headwater chub	Yes
				Meda fulgida	spikedace	Yes
				Rhinichthys osculus	speckled dace	Yes
				Tiaroga cobitis	loach minnow	Yes
			Catostomidae	*Catostomus insignis*	Sonora sucker	Yes
				Pantosteus clarkii	desert sucker	Yes
		Salmoniformes	Salmonidae	*Oncorhynchus gilae*	Gila trout	No
	Nonnative	**Cypriniformes**	Cyprinidae	*Cyprinus carpio*	common carp	Yes
	Actinopterygii			*Cyprinella lutrensis*	red shiner	Yes
				Pimephales promelas	fathead minnow	Yes
		Siluriformes	Siluridae	*Ameiurus natalis*	yellow bullhead	Yes
				Ictalurus punctatus	channel catfish	Yes
				Pylodictis olivaris	flathead catfish	Yes
		Salmoniformes	Salmonidae	*Oncorhynchus mykiss*	rainbow trout	Yes
				Salmo trutta	brown trout	Yes
		Cyprinodontiformes	Poeciliidae	*Gambusia affinis*	western mosquitofish	Yes
		Perciformes	Centrarchidae	*Lepomis cyanellus*	green sunfish	Yes
				Micropterus dolomieu	smallmouth bass	Yes
				Micropterus salmoides	largemouth bass	No

Chapter 4 - Metapopulation analysis indicates that native and nonnative fishes respond differently to wildfire in a desert stream

Abstract

Ash flows and flooding associated with forest fires represent important but understudied sources of disturbance for fish populations in forested regions of the American Southwest. Knowledge concerning these disturbances is especially limited for larger streams where warmwater species dominate fish assemblages. Fire-related disturbances can have disproportionate negative effects on nonnative fishes, although this hypothesis has only been tested for coldwater salmonids. The objective of our research was to contrast effects of broad-scale forest fires followed by extreme flooding on metapopulations of native and nonnative fishes in the upper Gila River of southwest New Mexico. Probabilities of occupancy, colonization, and local extinction of fishes were calculated across sites before and during disturbance, and were also measured across a broader spatial scale during disturbance to identify potential refuge locations. Occupancy was higher for native fishes relative to nonnatives, but we found that multiple forest fires and flood events increased extinction probabilities of all native species (and especially imperiled ones). Rather than being uniformly negative, responses of nonnative species to forest fires were mixed. Extinction probabilities of nonnative coldwater salmonids increased during disturbance, while those of several warmwater species remained unchanged or decreased. Undisturbed habitats were poor refugia for most native species, as they were previously comprised by anthropogenic activities (nonnative piscivore introductions, dewatering, and fragmentation). Despite exposure to multiple disturbances, sites located in large tributary and valley reaches were consistently occupied by native species, suggesting these habitats provide refugia from which colonists can repopulate other habitats. The uniformly negative response by native fishes to disturbance may be related to the unusual size and severity of wildfire and flood disturbance resulting from fire suppression and climate change. We suggest that management actions (forest thinning; prescribed burning) that restore a more natural disturbance regime of small and less severe fires coupled with habitat remediation activities (nonnative removal; decreased water withdrawal; improved connectivity) might diminish extinction risk for native fishes.

Introduction

The size, severity, and frequency of forest fires in the southwestern United States have increased in recent decades (Westerling et al., 2006). The frequent, low-intensity surface fires that once characterized southwestern fire regimes are being supplanted by large, stand-replacing crown fires that were historically a rare component of the landscape (Swetnam and Baisan, 1996; Margolis and Balmat, 2009; Swetnam and Brown, 2011). Changes in fire regime are related to increased fuel loads that resulted from a century of fire suppression and recent (i.e., post-1985) climatic changes associated with higher temperatures and earlier snowmelt (Covington and Moore, 1994; Westerling et al., 2006; Hurteau et al., 2013). Such changes are predicted to both accelerate and intensify in coming decades (Brown et al., 2004; McKenzie et al., 2004), as climate change projections indicate increased temperatures, reduced snowpack, and earlier snowmelt in the region (Seager et al., 2007; Seager and Vecchi, 2010; Kunkel and Redmond, 2012). Managing forests to ameliorate effects of climate-related changes to the fire regime and thus regional terrestrial and aquatic biodiversity will be a central conservation challenge during the 21st century (Hurteau et al., 2013).

Forest fires have numerous direct and indirect effects on abiotic components of stream ecosystems, which can impact fish populations (Gresswell, 1999; Bisson et al., 2003; Rieman et al., 2012). Direct effects occur when a wildfire burns the riparian area of a stream, increasing temperature (Minshall and Brock, 1991; Hitt, 2003), pH (Cushing and Olson, 1963), and phosphorus and nitrogen concentrations (Bayley et al., 1992; Earl and Blinn, 2003). These effects can be catastrophic for species highly-sensitive to changes in temperature and water quality such as salmonids (Howell, 2006), but are generally of a short duration and limited to smaller streams because increasing water volume buffers changes in water quality (Minshall and Brock, 1991; Rieman et al., 1995; Rieman et al., 2012).

Indirect effects of forest fires result from alteration of catchment vegetation and soil characteristics. Indirect effects include increased temperature and sunlight (Johnson and Jones, 2000; Dunham et al., 2007), altered inputs of large woody debris (May and Gresswell, 2003), increased sedimentation (Benda et al., 2003), and greater discharge (Legleiter et al., 2002). These habitat changes can have negative, neutral, or positive effects on fish populations, with the degree of impact dependent upon an interaction between post-fire runoff and the size and severity of the fire, the size of the stream, and the streams spatiotemporal proximity to the

wildfire (Rieman et al., 2012). In Fig. 4.1, we summarize the context dependency of wildfire effects on fish populations. For example, an extremely severe form of indirect wildfire effect occurs when moderate to heavy runoff from a recently burned catchment flows into a stream, resulting in ash flows, debris torrents, and sediment slugs. The severity of ash flows is dictated by an interaction between precipitation, catchment relief, and soil characteristics, with the most severe ash flows occurring after moderate precipitation in a high-relief catchment with hydrophobic soils (Rieman et al., 2012). Ash flows from moderate runoff result in hypoxia and lethal concentrations of trace metals, ferrocyanides, and residual fire retardants (Novak and White, 1990; Miller et al., 2003; Lyon and O'Connor, 2008). These ash flows may result in extirpation of fish (Propst et al., 1992; Rinne, 1996; Lyon and O'Connor, 2008). Ash flows from heavier runoff may have less toxic water chemistry from a dilution effect, but can produce severe flooding and have moderate effects on fish. Ash flows are especially common in streams of the American Southwest, where the monsoon season (July-September) directly follows the fire season (May-June; Rinne, 1996; Adams and Comrie, 1997).

The preponderance of information concerning the effects of wildfire on stream habitats and fishes comes from cold headwater streams that are proximal to the fire perimeter and are primarily inhabited by native or nonnative salmonids (Gresswell, 1999; Bisson et al., 2003; Rieman et al., 2012). Although these studies have greatly enhanced our knowledge regarding the effects of wildfire on stream fishes, major questions remain concerning the response of streams more distal from the fire perimeter that are inhabited by warmwater fishes, which may exhibit different responses to forest fires given their different temperature and water quality tolerances (Olden et al., 2006). This information could be important to conservation of imperiled fishes in the American Southwest, where the majority of native species are non-salmonids living in cool and warmwater systems (Olden et al., 2006). Similarly, numerous nonnative warmwater fishes now inhabit Southwestern streams, where they generally outnumber native species in terms of richness by two to one (Strecker and Olden, 2014).

Of special interest to forest and fisheries managers are responses of native and nonnative fishes to changes wrought by forest fires. Dunham et al. (2003) hypothesized that because nonnative fishes may lack evolutionary experience with forest fires and ash flows, their populations could be more negatively affected than native species. Native fish adaptations to wildfire generally promote resilience rather than resistance, and include complex life history

strategies with mixed migratory behaviors and overlapping generations, both of which allow for rapid recolonization by natives from unburned reaches (Rieman et al., 1995). Alternatively, forest fires could conceivably have greater negative impacts on native fish populations and fewer on nonnatives, as fire-related habitat degradation (e.g., sedimentation, thermal stress, eutrophication, and hypoxia), when resulting from anthropogenic activities (e.g., logging, mining, and agriculture), is associated with increased invasion success of nonnatives (Moyle and Light, 1996; Dunham et al., 2003). Further, if biotic resistance by native communities is responsible for limiting nonnative spread, disturbances that decrease native populations could tip the balance towards nonnative success, even if environmental conditions return to pre-disturbance values (Dunham et al., 2003). Finally, depleted dissolved oxygen concentrations and increased concentrations of toxic compounds (e.g. ferrocyanide, trace metals, and fire retardants) resulting from ash flows may negatively impact both natives and nonnatives equally, as few species have the ability to tolerate such harsh abiotic conditions (Minshall et al., 1997; Barber et al., 2003; Lyon and O'Connor, 2008). Determining the influence of fire-related disturbance on native and nonnative extinction risk has important management implications, given that humans can partially control these disturbances via fire suppression, forest thinning, and prescribed burning (Arkle and Pilliod, 2010).

Post-fire responses of native and nonnative fish populations to ash flows and flooding are expected to be related to their metapopulation dynamics (Gotelli and Taylor, 1999a; Taylor and Warren, 2001; Vaughn, 2012); specifically probabilities of occupancy, colonization, and extinction. Because these probabilities operate in currencies of interest to conservation biology (proportion of sites occupied, local extinction risk, recolonization potential following local extinction) they provide a promising avenue for investigating interactive effects of disturbance and nonnatives on native metapopulations. However, metapopulation dynamics also respond spatially to variation in habitat characteristics, with colonization and occupancy increasing and extinction decreasing with habitat size, quality, and connectivity (Schlosser, 1987; Gotelli and Taylor, 1999a; Taylor and Warren, 2001). Spatial habitat heterogeneity and temporal disturbances govern important spatial processes, including source-sink dynamics and rescue effects (Brown and Kodric-Brown, 1977; Dunning et al., 1992; Schlosser, 1994) that, in turn, dictate local population resilience (i.e. recovery time following disturbance; Hanski, 1999).

Recovery rates are also related to species-specific traits and local abundances in the metapopulation (Gotelli and Taylor, 1999b; Hitt and Roberts, 2012). For example, vagile species, abundant species, or species with more populations may be more resilient following disturbance (Albanese et al., 2009; Stoll et al., 2014), and species with larger body size and greater swimming performance may be resistant to disturbances such as flooding because they can relocate more easily (Minckley and Meffe, 1987). A thorough understanding of interactions among disturbance and metapopulation dynamics of native and nonnative fishes thus requires documentation of probabilities in habitats of varying characteristics and community composition (Dunham et al., 2003). This information also enables identification of potential refuge habitats.

We estimated probabilities of occupancy, local extinction, and recolonization to investigate responses of native and nonnative fishes to extreme wildfire and flood disturbance in the upper Gila River Basin of southwest New Mexico in habitats of varying characteristics and community composition. Our specific objectives were to 1) test the hypothesis that metapopulation probabilities of native and nonnative fishes respond differently to forest fires; 2) compare the impacts of three forest fires on local extinction of native and nonnative fishes; and 3) identify potential source populations that could aid in native species recovery following disturbance. Given their limited evolutionary history with high-intensity wildfire, we predicted that nonnative occupancy and colonization would decrease while extinction would increase following these disturbances, whereas the metapopulation probabilities of native fishes were predicted to remain unchanged (Lytle and Poff, 2004; Waples et al., 2008). Further, wildfires of greater size and severity were predicted to increase likelihood of extinction for both native and nonnative fishes. Finally, habitats receiving minimal impact (i.e., downstream, greater water volume, or in unburned tributaries) from wildfire were predicted to maintain high occupancy and low extinction of native fishes, and thus serve as potential sources for populating decimated habitats.

Methods

Study Area

Our study was conducted in the upper Gila River basin of southwestern New Mexico (Fig. 4.2). Much of the watershed is managed by the United States Forest Service or Bureau of Land Management, but water diversions downstream of the Mogollon Creek-Gila River

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confluence create a gradient of anthropogenic habitat alteration. The stream network was partitioned into five habitat types according to stream size, dominant features of the catchment, and degree of anthropogenic habitat alteration. Between two and five study sites were on each of five Gila River habitats over an 898 m elevation gradient (Table 4.1). Habitat types included small tributaries (n=4 sites), large tributaries (n=5 sites), canyon-bound mainstem (n=3 sites), low modification valley mainstem (n=2 sites), and high modification valley mainstem (n=2 sites). Small tributary, large tributary, and canyon habitats were relatively pristine, whereas anthropogenic activities in valley habitats results in increased nitrogen concentrations and diminished discharge (Whitney et al., 2014; Fig. 4.3).

Forest types in the watershed included high elevation (≥2,440m above sea level [a.s.l.]) mixed conifer forests (Douglas-fir *Pseudotsuga menziessi*; southwestern white pine *Pinus strobiformis*; white fir *Abies concolor*), mid-elevation (1675-2590m a.s.l.) pine forests (ponderosa pine *Pinus ponderosa*; Gambel oak *Quercus gambelii*; *Juniperus* spp.), lower elevation (1220-2285m a.s.l.) woodlands (*Pinus* spp.; *Juniperus* spp.; *Quercus* spp.), and grasslands or Chihuahua Desert occurring at the lowest elevations (1220-1370m and ≤ 1220m a.s.l., respectively). Riparian forests were generally composed of cottonwood (*Populus* spp.), willow (*Salix* spp.), and sycamore (*Platanus* spp.) species regardless of elevation. The four small tributary sites were located on 1st or 2nd order streams in a mountainous landscape with catchments composed primarily of mid to high elevation forests. The five large tributary sites were on 2nd and 3rd order streams and also occurred in a mountainous landscape with middle to high elevation forests. The three canyon-bound sites were on the 4th order Gila River mainstem in the Upper Box canyon, which had a narrow riparian corridor with steep canyon walls and a riverine landscape similar to that of the small and large tributary sites. Canyon 1 and Canyon 3 delimited the up- and downstream points of the Upper Box Canyon. The low modification valley mainstem habitat began where the canyon-bound Gila River flows onto the low-gradient, low-elevation Cliff-Gila valley with cultivated fields and pasture on the adjacent floodplain, minimal riparian forest, and sparse human settlement. From there, it flowed through the Middle Box canyon that began 7.3 river kilometers (rkm) downstream of the low modification Valley 2 site and ended 5.7 rkm above the upstream high modification valley site. Sites in the high modification valley occurred in the Chihuahua Desert and had greater anthropogenic habitat alteration relative to low modification valley sites. Consequently, complete drying of sites often

occurred during peak irrigation demand (Fig. 4.3). The most downstream site was located just below Sunset Canal diversion dam (dam height ~ 3m). Below Sunset Diversion, the Gila River was frequently dry.

Chronology of Natural Disturbance

During the course of our study (June 2008 through October 2013) a series of extreme natural disturbances occurred. From 17 April 2011 through 6 June 2011, the Miller Fire burned 35,950 hectares (ha) in the Little Creek, Turkey Creek, West Fork Gila River, and Middle Fork Gila River drainages (Fig. 4.2). Fire-generated ash was washed through these tributaries to the mainstem Gila River during a moderately strong monsoon season (mean daily discharge [MDD] in the unmodified canyon reach during 01 July- 30 Sept= 2.72 m^3 s^{-1}; maximum MDD= 31.7 m^3 s^{-1}) that began 48 days after the fire (Fig. 4.3a). In the following year, during 9 May through 23 July, the largest wildfire in New Mexico history (Whitewater-Baldy Fire) burned 120,535 ha in the West Fork, Middle Fork, Turkey Creek, and Mogollon Creek drainages.   Ash from this wildfire was dispersed to downstream reaches during a weak monsoon (MDD=1.81 m^3 s^{-1}; max MDD= 5.24 m^3 s^{-1}) that began on 4 July while the fire was still active. During 7 June – 11 July 2013 the Silver Fire burned 56,132 ha that included Black Canyon and lower East Fork drainages. This period of disturbance concluded in September 2013 with an extremely strong monsoon season (MDD= 25.3 m^3 s^{-1}; max MDD= 351.1 m^3 s^{-1}), which caused severe flooding exacerbated by a denuded upper watershed, and the third largest recorded discharge (815 m^3 s^{-1}) on the Gila River (Fig. 4.3a).   All sites, except large tributary 1 and small tributary 4, were visibly affected by this large flow event. We expected impacts to be most severe in small tributaries and that impacts would attenuate downstream as increased water volume and distance from fire increased dilution of entrained ash and fine sediments (Fig. 4.1; Fig. 4.4).

Fish Sampling

We used two datasets to characterize metapopulation responses of native and nonnative fishes to variation in disturbance, habitat characteristics, and community composition. The first dataset (hereinafter the 'disturbance' dataset) included samples taken from six sites every June and October during 2008-2011 (pre-disturbance; n=6 sampling occasions) and 2011-2013 (disturbance; n=6 sampling occasions) from sites located in large tributary, canyon, and low modification valley habitats (Table 4.1). The temporal sampling extent (5.5 years) was greater

than the age of maturity for all fish species in the upper Gila River (0.1 - 4.5 years [Olden et al., 2006]) and included sufficient time for recruitment and reproduction by at least one generation of each species, thus providing an adequate representation of temporal dynamics (Connell and Sousa, 1983). Further, our sampling preceded and followed major changes in the flow regime and fish population cycles (i.e. June sample quantified survival following spring snowmelt and spawning but preceded summer monsoon while the October sample followed summer monsoon and provided an estimate of spawning success; Fig. 4.3) that influenced metapopulation probabilities in the upper Gila River (Propst et al., 2008; Stefferud et al., 2011; Gido et al., 2013). This sampling interval allowed our estimated metapopulation probabilities to adequately approximate actual system dynamics (Diamond and May, 1977; Clark and Rosenzweig, 1994; Taylor and Warren, 2001). To obtain broader-scale evaluation of potential refuge habitats, the second dataset (hereinafter the 'refuge' dataset) included samples taken from 16 sites every March, June, and October during the period of disturbance in 2012-2013 (n=6 sampling occasions). Refuge sites encompassed the entire suite of habitat types and disturbance frequencies found in the upper Gila River, and were expected to enable identification of important source habitats that might aid in post-disturbance recovery. Fishes were sampled with single pass backpack electrofishing with 1-2 dipnetters and seining (4.6 x 1.2m, 3.2mm mesh) in 4-6 pool and riffle mesohabitats at each site. In addition, to estimate species detection probabilities, two passes were made at each of the disturbance dataset sites between June 2008 and June 2011 (n=7 sampling occasions). Identical methods were used on each pass, with the second pass occurring 12-24 hours after the first. To prevent movement into or out of sites between the two passes by larger more-mobile individuals, block nets (4 cm mesh) were deployed at the up- and downstream end of each site prior to the first pass.

Metapopulation Calculation

Metapopulation probabilities were calculated for each fish species following methods of Gotelli and Taylor (1999a), and included probability of occupancy (p_o: number of samples occupied/total number of samples), colonization (p_c: number of colonization events/number of colonization opportunities), and extinction (p_e: number of extinction events/number of extinction opportunities). A colonization event was defined as a site going from unoccupied to occupied between two consecutive time periods, and an extinction event occurred when a site went from

occupied to unoccupied between two consecutive time periods. By definition, colonization events cannot occur if the site is always occupied, and extinctions cannot occur if the site is never occupied. Colonization and extinction opportunities were the number of times a site was unoccupied or occupied, respectively. These probabilities were calculated for the disturbance dataset during June 2008 through October 2010 (pre-disturbance values) and June 2011 through October 2013 (disturbance values), for the refuge dataset during March 2012 through October 2013, and as an overall weighted-average for each species across sites and sample periods for both datasets.

Detection Probabilities

Because our sampling design consisted of a single pass for the majority of samples our analysis assumed that detection probabilities were sufficiently high so that naïve and detection-corrected metapopulation probabilities do not differ. To assess the validity of this assumption we calculated robust-design detection and occupancy probabilities (MacKenzie et al., 2003) using the 2-pass samples collected across the disturbance sites during 2008-2011 using the unmarked package (Fiske and Chandler, 2011) in program R version 2.13.0 (R Development Core Team, 2011). Detection-corrected occupancy estimates were compared to naïve occupancy estimates calculated over the same time period with a t-test and Pearson correlation coefficient to evaluate if conclusions differed when accounting for imperfect detection. If significant differences were found between naïve and detection-corrected estimates we adjusted our presence-absence matrix to account for imperfect detection. Otherwise, we used naïve estimates. We note that naïve estimates are preferred because they required no assumptions concerning the likelihood of detection at locations where that probability was not calculated.

Data Analysis

Statistical analyses were performed in R version 2.13.0 (R Development Core Team, 2011). Results were considered statistically significant at $\alpha \leq 0.05$ and marginally significant at $\alpha \leq 0.10$. Using the disturbance dataset we evaluated the hypothesis that natives and nonnatives responded differently to disturbance by comparing metapopulation probabilities using generalized linear models (GLMs). For this test, binomial distribution of error variance and analysis of deviance with interactive effects of origin (native or nonnative) and disturbance (pre- or intra-) (Crawley, 2007) were implemented, unless overdispersion was present (residual

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deviance >> residual degrees of freedom). In that case, we used the quasibinomial error distribution instead of the binomial (Crawley, 2007). Analysis of deviance and the binomial or quasibinomial error distribution were chosen because the response variables (metapopulation probabilities) are bound between 0 and 1 and the predictor variables are categorical (McCullagh and Nelder, 1989). This design is similar to analysis of variance (ANOVA), with the key differences being the distribution of the response variable (bound between 0 and 1 rather than negative infinity and positive infinity) and the error structure (binomial rather than Gaussian).

We evaluated the severity of each disturbance to the upper Gila River Basin as a whole by calculating extinction probabilities of natives and nonnatives for each disturbance event using the refuge dataset; the Silver Fire and flood of September 2013 were treated as a single event because we did not have the temporal sampling resolution to disentangle their respective effects. Because of its size and severity, we predicted the Whitewater-Baldy Fire would result in greater native and nonnative extinctions than other disturbances. The severity of this event was likely exacerbated by post-fire low-magnitude monsoonal flows wherein concentrations of ash and fine sediment were not diluted and thus likely more problematic for fish (Rinne, 1996; Earl and Blinn, 2003).

Analysis of deviance, using the refuge dataset, was used to compare metapopulation probabilities of natives and nonnatives among our five habitats and to identify potential refuge populations. We reasoned that habitats with high occupancy could serve as potential native refuge populations during recovery, and that these habitats would be those subject to little or no disturbance. Non-metric multidimensional scaling (NMDS) on a Bray-Curtis distance matrix of occupancy probabilities from the refuge dataset was used to identify which habitats provided potential sources for each species. The optimum number of axes for the NMDS was determined iteratively by minimizing stress values, with stress defined as the ability of the NMDS to preserve Bray-Curtis distance in a reduced set of axes. To remove the influence of rare species, those with an occupancy probability of <0.15 were removed from NMDS analysis.

Results

Species Detection and Metapopulation Probabilities

Detection probabilities were high for most species (mean = 0.77; Table 4.2) and differences between detection-corrected and naïve occupancy estimates were marginally-

significant (t = 1.79; P = 0.08), but highly-correlated (r = 0.78; P < 0.01). Given this result, we reasoned that metapopulation estimates uncorrected for detection probabilities could provide an accurate representation of metapopulation probabilities, and did not adjust presence-absence matrices for imperfect detection for any other analyses. Nine native and 12 nonnative fish species were collected during the study. Among native fishes, Longfin Dace (*Agosia chrysogaster*), Desert Sucker (*Pantosteus clarkii*), and Sonora Sucker (*Catostomus insignis*) tended to have the highest occupancy, highest colonization, and lowest extinction probabilities (Table 4.2). Nonnative occupancy and colonization were generally lower and extinction higher compared to natives, with Red Shiner (*Cyprinella lutrensis*), Western Mosquitofish (*Gambusia affinis*), and Smallmouth Bass (*Micropterus dolomieu*) having the only nonnative $p_o > 0.50$.

Response to Disturbance

High overdispersion necessitated using quasibinomial error distributions for all generalized linear models (GLMs). The main effects of origin ($F_{1,21} = 19.8$; $P < 0.01$) and disturbance ($F_{1,22} = 3.09$; $P = 0.09$) were significant or marginally significant, respectively, but there was not a significant interaction ($F_{1,20} = 0.62$; $P = 0.44$) between these factors. Regardless of disturbance period, native fishes always had greater occupancy (mean $p_o = 0.56$) than nonnatives (mean $p_o = 0.31$; Fig. 4.5a), and occupancy for both groups decreased during the period of disturbance from a mean of 0.48 to 0.39 (Fig. 4.5b). These results supported our prediction of decreased nonnative occupancy during disturbance, but refuted our prediction of no response to disturbance by natives. Native species associated with decreased occupancy included Headwater Chub (*Gila nigra*) and Spikedace (*Meda fulgida*), which had 54% and 33% reductions in their respective occupancy probabilities during disturbance. Other natives had reductions of 10-20%. No native species increased occupancy during disturbance (Table 4.2). Although nonnative extinction probabilities exhibited an overall increase, response by individual species varied. Nonnatives having the largest decrease in occupancy during disturbance were Rainbow Trout (*Oncorhynchus mykiss*), Brown Trout (*Salmo trutta*), and Channel Catfish (*Ictalurus punctatus*), which had 92%, 77% and 70% decreases, respectively. Nonnatives that exhibited no change or increased occupancy during disturbance, were Fathead Minnow (*Pimephales promelas*, no change), Largemouth Bass (*M. salmoides*, no change), Flathead Catfish (*Pylodictis olivaris*, 14% increase), Yellow Bullhead (*Ameiurus natalis*, 21% increase),

Western Mosquitofish (65% increase), and Common Carp (*Cyprinus carpio*, 225% increase). Neither additive nor interactive effects of origin and disturbance on colonization were significant ($P \geq 0.27$), as colonization for both groups was low ($p_c < 0.20$) across both time periods. A significant origin by disturbance interaction influenced the probability of extinction ($F_{1,20} = 4.38$; $P = 0.05$). Extinction probabilities of natives and nonnatives increased during disturbance, but extinction increased by a greater magnitude for natives so that their extinction (mean $p_e = 0.29$) was no longer statistically less than that of nonnatives (mean $p_e = 0.43$; Fig. 4.5c). These results supported our predictions regarding nonnatives, but not for natives. Increases in extinction probability were greatest for Spikedace (157% increase), Headwater Chub (117% increase), and Loach Minnow (*Tiaroga cobitis*; 43% increase). Increases in extinction risk for other natives were < 25% and did not decrease for any. Similar to occupancy, nonnative species responses were mixed; Channel Catfish, Rainbow Trout, and Brown Trout extinction probabilities increased by 100%, 300%, and 333%, respectively, whereas those of Western Mosquitofish (86%), Yellow Bullhead (53%), and Common Carp (9%) decreased.

Extinction probabilities for both natives ($p_e = 0.29$) and nonnatives ($p_e = 0.50$) were highest following the 2013 Silver Fire and flood. Extinction probabilities were intermediate following the 2012 Whitewater-Baldy Fire (native and nonnative $p_e = 0.24$) and lowest after the 2011 Miller Fire (native $p_e = 0.14$; nonnative $p_e = 0.17$).

Identification of Refuge Habitats

Interactive effects of origin and habitat were found to influence occupancy probabilities ($F_{4,22} = 5.22$; $P < 0.01$). Natives had greatest occupancy in large tributaries and the low modification valley, whereas nonnatives had greatest occupancy in the high modification valley. Nonnative occupancy was greater, on average, than native occupancy in canyon and highly-modified valley habitats, but was lowest relative to natives in small tributary habitat. Mean native occupancy was 12 times greater than that of nonnatives in small tributaries (Fig. 4.6a). These results supported our prediction that small tributary (only half of sites affected), low-modification valley (low-intensity ash flows), and large tributary habitats (East Fork unaffected) that were less severely impacted by fires might serve as refuge habitats. Despite their greater water volume, canyon habitats that were influenced by fire provided poor refuge habitat. High native occupancy in large tributaries was not driven by East Fork sites that were minimally

impacted by forest fires, as native occupancy was higher in other large tributary localities that were severely impacted by fire (Table 4.3). Although high-modification valley habitats were presumably less affected by ash flows because of their distance from the burned areas, they also did not have high native occupancy. Interactive effects of origin and habitat were found to influence colonization probabilities ($F_{4,22} = 3.03$; $P = 0.04$). Nonnative colonization exceeded native colonization in the canyon and both valley habitats, but was lower than natives in the two tributary habitats (Fig. 4.6b). Colonization for both groups tended to be lowest in the small tributary habitat ($p_c \leq 0.04$), but was generally low for both natives ($p_c \leq 0.15$) and nonnatives ($p_c \leq 0.25$) across all habitats. Extinction probabilities were not influenced by interactive effects ($F_{4,19} = 0.67$; $P = 0.62$), although additive effects of habitat ($F_{4,24} = 4.66$; $P < 0.01$) and origin ($F_{1,23} = 12.7$; $P < 0.01$) were significant. Extinction rates were highest for both natives and nonnatives in the canyon habitat (mean $p_e = 0.42$) and were 3.2 times greater than the lowest mean extinction rate ($p_e = 0.13$) in the high modification valley (Fig. 4.6c). Nonnative extinction probabilities (mean $p_e = 0.36$) were double that of native fishes (mean $p_e = 0.18$; Fig. 4.6d). Native extinction was greater than colonization across all sites, except small tributary 2 and large tributary 4 and 5. Nonnative extinction exceeded colonization across all sites (Table 4.3).

A two-axis configuration was the optimal solution for the NMDS analysis, and had a stress value of 0.07. The first axis of the NMDS separated sites with high native occupancy (positive NMDS1 scores) from those with high nonnative occupancy (negative NMDS1 scores), whereas the second axis tended to separate tributary habitats (positive NMDS2 scores) from mainstem habitats (negative NMDS2 scores) with some exceptions (e.g. canyon-1 had positive NMDS2 scores, small tributary 3 and 4 had negative scores; Fig. 4.7). NMDS illustrated that the likelihood a habitat might provide refuge during disturbance was dependent upon the species of interest. Speckled Dace (*Rhinichthys osculus*) most often occupied small and large tributary habitats, Spikedace characterized large tributary (especially large tributary 3) and low modification valley habitats, and Loach Minnow characterized low and high modification valley habitats, large tributary 4, and canyon 1 (Table 4.4; Fig. 4.7). Longfin Dace, Desert Sucker, and Sonora Sucker had relatively high occupancy across all habitats, with several exceptions (Table 4.4). Nonnative occupancy during disturbance was greatest in large tributary, canyon, and high modification valley habitats. Smallmouth Bass and Yellow Bullhead characterized large tributaries, Common Carp and Flathead Catfish characterized the canyon, Channel Catfish,

Fathead Minnow, and Red Shiner characterized canyon and both valley habitats, and Western Mosquitofish had high occupancy in all habitats, excluding those in the small tributary (Table 4.4; Fig. 4.7).

Discussion

Historical versus Contemporary Disturbance Regime

Our study documented decreases in occupancy and increases in local extinction of fishes, especially native fishes, during disturbance. Native fish extinction probabilities were lower than nonnatives prior to fires and flooding, but increased disproportionately during disturbance, resulting in statistically similar probabilities of extinction. We assumed that natives would be less affected by fire-related disturbance because of their evolutionary experience with wildfire and flooding, but this expectation was not borne out in this study. The extreme extent and severity of these disturbances relative to the historical disturbance regime might have overwhelmed the inherent ability of native fishes to cope with such catastrophic natural events. Burn scar data from the Gila National Forest indicated that fires between 1700 and 1900 occurred every 4-5 years and rarely occurred in consecutive years (Swetnam, 1990). Large wildfires (>1,000 ha) occurred only every 15-25 years (Dietrich, 1983). These were typically low-intensity surface fires that did not result in tree mortality (Hurteau et al., 2013). The largest fire in the Gila National Forest between 1909 and 1986 was ~25,000 ha and other fires during this time period were ≤10,000 ha (Swetnam, 1990). In comparison, three wildfires that ranged from 35,950 ha to 120,535 ha with associated ash flows occurred in the three consecutive years of this study. In addition to being large, these were also high-intensity, stand-replacing crown fires. Stream flow regimes, which are indicative of fire conditions (extreme low flow from limited precipitation) and are influenced by wildfire (increased runoff from altered soil and vegetation), make interpretation of these results complex (Fig. 4.1). In the latter 3 years of our study, mean daily discharge in July was < 0.6 m^3 s^{-1} (USGS Gila River near Gila gage #09430500), among the lowest on record for that month, yet in September 2013, the third largest recorded discharge occurred. The maximum instantaneous discharge during the flood was 815 m^3 s^{-1}, 2 orders of magnitude greater than the mean period of record (1927-2013) discharge of 4.3 m^3 s^{-1} (USGS Gila River near Gila gauge #09430500). This flood coupled with the Silver Fire resulted in 2013 having the largest event extinction probabilities, although it is possible that

the effects of 2013 disturbances were enhanced by wildfires in preceding years. Indeed, extinction probabilities for both native and nonnative fishes increased with each consecutive disturbance. While native fishes of the Gila River evolved in highly variable systems, the extent, intensity, and frequency of recent events evidently exceeded their tolerance.

Refuge Populations and Rescue Effects

Recovery of native Gila River fishes following disturbance will depend upon among-habitat recolonization and within-habitat recruitment. Recovery will be partially dictated by marginally impacted source populations providing colonists for de-populated habitats, which is determined by species dispersal ability and distance from source (Brown and Kodric-Brown, 1977; Rieman and Clayton, 1997; Rieman and Dunham, 2000). Unfortunately, the large size and frequency of disturbance in the upper Gila River spared few refuge habitats. Habitats that escaped ash flows and flooding were Upper East Fork (upstream of Black Canyon confluence) and Blue Creek. But, native fish populations in the Upper East Fork were compromised by high occupancy of nonnative piscivores (Yellow Bullhead, Smallmouth Bass; Pilger et al., 2010), as evidenced by it having one of the highest native extinction probabilities in the upper Gila River despite experiencing no disturbance. Had invasions not occurred, the East Fork may have served as an important refuge habitat for all native species. For instance, federally-protected Spikedace and Loach Minnow historically occurred in the East Fork drainage, but are now likely absent in this tributary (Propst et al., 2008). Given its currently high occupancy by piscivorous nonnatives, the East Fork may now only function as a source population for large-bodied Headwater Chub, Sonora Sucker, and Desert Sucker. Nonnative removal in this tributary could potentially restore populations of imperiled species (Propst et al., 2014), increasing the number of potential refuge populations and enhancing native fishes resilience to future disturbances (Young, 2012). Although not compromised by nonnative occupancy, the native source population in Blue Creek is depauperate because of its small size and isolation, and supported only Speckled Dace, Longfin Dace, and Desert Sucker. This habitat was also isolated from the Gila River mainstem by a >10 km reach that is dry for a large proportion of the year. For these reasons, neither upper East Fork nor Blue Creek will provide Spikedace or Loach Minnow colonists for depopulated reaches. Lastly, although minimally impacted by wildfires, anthropogenic flow alteration and high occupancy by nonnative species likely precluded the high-modification valley from

supporting native fish populations that could contribute to recovery of depopulated reaches. Interrupted flows in this and lower reaches of the Gila River in Arizona compromised potential of this reach to provide refuge habitat, and Sunset Diversion Dam impeded upstream movement of fishes under typical flow conditions. These conditions highlight how anthropogenic stressors (nonnative species, fragmentation, dewatering) can interact with natural disturbance (wildfire and flooding) to abnormally diminish native fishes' resistance and resilience.

Recovery of native fishes in the upper Gila River will also be dependent upon within-habitat recruitment from populations that persisted despite disturbance (Lamberti et al., 1991). Although occupancy decreased and extinction increased for natives following the series of disturbances, no native species was extirpated from the upper Gila River drainage. Our among-habitat quantification of metapopulation probabilities indicated that habitats especially important as source habitats were small tributary sites for Speckled Dace, West Fork for Spikedace, and the low modification valley for Loach Minnow (Fig. 4.4). Maintaining an unfragmented stream network will help ensure that connections among these sources and other habitats remain and that populations can recover from disturbance (Dunham and Rieman, 1999; Rieman and Dunham, 2000). Among-habitat recolonization may be less important for species present at a large number of sites such as Longfin Dace, Desert Sucker, and Sonora Sucker. Headwater Chub, Rio Grande Sucker (*Pantosteus plebius*), and Gila Trout (*Oncorhynchus gilae*) had low occupancy regardless of disturbance, meaning other conservation measures (e.g. nonnative removal and native fish augmentation) may be required to maintain these populations. Because of low occupancy and high extinction of native fishes in the canyon and high-modification valley, it does not appear that either of these habitats will aid in the recovery of the upper Gila River fishes (Fig. 4.4).

Native versus Nonnative Response

It has been hypothesized that disturbance from forest fires can disproportionately impact populations of native or nonnative fishes (Dunham et al., 2003). Studies investigating effects of wildfire and species (native and nonnative) responses are limited, but suggest low resistance and high resilience by both groups to wildfire disturbance (Lyon and O'Connor, 2008; Sestrich et al., 2011; Young, 2012). Excluding the study by Lyon and O'Connor (2008) on Australian fishes, these studies were conducted on salmonid species in coldwater systems that were proximal to

fire perimeters. Results for nonnative salmonids and native fishes from our study are consistent with findings of others, in that decreases in occupancy and increases in extinction were observed. However, we found that fish populations did not have to be in the fire perimeter to experience negative fire effects. Furthermore, we also found that nonnative warmwater species such as Common Carp, Flathead Catfish, Yellow Bullhead, and Western Mosquitofish increased in occupancy and were less prone to extinction during disturbance than were native species. Each is a habitat generalist and tolerant of harsh abiotic conditions (Olden et al., 2006) and Flathead Catfish are capable of withstanding large floods (Minckley and Meffe, 1987). Increased occupancy and low extinction of these nonnative species might be related to drought, which might have limited negative effects or potentially favor nonnatives, especially those that prefer low velocity habitats (Propst et al., 2008). Thus, disturbances with unbalanced influence on natives and nonnatives could, over successive disturbances, results in drastic shifts in community composition.

Study Limitations

Because naïve and detection-corrected probabilities were highly-correlated and only marginally different we did not account for imperfect detection in any of our analyses. However, we acknowledge that imperfect detection may have influenced some of our results. For instance, because detection probabilities were generally lower for many nonnative species, we may have underestimated their occupancy and overestimated their extinction probabilities. Given the high detection and limited differences between naïve and detection-corrected estimates of native fishes, we believe that our major conclusion that wildfires had greater effects on native occupancy and extinction relative to nonnatives is sound. If anything, the difference between native and nonnative metapopulation probabilities is even less than we report, with even more serious conservation implications for native fishes.

Conclusions

Our study documented decreases in occupancy and increases in extinction for native and nonnative fishes during a series of large and intense wildfires and flooding, but were especially detrimental to imperiled native fishes. Although recent wildfires may be unprecedented in magnitude, at least within the past 300 years, their occurrence resulted from elevated fuel loads after decades of fire suppression and climate change (Swetnam, 1990; Westerling et al., 2006).

Future climate projections indicate that large, frequent wildfires will become the rule rather than the exception in coming decades (Brown et al., 2004; McKenzie et al., 2004; Moritz et al., 2012), thereby increasing extinction risk for native fishes. Large and severe wildfires represent an additional threat to native fish persistence, with the negative effects of wildfire compounded by the presence of nonnative species, fragmentation, and dewatering (Dunham et al. 2003). Preservation of physically-linked habitats coupled with management actions that limit native fish exposure to ash flows (e.g. evacuation; Brooks, 2006) or that help restore the natural regime of smaller, less severe fires (e.g. prescribed burning, forest thinning; Covington et al., 1997; Reinhardt et al., 2008) will be critical to conserving native fish populations in a changing climate.

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Figure 4.1 Conceptual diagram describing the impact of forest fires on stream fish populations. Impacts are dictated by an interaction between post-fire runoff and stream proximity to fire, fire severity, stream size, and time since fire. Runoff is influenced by precipitation, catchment relief, and soil characteristics. Moderate runoff will be most harmful to fish because of toxic water chemistry, heavy runoff will have moderate effects because of a dilution effect, while low runoff will result in habitat changes only (e.g. temperature, light, sedimentation, wood input).
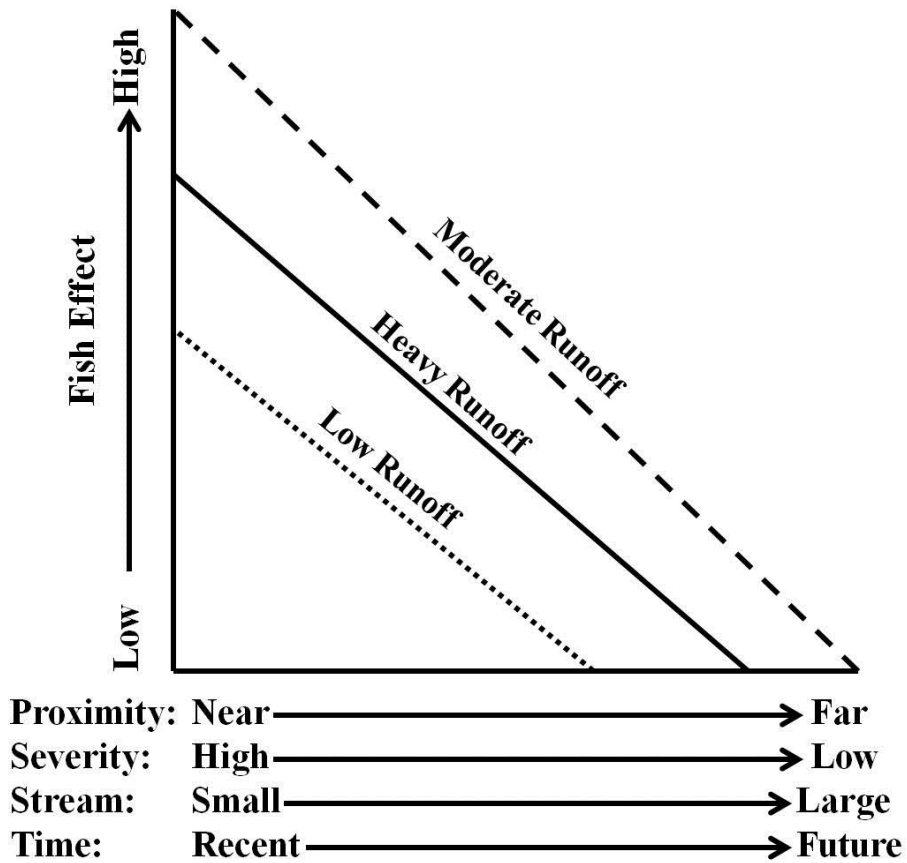
Figure 4.2 Map of the upper Gila River basin, New Mexico with fish community sampling sites and USGS gage positions indicated. Shaded areas represent area burned by consecutive fires between 2011 and 2013
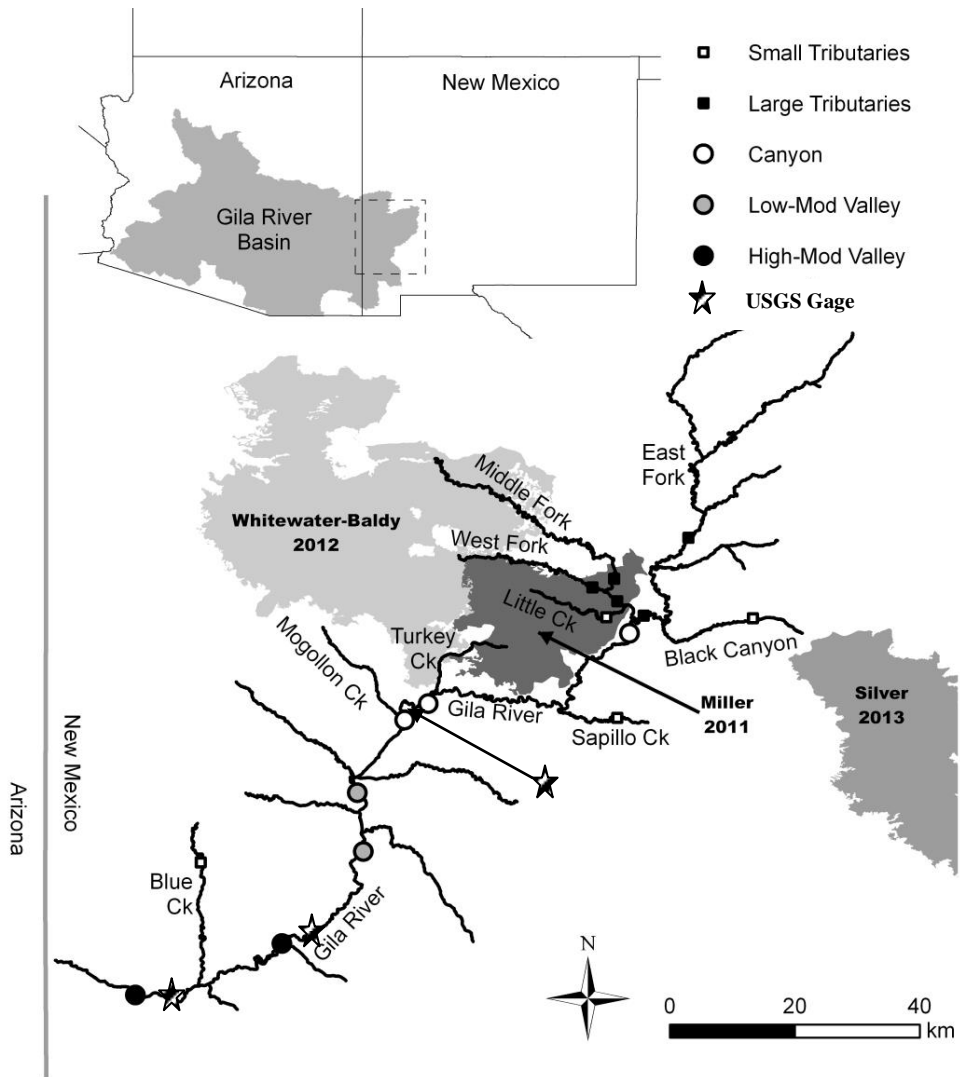
Figure 4.3 Mean daily discharge on the Gila River mainstem in reaches with no, low, and high modification of discharge from irrigation diversions (a) during 01 January 2008 to 31 December 2013 and (b) as an annual average during the period of peak irrigation demand (May-August) to demonstrate major differences in flow regime resulting from modification. Data for the unmodified reach came from the United States Geological Survey (USGS) gage# 09430500, data for the low modification reach came from USGS gage# 09431500, and data for the high modification reach came from USGS gage# 09432000. See Fig. 4.2 for USGS gage locations. Hatched bars in panel (a) indicate timing and duration of forest fires; + denote timing of sampling for the disturbance dataset and # denote timing of sampling for refuge dataset.
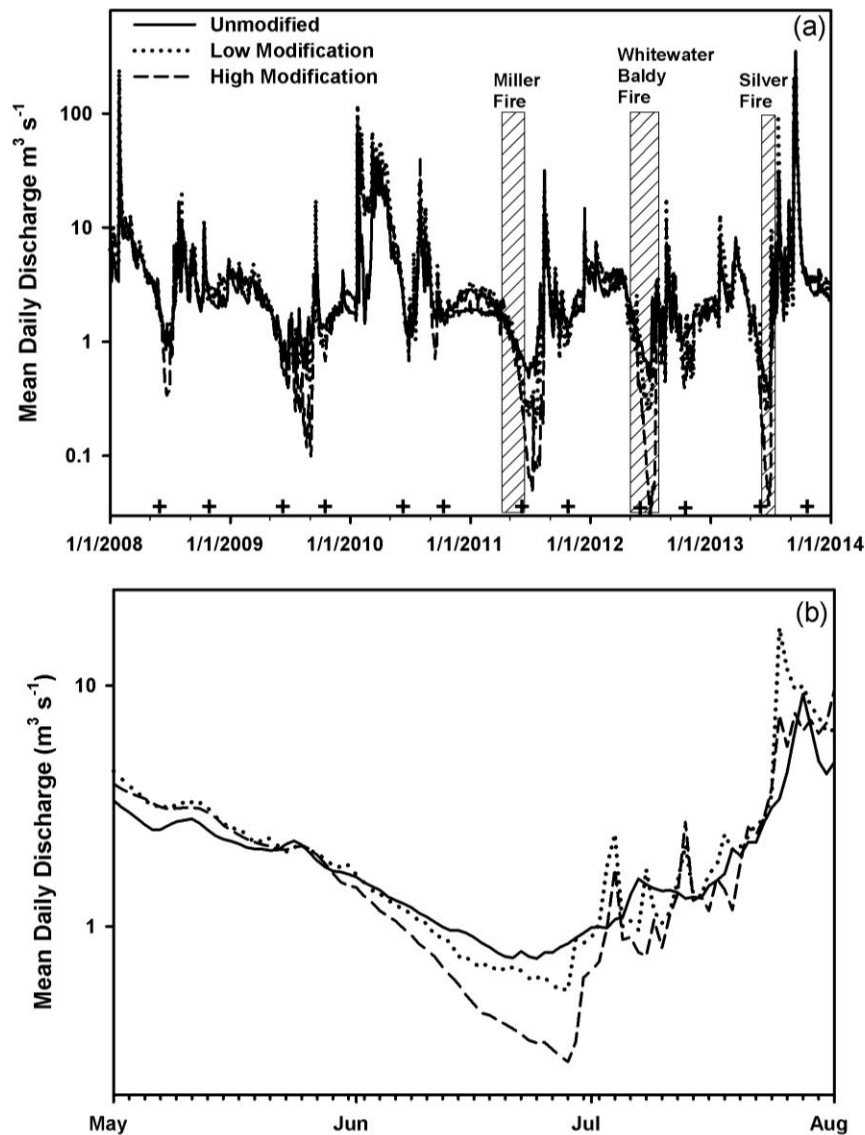
Figure 4.4 Conceptual diagram describing longitudinal gradients of anthropogenic alteration, fire impacts, and native and nonnative fish occupancy in the upper Gila River, NM, USA. Percentages listed for fire impact are the percentage of sample sites that were affected by at least one forest fire during the study. Shape width is proportional to the magnitude of impact or occupancy, i.e. wider shapes equate to higher impact or occupancy; width (magnitude) decreases longitudinally because of presumed dilution conferred by larger streams and increasing distance from fire (Fig. 4.1). Stars denote potentially-important source habitats for native fish recovery following disturbance.
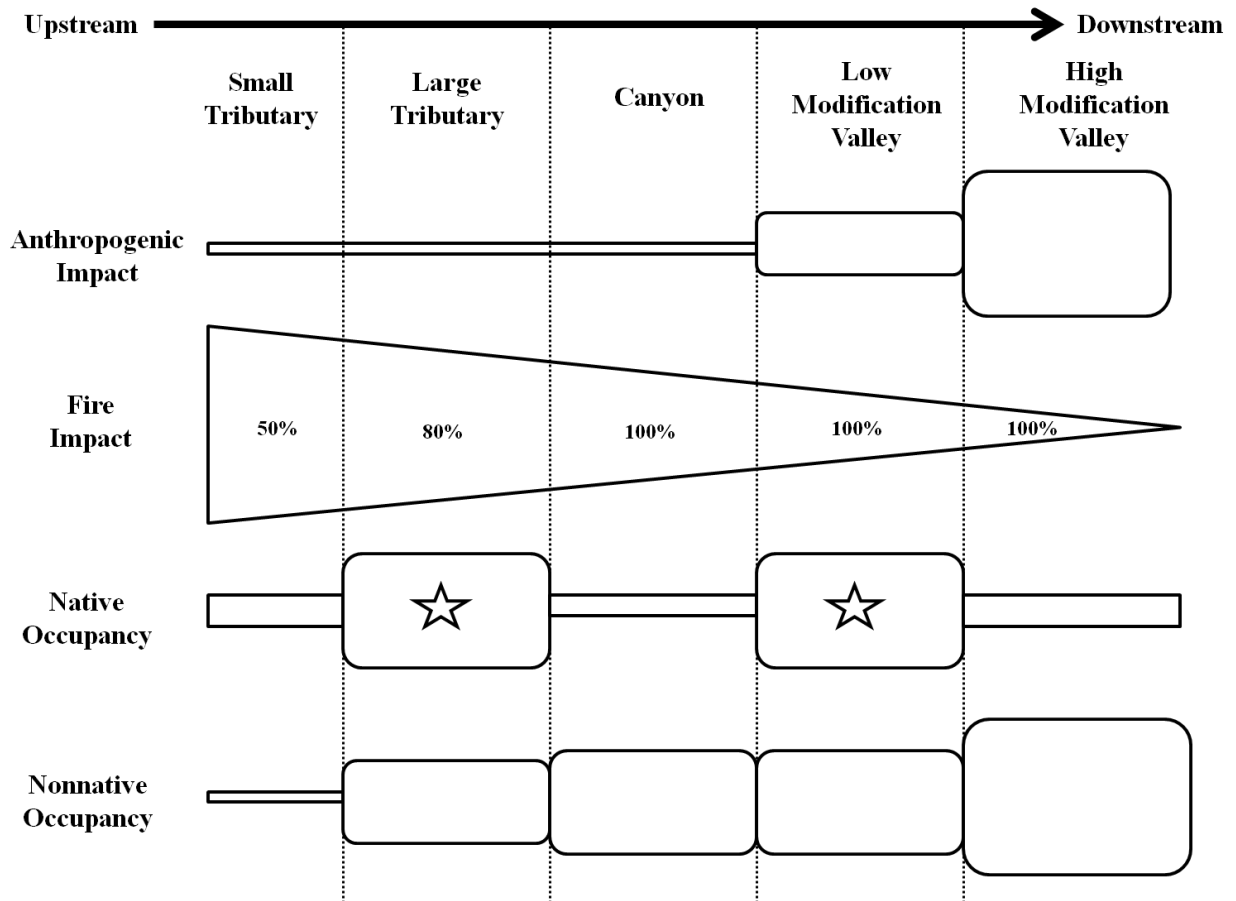
Figure 4.5 Differences in (a) occupancy between native and nonnative fishes or (b) before and during disturbance, and differences in (c) extinction between natives and nonnative before and during disturbance across 6 sites in the upper Gila River Basin, NM. SD= standard deviation.
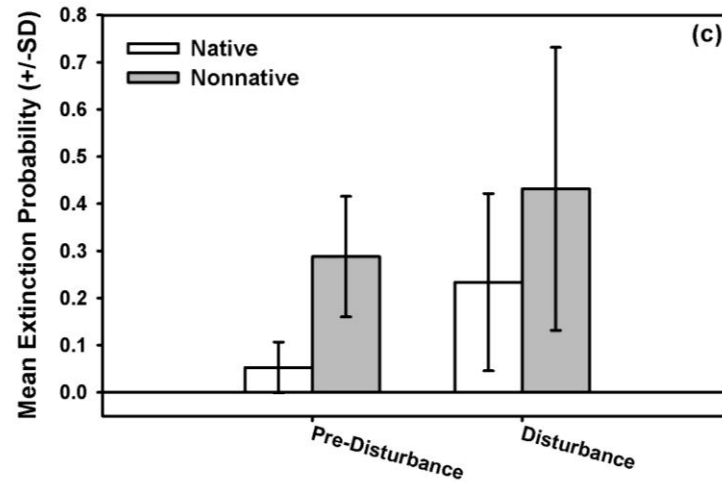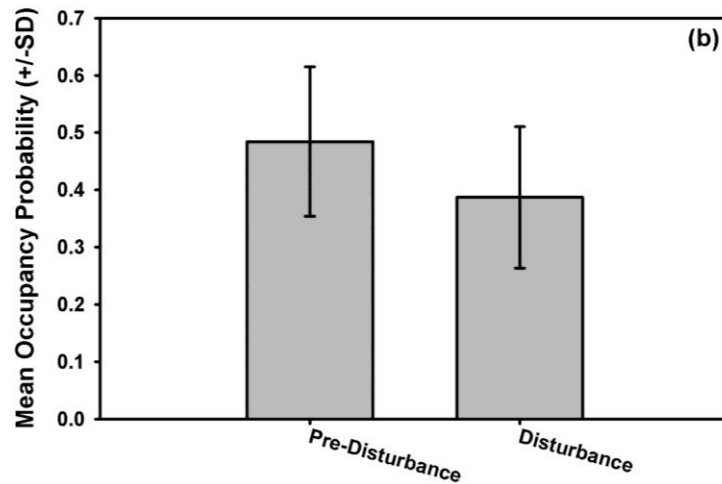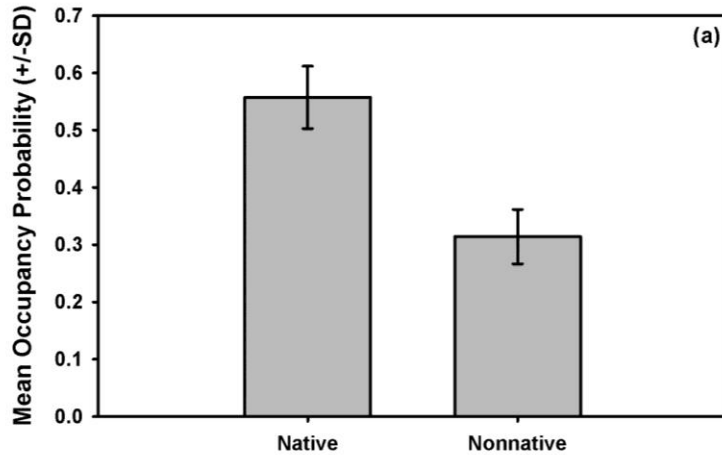
Figure 4.6 Differences in (a) probabilities of occupancy and (b) colonization between native and nonnative fishes among habitats, and differences in extinction probabilities (c) among habitats or (d) between native and nonnative fishes. SD= standard deviation.
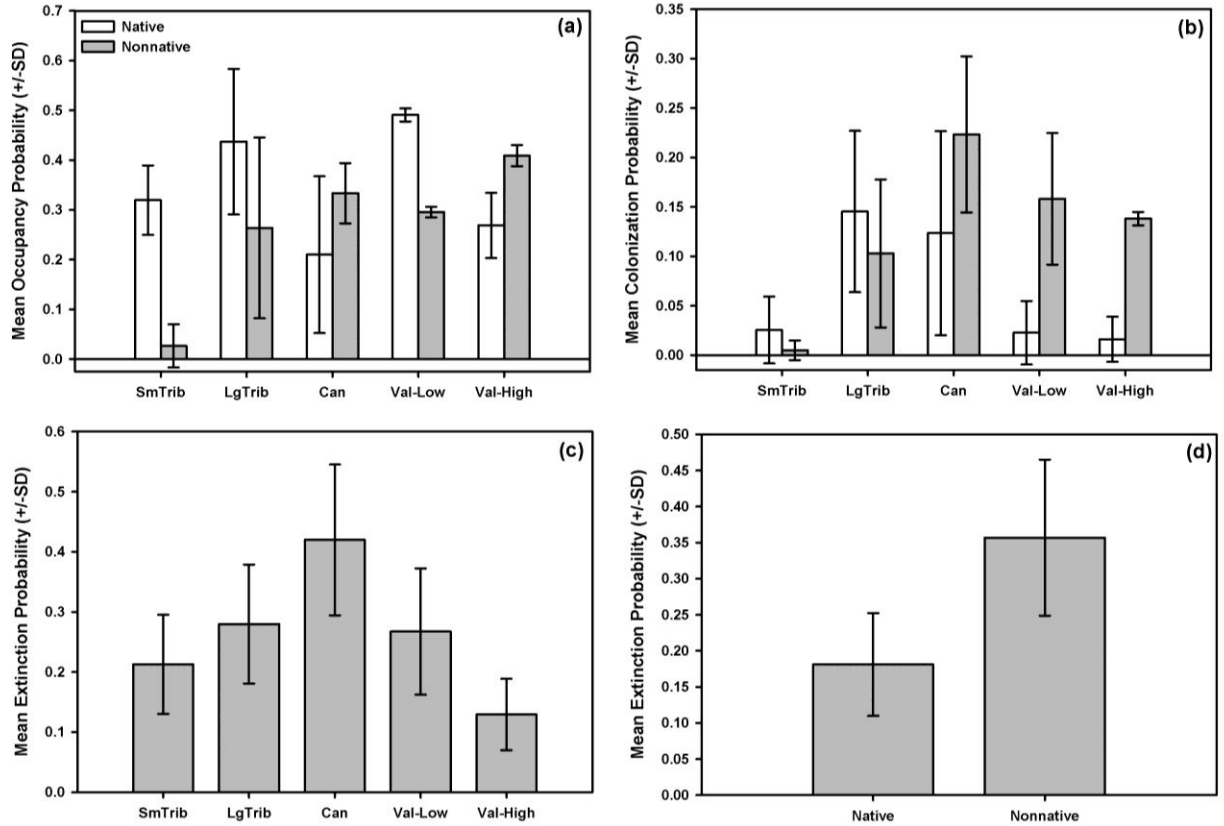
Figure 4.7 Non-metric multidimensional scaling (NMDS) biplots summarizing (a) among-site and (b) interspecific variation in occupancy probabilities for the refuge dataset. See Table 4.1 for site abbreviations. Species codes are the first three letters of the genus and the first three letters of the specific epithet; see Table 4.2 for common names. Nonnative species codes are underlined
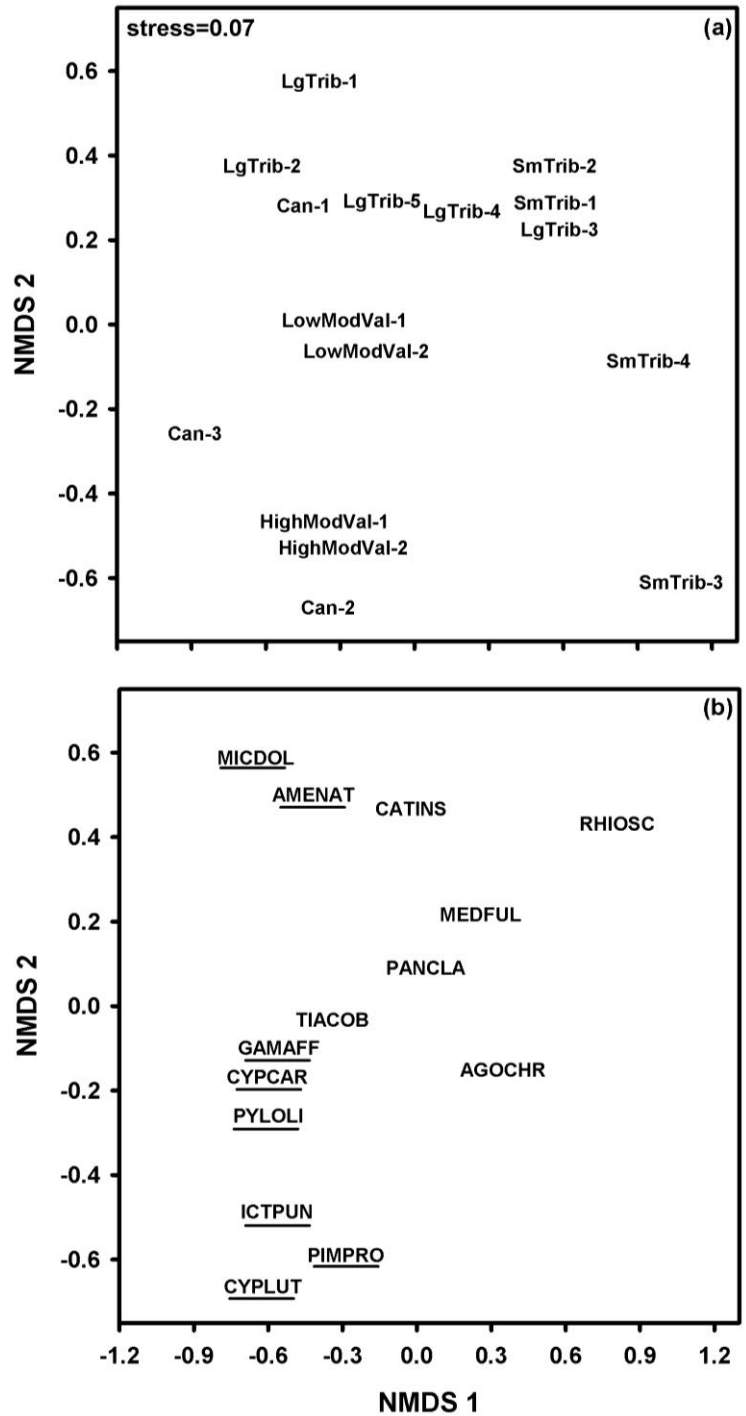
Table 4.1 Stream size and catchment characteristics of the 16 study sites located in the upper Gila River, NM, USA. See Figure 4.1 for site locations.

Site Name	Water Body	Habitat Type Name	Elevation (m a.s.l.)	Mean Width[a] (m)	Mean Length[a] (m)	Discharge[a] ($m^3 s^{-1}$)	Temperature[a] (°C)
Sm Trib 1	Black Canyon	Small Tributary	2059	3.2	122	<0.01	16.2
Sm Trib 2	Little Creek	Small Tributary	1729	3.1	134	0.02	19.6
Sm Trib 3	Sapillo Creek	Small Tributary	1783	2.8	78	0.01	18.3
Sm Trib 4	Blue Creek	Small Tributary	1422	3.6	122	0.00	22.4
Lg Trib 1	East Fork	Large Tributary	1878	4.7	210	0.41	21.5
Lg Trib 2	East Fork	Large Tributary	1694	6.8	210	0.42	21.7
Lg Trib 3[b]	**West Fork**	**Large Tributary**	**1738**	**4.1**	**241**	**0.08**	**20.2**
Lg Trib 4	West Fork	Large Tributary	1711	6.8	200	0.22	21.9
Lg Trib 5	**Middle Fork**	**Large Tributary**	**1725**	**8.2**	**278**	**0.17**	**20.6**
Can 1	**Gila River**	**Canyon**	**1691**	**9.4**	**333**	**0.77**	**21.5**
Can 2	Gila River	Canyon	1448	11.0	236	0.51	21.7
Can 3	**Gila River**	**Canyon**	**1412**	**10.0**	**205**	**0.66**	**22.0**
Low Val 1	**Gila River**	**Low-Mod Valley**	**1360**	**11.3**	**272**	**0.36**	**21.6**
Low Val 2	**Gila River**	**Low-Mod Valley**	**1331**	**10.6**	**296**	**0.24**	**23.4**
High Val 1	Gila River	High-Mod Valley	1240	4.5	264	0.01	23.3
High Val 2	Gila River	High-Mod Valley	1161	2.9	198	0.02	20.6

[a] Calculated for the month of June in 2012 and 2013 and then averaged; see Whitney et al. (2014) for methods

[b] Sites in bold were used for the disturbance dataset that included samples taken every June and October during 2008-2013; whereas samples from non-bold sites were taken every March, June, and October during 2012-2013. All sites were used for the refuge dataset.

Table 4.2 Occupancy (p_o), colonization (p_c), extinction (p_e), and detection probabilities of native and nonnative fishes in the upper Gila River, NM, USA. 6= 6 site disturbance dataset; 16= 16 site refuge dataset; ρ = detection probability; Ψ = detection-corrected occupancy; Naïve = occupancy uncorrected for detection. Species codes are first three letters of the genus and first three letters of the specific epithet. Native species are in bold.

Code	Common Name	Occupancy 6 Pre	Occupancy 6 During	Occupancy 16	Colonization 6 Pre	Colonization 6 During	Colonization 16	Extinction 6 Pre	Extinction 6 During	Extinction 16	Detection 6 ρ	Detection 6 Ψ	Detection 6 Naïve
AGOCHR	**Longfin Dace**	0.94	0.81	0.74	1.00	0.60	0.35	0.00	0.20	0.13	0.96	0.95	0.95
GILNIG	**Headwater Chub**	0.36	0.17	0.11	0.10	0.08	0.07	0.23	0.50	0.56	0.80	0.40	0.36
MEDFUL	**Spikedace**	0.67	0.44	0.19	0.20	0.06	0.06	0.08	0.21	0.33	1.00	0.67	0.67
RHIOSC	**Speckled Dace**	0.47	0.42	0.41	0.06	0.17	0.11	0.00	0.25	0.18	0.91	0.51	0.48
TIACOB	**Loach Minnow**	0.56	0.47	0.32	0.21	0.13	0.09	0.10	0.14	0.17	0.92	0.58	0.55
PANCLA	**Desert Sucker**	1.00	0.81	0.69	1.00	0.40	0.27	0.00	0.16	0.19	1.00	1.00	1.00
PANPLE	**Rio Grande Sucker**	X[a]	X	0.06	X	X	0.00	X	X	0.00	—[b]	—	—
CATINS	**Sonora Sucker**	1.00	0.89	0.63	1.00	1.00	0.07	0.00	0.14	0.10	0.99	1.00	1.00
ONGCIL	**Gila Trout**	0.06	0.00	0.01	0.04	0.00	0.01	1.00	1.00	1.00	—	—	—
CYPLUT	Red Shiner	0.58	0.50	0.33	0.42	0.21	0.06	0.19	0.25	0.19	0.62	0.77	0.57
CYPCAR	Common Carp	0.11	0.36	0.17	0.11	0.32	0.16	0.50	0.45	0.62	0.35	0.45	0.12
PIMPRO	Fathead Minnow	0.25	0.25	0.22	0.32	0.18	0.05	0.56	0.63	0.37	0.58	0.53	0.26
AMENAT	Yellow Bullhead	0.39	0.47	0.31	0.16	0.00	0.09	0.14	0.07	0.22	0.87	0.48	0.40
ICTPUN	Channel Catfish	0.28	0.08	0.23	0.14	0.07	0.14	0.50	1.00	0.59	0.56	0.60	0.26
PYLOLI	Flathead Catfish	0.39	0.44	0.26	0.21	0.33	0.19	0.36	0.40	0.57	0.51	0.81	0.38
ONCMYK	Rainbow Trout	0.33	0.03	0.14	0.10	0.00	0.04	0.25	1.00	0.69	0.92	0.32	0.31
SALTRU	Brown Trout	0.36	0.08	0.00	0.11	0.00	X	0.15	0.67	X	0.88	0.42	0.36
GAMAFF	Western Mosquitofish	0.47	0.78	0.56	0.50	0.17	0.21	0.29	0.04	0.15	0.40	0.97	0.50
LEPCYA	Green Sunfish	0.44	0.22	0.15	0.41	0.13	0.10	0.38	0.57	0.62	0.77	0.60	0.43
MICDOL	Smallmouth Bass	0.53	0.31	0.23	0.35	0.05	0.03	0.26	0.36	0.33	0.85	0.60	0.52
MICSAL	Largemouth Bass	0.03	0.03	0.04	0.03	0.03	0.04	1.00	1.00	1.00	—	—	—

[a] species was not encountered during sampling for the dataset
[b] probability could not be estimated because if insufficient data

Table 4.3 Occupancy (p_o), colonization (p_c), extinction (p_e) for native and nonnative fishes in the upper Gila River, NM, USA across sites before and during disturbances

Dataset	Disturbance Period	Habitat	Site	Native p_o	p_c	p_e	Nonnative p_o	p_c	p_e
Disturbance	Before	Large Tributary	3	0.73	0.23	0.09	0.18	0.02	0.08
			5	0.73	0.08	0.03	0.44	0.24	0.23
		Canyon	1	0.63	0.22	0.07	0.37	0.22	0.33
			3	0.45	0.12	0.14	0.43	0.24	0.29
		Low Mod Valley	1	0.63	0.00	0.00	0.35	0.17	0.35
			2	0.63	0.00	0.00	0.31	0.24	0.45
	During	Large Tributary	3	0.63	0.07	0.08	0.00	0.00	1.00
			5	0.53	0.30	0.25	0.35	0.09	0.28
		Canyon	1	0.48	0.29	0.32	0.45	0.20	0.20
			3	0.15	0.06	0.56	0.37	0.11	0.28
		Low Mod Valley	1	0.55	0.00	0.04	0.28	0.21	0.53
			2	0.53	0.00	0.16	0.28	0.08	0.30
Refuge	During	Small Tributary	1	0.37	0.00	0.20	0.02	0.00	1.00
			2	0.39	0.07	0.06	0.00	0.00	—[a]
			3	0.26	0.03	0.17	0.09	0.02	0.20
			4	0.26	0.00	0.08	0.00	0.00	—
		Large Tributary	1	0.33	0.14	0.41	0.42	0.06	0.13
			2	0.24	0.08	0.22	0.39	0.19	0.38
			3	0.54	0.05	0.08	0.00	0.00	—
			4	0.59	0.22	0.19	0.15	0.11	0.70
			5	0.48	0.23	0.16	0.35	0.15	0.43
		Canyon	1	0.39	0.24	0.25	0.39	0.31	0.45
			2	0.15	0.08	0.57	0.27	0.18	0.53
			3	0.09	0.05	0.60	0.33	0.17	0.50
		Low Mod Valley	1	0.50	0.05	0.09	0.29	0.21	0.50
			2	0.48	0.00	0.16	0.30	0.11	0.37
		High Mod Valley	1	0.31	0.03	0.07	0.42	0.13	0.20
			2	0.22	0.00	0.00	0.39	0.14	0.20

[a]The group (native or nonnative) was not encountered during sampling

Table 4.4 Occupancy (p_o), colonization (p_c), and extinction (p_e) probabilities across 16 sites in 5 habitats during March 2012-October 2013 in the upper Gila River, NM, USA.

Probability			Small Tributary				Large Tributary					Canyon			Low Valley		High Valley	
	Origin	Species	1	2	3	4	1	2	3	4	5	1	2	3	1	2	1	2
p_o	Native	Longfin Dace	0.83	0.67	1.00	1.00	0.33	0.17	1.00	1.00	0.67	0.33	0.50	0.33	1.00	1.00	1.00	1.00
		Headwater Chub	0.00	0.00	0.00	0.00	0.67	0.00	0.17	0.33	0.50	0.17	0.00	0.00	0.00	0.00	0.00	0.00
		Spikedace	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.33	0.17	0.17	0.00	0.00	0.50	0.83	0.00	0.00
		Speckled Dace	0.83	1.00	0.17	1.00	0.33	0.00	1.00	1.00	0.83	0.33	0.00	0.00	0.00	0.00	0.00	0.00
		Loach Minnow	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.83	0.17	0.83	0.17	0.00	1.00	0.83	1.00	0.00
		Desert Sucker	0.83	1.00	0.00	0.33	0.67	0.67	0.67	0.83	1.00	0.67	0.67	0.00	1.00	0.83	0.83	1.00
		Rio Grande Sucker	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Sonora Sucker	0.83	0.83	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.50	1.00	0.83	0.00	0.00
		Gila Trout	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Nonnative	Red Shiner	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.17	0.33	0.83	0.83	0.50	0.50	1.00	1.00
		Common Carp	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.50	0.50	0.17	0.33	0.33	0.00	0.50	0.17
		Fathead Minnow	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.50	0.00	0.33	0.00	0.00	0.67	0.67	1.00
		Yellow Bullhead	0.00	0.00	0.00	0.00	1.00	0.83	0.00	0.50	1.00	0.83	0.00	0.00	0.00	0.67	0.00	0.17
		Channel Catfish	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.50	0.33	0.33	0.33	1.00	0.50
		Flathead Catfish	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.50	0.50	0.33	0.67	0.17	0.17	0.67	0.50
		Rainbow Trout	0.17	0.00	0.83	0.00	0.00	0.33	0.00	0.33	0.17	0.33	0.00	0.00	0.00	0.00	0.00	0.00
		Western Mosquitofish	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.33	0.67	0.83	0.50	0.83	1.00	1.00	0.83	1.00
		Green Sunfish	0.00	0.00	0.00	0.00	0.67	0.33	0.00	0.00	0.00	0.50	0.33	0.33	0.17	0.00	0.00	0.00
		Smallmouth Bass	0.00	0.00	0.00	0.00	1.00	0.83	0.00	0.17	0.33	0.50	0.00	0.33	0.50	0.00	0.00	0.00
		Largemouth Bass	0.00	0.00	0.17	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
p_c	Native	Longfin Dace	—[a]	0.50	—	—	0.00	0.20	—	—	1.00	0.33	0.50	0.33	—	—	—	—
		Headwater Chub	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.67	0.33	0.20	0.00	0.00	0.00	0.00	0.00	0.00
		Spikedace	0.00	0.00	0.00	0.00	0.00	0.00	—	0.25	0.20	0.25	0.00	0.00	0.50	—	0.00	0.00
		Speckled Dace	—	—	0.00	—	0.67	0.00	—	—	1.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00
		Loach Minnow	0.00	0.00	0.00	0.00	0.00	0.25	0.00	1.00	0.20	1.00	0.20	0.00	—	—	—	0.00
		Desert Sucker	—	—	0.00	0.00	1.00	0.50	0.50	—	—	0.50	1.00	0.00	—	—	1.00	—
		Rio Grande Sucker	0.00	0.00	—	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Sonora Sucker	—	1.00	0.00	0.00	—	—	—	—	—	—	0.00	0.50	—	—	0.00	0.00
		Gila Trout	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Red Shiner	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.25	—	1.00	0.00	0.00	—	—
		Common Carp	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.50	0.67	0.25	0.67	0.50	0.00	0.50	0.20
		Fathead Minnow	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	1.00	1.00	—
		Yellow Bullhead	0.00	0.00	0.00	0.00	—	—	0.00	1.00	—	1.00	0.00	0.00	0.00	1.00	0.00	0.25

Probability	Origin	Species	Small Tributary				Large Tributary					Canyon			Low Valley		High Valley	
			1	2	3	4	1	2	3	4	5	1	2	3	1	2	1	2
p_c	Nonnative	Channel Catfish	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.67	0.33	0.50	0.33	—	0.67
		Flathead Catfish	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.67	0.33	1.00	0.25	0.25	1.00	0.33
		Rainbow Trout	0.00	0.00	—	0.00	0.00	0.33	0.00	0.33	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
		Western Mosquitofish	0.00	0.00	0.00	0.00	—	—	0.00	0.33	1.00	1.00	1.00	1.00	—	—	1.00	—
		Green Sunfish	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	1.00	0.33	0.00	0.25	0.00	0.00	0.00
		Smallmouth Bass	0.00	0.00	0.00	0.00	—	—	0.00	0.25	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00
		Largemouth Bass	0.00	0.00	0.20	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00
p_e	Native	Longfin Dace	0.20	0.00	0.00	0.00	0.50	—	0.00	0.00	0.67	0.50	0.67	0.50	0.00	0.00	0.00	0.00
		Headwater Chub	—	—	—	—	0.50	—	1.00	1.00	0.00	—	—	—	—	—	—	—
		Spikedace	—	—	—	—	—	—	0.00	1.00	—	1.00	—	—	0.67	0.20	—	—
		Speckled Dace	0.20	0.00	1.00	0.00	1.00	—	0.00	0.00	0.25	1.00	—	—	—	—	—	—
		Loach Minnow	—	—	—	—	—	1.00	—	0.25	—	0.25	—	—	0.00	0.20	0.00	—
		Desert Sucker	0.20	0.00	—	0.50	0.50	0.33	0.33	0.20	0.00	0.00	0.50	—	0.00	0.20	0.25	0.00
		Rio Grande Sucker	—	—	0.00	—	—	—	—	—	—	—	—	—	—	—	—	—
		Sonora Sucker	0.20	0.25	—	—	0.00	0.00	0.00	0.00	0.00	0.00	—	0.67	0.00	0.20	—	—
		Gila Trout	—	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—
	Nonnative	Red Shiner	—	—	—	—	—	—	—	—	—	1.00	0.00	0.20	0.25	0.33	0.00	0.00
		Common Carp	—	—	—	—	—	1.00	—	—	0.33	0.50	1.00	1.00	1.00	—	0.33	—
		Fathead Minnow	—	—	—	—	—	—	—	0.50	0.50	—	0.50	—	—	0.50	0.50	0.00
		Yellow Bullhead	—	—	—	—	0.00	0.20	—	0.67	—	0.00	0.25	—	—	0.25	—	1.00
		Channel Catfish	—	—	—	—	0.33	—	—	—	—	—	1.00	1.00	1.00	1.00	0.00	1.00
		Flathead Catfish	—	—	—	—	—	0.50	—	—	0.67	0.50	0.50	0.50	1.00	1.00	0.50	0.50
		Rainbow Trout	1.00	—	0.20	—	—	1.00	—	1.00	1.00	1.00	—	—	—	—	—	—
		Western Mosquitofish	—	—	—	—	0.00	0.00	—	0.50	0.50	0.25	0.67	0.25	0.00	0.00	0.00	0.00
		Green Sunfish	—	—	—	—	0.25	1.00	—	—	—	1.00	0.50	0.50	1.00	—	—	—
		Smallmouth Bass	—	—	—	—	0.00	0.20	—	1.00	0.50	0.33	—	0.50	0.67	—	—	—
		Largemouth Bass	—	—	—	—	1.00	—	—	—	—	—	—	—	1.00	—	—	—

[a]Indicates a species was always present for a colonization probability, or a species was always absent for an extinction probability

Chapter 5 - And the pendulum swings: changing patterns of native and nonnative success in response to uncharacteristic wildfire

Monitoring of biotic properties before and after a series of large wildfires revealed a swinging pendulum of native and nonnative success in the upper Gila River. Chapters 2, 3, and 4 revealed that prior to the wildfires native fishes were generally more productive, had higher occupancy, and lower extinction relative to nonnatives, with few exceptions. This high native success was supported by an extremely productive community of primary producers and macroinvertebrates. During and after the series of forest fires native biomass and occupancy dropped precipitously while extinction increased, with simultaneous decreases in the biomass of basal resources. This decrease in success of native fauna was not matched by concomitant decreases in the nonnative community, as most nonnatives other than salmonids were left unaffected by the series of forest fires. These patterns yielded novel insights into the management of native taxa in the presence of nonnatives, because they are the first to compare native and nonnative success in a catchment largely devoid of anthropogenic alterations, and are the only to compare the responses of a warmwater assemblage of native fishes and nonnative fishes, crayfish, and tadpoles to wildfires. Given that natives were more successful than nonnatives prior to the wildfires, it could be predicted that the pendulum of success will swing back in favor of native taxa in the years to come, but continued monitoring will be required to determine if this is indeed the case.

It is believed that where natural environmental conditions remain (e.g., disturbance regimes) native fauna will outperform nonnative species (Poff et al. 1997; Bunn and Arthington 2002; Lytle and Poff 2004). Prior to the series of wildfires we found this pattern to be true in the free-flowing and largely-unmodified upper Gila River, although the productivity of several nonnatives (Flathead Catfish, Common Carp, Virile Crayfish, American Bullfrog tadpoles) could approach or exceed that of native taxa at certain sites during specific times. The results from Chapter 1 suggested that the natural flow regime and pristine habitats could promote but did not guarantee greater native success relative to nonnatives. These findings partially support the efficacy of management strategies of flow regime and habitat restoration for native conservation in the presence of nonnatives, and suggest that naturally functioning habitats should be left unmodified when possible. However, results from Chapter 2 also suggest that targeted removal

of nonnative species at specific problem locations may be required to ensure native persistence (Propst et al. 2014). Combining strategies of restoration, preservation, and mechanical removal will be vital tools in conserving native species under a changing climate, but will be challenging as water demand increases in the desert southwest.

The free-flowing and pristine character of the upper Gila River is currently under threat as a result of the Arizona Water Settlements Act (AWSA) of 2004. The AWSA has apportioned up to $128 million in federal funds for a water development project on the upper Gila River, and would allow additional diversions of up to 17.3 million m^3 per year (Fort 2012). Several competing development projects are currently under review, some of which would result in fragmentation of the upper Gila River (O'Leary 2013). This alteration of flow and fragmentation could decrease native success, limit re-colonization in wildfire-impacted habitats, and prevent the pendulum of success swinging back in the favor of native fauna, further increasing the vulnerability of fishes to wildfire and climate change, as small, isolated populations are at increased risk of extirpation (Rieman et al. 2003).

Climate change is predicted to results in wildfires becoming a more frequent and more severe disturbance for streams draining dryland forested biomes (Brown et al. 2004; McKenzie et al. 2004; Moritz et al. 2012). This prediction is of great concern for conservation of native fauna in the upper Gila River and potentially elsewhere, as the findings in Chapters 2 and 3 of this dissertation suggest disproportionate negative effects on native taxa relative to nonnatives. This result suggests that the traits that allow for successful invasion (habitat generalist, high environmental tolerance) may also confer resistance to extreme disturbance (Moyle and Light 1996; Kolar and Lodge 2001). In contrast, the traits of native fauna left them unprepared to cope with the uncharacteristically large wildfire disturbances that occurred during our study (Dietrich 1983; Swetnam 1990; Hurteau et al. 2013). Experiments that test the physiological tolerance of native and nonnative taxa to water chemistry resulting from ash flows could help elucidate the mechanisms promoting native declines versus nonnative persistence in the face of wildfire. Furthermore, studies comparing the effects of historical (smaller size, lower intensity) versus contemporary (large size, high intensity) fires and the ash flows (or lack thereof) they produce on stream ecosystems could also provide insight. Did historical fires have benign effects on stream ecosystems, thus explaining the lack of adaptation of native fishes to resist current wildfires? Also, comparing responses of natives in communities with and without nonnative species could

prove formative. Did negative interactions with nonnatives prior to wildfires leave the native community more vulnerable to disturbance, or would the pronounced negative effects have been observed regardless? In any case, management will be required to conserve native fishes in the presence of uncharacteristic fire and nonnative species. Findings from Chapters 3 and 4 suggest management activities (logging; prescribed burning) that help reduce fire size and intensity could be beneficial to native fauna (Covington et al. 1997; Reinhardt et al. 2008). The upper Gila River Basin provides a prime opportunity for these management activities to occur, as it contains a largely-intact assemblage of imperiled fauna, is remote, and has a high potential for uncharacteristic wildfire (Bisson et al. 2003; O'Laughlin 2005). However, it is important to ensure that these management actions are not more harmful to natives than wildfire itself, as logging and road building required to conduct logging can result in many of the same effects (altered sedimentation, temperature, instream wood recruitment, and allochthonous resource inputs) as wildfire (Rieman et al. 2003; O'Laughlin 2005). Increasing inherent ecosystem resilience by keeping the upper Gila River unfragmented coupled with targeted nonnative removal in problem areas may be more beneficial to native fauna than these other management options (Bisson et al. 2003; Rieman et al. 2003). These activities may help ensure the pendulum of success swings back in favor of native fauna in the upper Gila River and elsewhere, as changing climate leads to more frequent and severe disturbances.

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