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Experimental Nonnative Wood Addition Enhances Instream Habitat for Native Fishes and Investigating Dryland River Alterations

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EXPERIMENTAL NONNATIVE WOOD ADDITION ENHANCES INSTREAM HABITAT FOR NATIVE FISHES AND INVESTIGATING DRYLAND RIVER ALTERATIONS

by

Benjamin J. Miller

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Phaedra Budy, Ph.D. Major Professor	Peter Wilcock, Ph. D. Committee Member
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UTAH STATE UNIVERSITY
Logan, Utah

2024

ABSTRACT

Experimental Nonnative Wood Addition Enhances Instream Habitat for Native Fishes and Investigating Dryland River Alterations

by

Benjamin J. Miller, Master of Science

Utah State University, 2024

Major Professors: Dr. Casey Pennock and Dr. Phaedra Budy
Department: Watershed Sciences

The extensive alteration of rivers in the western United States, driven in part by flow regulation, water overallocation, and the proliferation of invasive riparian vegetation (primarily tamarisk *tamarix spp.* and Russian olive *Elaeagnus angustifolia*), has led to widespread habitat loss and simplification, which is a major contributor to the imperilment of native fishes in the Colorado River Basin (CRB). Here, we assessed the effectiveness of enhancing native fish habitat by experimentally adding wood from invasive Russian olive to the main channel of the San Juan River, a highly simplified dryland river. Additionally, we quantified channel narrowing and vegetation encroachment, which are conspicuous indicators of riverine habitat alteration, for three dryland CRB tributaries by conducting a comparative analysis of remotely sensed data between historical and contemporary time periods. After wood addition, total native fish densities were 2.2x higher in treatments compared to references, whereas total nonnative fish densities exhibited no response. Macroinvertebrate densities were 6.8x higher, and habitat complexity increased in treatments. Counts of geomorphic features in treatments increased from 1 to a maximum of 11 following wood addition, while the number of features in references remained unchanged. The historical-contemporary comparative analysis revealed that, coinciding with a general decrease in flows over time, all three rivers underwent substantial channel narrowing, although the degree of narrowing varied among rivers (78%, 73%, and 29%). The magnitude of channel narrowing generally matched the deviation from historical spring floods, with large decreases in spring discharge corresponding to more pronounced channel narrowing. Contemporary woody cover was similarly high among all three rivers (39%, 31%, and 36% of valley bottom area), and there was a substantial increase in woody vegetation along the active channel (4% to 74%). Our results 1) suggest nonnative wood addition is an effective management action for enhancing native fish habitat, and 2) underscore the magnitude of river alteration in the region. Our findings emphasize that, when possible, preserving or restoring natural flows should be prioritized for the effective conservation of dryland rivers. In systems where flow management is not effective or is simply not an option, managers might consider non-flow physical habitat improvement alternatives, such as wood addition, to enhance habitat for native fishes.

(98 pages)

PUBLIC ABSTRACT

Experimental Nonnative Wood Addition Enhances Instream Habitat for Native Fishes and Investigating Dryland River Alterations

Benjamin J. Miller

The rivers of the Colorado River Basin (CRB) have been degraded by human activities such flow regulation, water overallocation, and the introduction of invasive riparian vegetation (primarily tamarisk *tamarix spp.* and Russian olive *Elaeagnus angustifolia*). These stressors have resulted in widespread habitat loss and simplification, which is a major contributor to the endangerment of native fishes in the CRB.

The objectives of this study were to 1) assess the effectiveness of enhancing native fish habitat by experimentally adding cut wood from nonnative Russian olive to the San Juan River, a highly degraded dryland river, and 2) determine the magnitude of channel narrowing and vegetation encroachment over time, which are indicators of riverine habitat alteration, for three dryland CRB tributaries. Addressing these objectives can provide valuable insights to assist managers in more effectively restoring habitats for endangered native fish species.

Our results indicate that wood addition can lead to increased local abundances of native fishes, which is likely due to the increased food resources and higher habitat quality that wood addition facilitated. Additionally, we demonstrated that all three study rivers underwent substantial vegetation encroachment and channel narrowing, the latter of which coincided with a general decrease in river flows over time, with large decreases in flows corresponding to more pronounced channel narrowing. We therefore provide

evidence supporting nonnative wood addition as an effective management action for enhancing native fish habitat while also underscoring the magnitude of river alteration in the region. Our findings emphasize that, when possible, preserving or restoring natural flows should be prioritized for the effective conservation of dryland rivers. In systems where managing flows is not feasible, managers may consider non-flow methods, like adding in-stream wood, to improve native fish habitats.

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CHAPTER 1

INTRODUCTION

Freshwater biodiversity is declining at a disproportionally high rate compared to other biomes, with freshwater vertebrate populations declining at rates roughly twice as high as those of marine and terrestrial systems (WWF 2020). Habitat loss and degradation is a major driver of riverine biodiversity decline and is largely the result of anthropogenic activities such as water overallocation, land use perturbations, and water control infrastructure such as dams and levees (Dudgeon et al. 2006, Vörösmarty et al. 2010). In North America, the imperilment rate of freshwater fishes continues to rise, with roughly 50% of all fish taxa either vulnerable, threatened, or endangered (Jelks et al 2008; Burkhead 2012). North America is home to a strikingly diverse array of fishes that hold immense economic, recreational, personal, and intrinsic value for the people also residing there. Tragically, over the past century, at least 57 freshwater fish taxa have been driven to extinction. On the other hand, thanks to the resilient nature of fishes as well as the dedicated efforts of conservators, scientists, environmentalists, and lawmakers, approximately 95% of all freshwater fish taxa still exist in North American waters. There remains a looming threat that an increasing number of fishes may face extinction as the 21st century progresses (Burkhead 2012). The recovery of imperiled fish populations to non-alarming levels has proven challenging for most species, primarily due to competing social demands impeding many potential avenues of conservation. Consequently, there is a need for conservators to persist in exploring varied strategies for native fish recovery, while also investigating historical trends that may aid in illuminating potential future approaches.

The Colorado River Basin (CRB), draining large portions of western North America, is one of the most extensively altered major river basins in the world. Human water consumption typically accounts for 100% of its annual flow; consequently, the Colorado River does not reach its terminus in the Gulf of California in most years. Euro-American settlement in the basin primarily occurred in the 1800s, and by the late 1900s, most native fish species were threatened or imperiled (Minckley and Deacon 1991). Although major successes have been made in the conservation of native CRB fishes, such as avoiding extinction in most species, the plight of native fishes remains precarious, as the majority of these native fish populations remain at-risk, and for the same reasons that initially threatened their existence (Propst et al. 2021). Despite these challenges, there remains hope that through advancements in scientific understanding, shifts in social attitudes, progresses in technology, and the development of novel perspectives, that native fishes can ultimately prevail.

The complexities surrounding the imperilment of native fish in the CRB can be simplified to two fundamental stressors: 1) invasion of nonnative fishes and 2) habitat loss. Nonnative fishes are theorized to compete with and predate on native fishes, particularly early life stages, thereby limiting or precluding native fish recruitment in many systems (e.g., Marsh and Langhorst 1998; USFWS 2018). The establishment of nonnative fishes is thus implicated in the decline of native fish populations across the basin (Tyus and Saunders 2000; Mueller 2005). The detrimental impacts of nonnative fishes are worsened by habitat loss and fragmentation, primarily a consequence of extensive river alterations throughout the basin that has resulted in the loss of important habitat features such as deltas, wetlands, floodplains, confluences, backwaters, and complex in-stream habitat (see Minckley 1973; Minckley et al. 2003). Efforts to improve habitat is severely hindered because the Colorado River serves as the primary source of water to 30 million people and 4 million acres of farmland (Wheeler et al. 2021). Consequently, water control practices and associated infrastructures typically take precedence over native fish conservation. Addressing habitat loss in the CRB, therefore, often necessitates exploring alternatives beyond addressing the evident root causes.

Large woody debris (wood) addition to streams and rivers is one such approach for enhancing habitat for fishes. Although extensive research has been conducted on wood addition in lotic systems, this approach has not been thoroughly investigated for large dryland rivers, particularly in the CRB. In Chapter 2, to investigate a potential approach to habitat enhancement, we experimentally added nonnative wood to the San Juan River, a major tributary to the Colorado River that has experienced substantial habitat degradation. Invasive trees, primarily tamarisk *tamarix spp.* and Russian olive *Elaeagnus angustifolia*, form dense thickets along the San Juan River, and many other rivers in the region, and contribute to habitat simplification (e.g., Laub et al. 2015; West et al. 2020). We hypothesized that the high abundance of invasive vegetation may serve as a potential resource for enhancing in-stream habitat when cut and added to the river. We predicted that nonnative wood addition would enhance habitat for native fishes by increasing structural, hydraulic, and geomorphic complexity as well as increasing food sources by promoting macroinvertebrate colonization of wood.

It is well-known that systems in the CRB have been negatively impacted by human activities, but alterations in many rivers have not been investigated and documented in the literature. In chapter 3, we quantified channel narrowing and riparian vegetation encroachment, two conspicuous indicators of river alteration, over large spatial extents for three tributaries of the Colorado River. We then compared riverine changes in the context of substantial and modest flow regime alterations. We expected the extent of channel narrowing and vegetation encroachment to generally relate to the degree to which spring flood magnitude and duration have been reduced in these three rivers.

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CHAPTER 2

EXPERIMENTAL INVESTIGATION OF NONNATIVE WOOD ADDITION FOR ENHANCING IN-STREAM HABITAT FOR NATIVE DRYLAND FISHES[1]

Abstract

Flow alteration and riparian vegetation encroachment are causing habitat simplification with severe consequences for native fishes. To assess the effectiveness of enhancing simplified habitat in a large dryland river, we experimentally added invasive wood at 19 paired treatment and reference (no wood added) subreaches (50 - 100m) within the main channel of the San Juan River. Using a before-after-control-impact design, we sampled fishes and macroinvertebrates, and quantified habitat complexity. After wood addition, total native fish densities were 2.2x higher in treatments compared to references, whereas total nonnative fish densities exhibited no response. Macroinvertebrate densities were 6.8x higher, and hydraulic and geomorphic complexity increased in treatments. Counts of geomorphic features in treatments increased from 1 to a maximum of 11 following wood addition, while the number of features in references remained unchanged. Wood addition has potential to instigate natural riverine processes, ultimately enhancing native fish habitat by increasing macroinvertebrate densities and habitat complexity in dryland rivers. Water overallocation and increasing aridity will continue to challenge efforts to improve habitat conditions with environmental flows

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[1] Co-Authored with Dr. Casey Pennock and Dr. Phaedra Budy

alone, and managers might consider integrating non-flow alternatives like addition of abundant, invasive wood to reduce habitat simplification.

Introduction

In riverine ecosystems, a natural flow regime is important for overall ecological health and is the major driver of diverse habitat creation and maintenance (Poff et al. 1997; Bunn and Arthington 2002; Humphries et al. 2020). However, few rivers retain a natural flow regime due to anthropogenic perturbations such as water abstraction, land use alteration, and the construction of dams and levees (Benke 1990; Dudgeon et al. 2006; Vörösmarty et al. 2010). Flow regime alteration results in the loss of stream power (e.g., spring floods) and can lead to instream habitat simplification through mechanisms such as channel width reduction, valley alluviation, channel incision, and a shift from a complex to a simple channel form (e.g., Benke 1990; Fortney et al. 2011; Grams et al. 2020). Habitat simplification from flow alteration is exacerbated by encroachment on formerly active channel features by riparian vegetation, which can be in the form of both native and invasives species, such as tamarisk (*tamarix spp.*) and Russian olive (*Elaeagnus angustifolia*). Vegetation encroachment reduces bank erosion and lateral channel migration, contributing to further habitat simplification (Friedman et al. 1998; Laub et al. 2015; West et al. 2020). Given the prevalence of flow regime alteration and associated habitat simplification, approaches to enhance instream habitat through direct measures are needed.

River managers have long recognized the importance of habitat complexity for aquatic organisms and have thus enacted many strategies to enhance instream habitat. Environments consisting of diverse and spatially heterogenous habitat are known to generally support higher biodiversity, promote increased productivity, and exhibit greater community stability (e.g., Holt 1984; Rooney et al. 2008; Scholl et al. 2023). Because stream fishes adapted to natural flow regime disturbances by developing life history strategies that exploit spatial and temporal heterogeneity in flow and habitat (Winemiller and Rose 1992; reviewed by Lytle and Poff 2004; Mims and Olden 2012), fishes require access to diverse and complimentary habitat types to complete their life cycle (Schlosser 1991). One method for restoring instream habitat in regulated rivers is through the implementation of environmental flow releases from dams, with the aim of mimicking important features of the natural flow regime (Acreman et al. 2014). However, the effectiveness of this approach is often hindered by conflicts between human water use and ecosystem need, limitations of infrastructure to deliver sufficiently large flows, and challenges of non–stationarity (Bruckerhoff et al. 2022; Pennock et al. 2022a; Wineland et al. 2022). Thus, in systems where environmental flow implementation is hindered or simply absent, efforts to directly manipulate physical habitat, such as the addition of large woody debris, may be required to enhance instream habitat (Buffington et al. 2014; Yarnell et al. 2018; Grantham et al. 2020).

Large woody debris (wood hereafter) is widely recognized as a vital component of many healthy riverine ecosystems and inclusion of wood in habitat enhancement efforts is a relatively common practice in rivers draining forested landscapes (Roni et al. 2008; Grabowski et al. 2019). Wood not only provides ecological benefits from within-structure processes and conditions but, through its interaction with flow and sediment regimes, wood is also an integral component of stream channel geomorphic processes at broader scales (Wohl et al. 2019). For example, wood influences channel geometry by forcing hydraulic diversity which can result in the formation of multiple habitat types in close proximity such as side channels, pools (i.e., low velocity), bars, islands, and channel avulsions (Gippel 1995; reviewed by Wohl et al. 2019). Wood addition can lead to local increases in fish and macroinvertebrate densities, biomass, and species richness (e.g., Angermeier and Karr 1984; Schneider and Winemiller 2008; Clark et al. 2019). Wood addition can also increase food resources for fishes by providing labile surfaces for both periphyton and macroinvertebrate production, which might be particularly beneficial in rivers with low productivity or dominated by unstable, mobile substrates (Benke et al. 1985; Crook and Robertson 1999). Woody debris can facilitate energetically favorable conditions (e.g., low-high velocity shear lines) and reduce intensities of predator-prey interactions by decreasing encounter rates due to diminished lines of sight and providing escape cover (Everett and Ruiz 1993; Sundbaum and Näslund 1998; Janssen et al. 2007). Due to its many benefits, wood addition often plays a crucial role in process-based restoration efforts, which aim to mitigate anthropogenic disruptions in river and floodplain ecosystems by restoring normative rates and magnitudes of natural processes with minimal corrective intervention (e.g., Beechie et al. 2010).

Despite the well-documented ecological role of wood and its significance in river restoration, there are still ecosystems, such as large dryland rivers, where the effects of wood addition remain relatively understudied. Rivers in the Colorado River basin (CRB), draining portions of the American Southwest and Northern Mexico, are pervasively affected by flow alteration, including large mainstem dams and water abstraction, as well as alterations in riparian vegetation due to invasion of woody species such as tamarisk and Russian olive (Stromberg et al. 2007; Macfarlane et al. 2017; Scott et al. 2018). Flow alteration and nonnative vegetation encroachment have played a major role in the loss of habitat complexity throughout the CRB, which in turn has contributed to dramatic declines in both the distribution and abundance of native fish populations, many of which remain in dire standing despite intensive, and expensive, management efforts (Minckley and Deacon 1968, 1991; Propst et al. 2021; Comte et al. 2022). In dryland CRB rivers, riparian woody vegetation cover has generally increased over time from relatively low historical levels (Webb and Leake 2006). Although abundant in-channel woody debris might not represent a historical precedent for restoration, enhancing habitat complexity with wood addition could initiate hydraulic and geomorphic processes that ultimately lead to diverse riverine geomorphology more representative of earlier conditions (e.g., Wohl et al. 2019; Wheaton et al. 2019).

Instream habitat is simplified in the San Juan River (SJR), a major tributary to the Colorado River, because of flow alteration and encroachment of invasive vegetation (Bliesner and Lamarra 2000, Franssen et al. 2007; Pennock et al. 2022b). Increases in riparian vegetation density, most recently by invasive Russian olive, has armored riverbanks, further reducing complex habitat formation through processes such as channel confinement and narrowing as well as reductions in channel form complexity (Bliesner and Lamarra 2000; Figure 1). Nevertheless, the existence of abundant nonnative woody vegetation may present a potential opportunity for enhancing simplified habitat through the addition of wood to the SJR. We conducted a field experiment in which we added Russian olive branches to the main channel of the SJR to assess the effectiveness of using additions of invasive woody vegetation to enhance in-stream habitat for native fishes in a large dryland river. We hypothesized wood addition would result in the following outcomes: 1) an increase in local abundances of native and nonnative fishes, 2) higher biomass of macroinvertebrates, and 3) improved physical habitat quality for fishes through reduced flow velocities and increased habitat complexity. The SJR is representative of other degraded dryland rivers in the CRB where flow regulation, overallocation of water, and establishment of nonnative riparian vegetation have contributed to broad scale habitat simplification. Results from this study are applicable to developing non-flow alternatives for enhancing habitat for native dryland fishes in the CRB, as well as in other dryland basins and sand-bed rivers.

Methods

Study area and background

The SJR originates in the San Juan Mountains of southwest Colorado and flows through portions of Colorado, New Mexico and Utah before joining the Colorado River in Lake Powell (Figure 1). Historically, the SJR exhibited large inter- and intra-annual variability in discharge, a characteristic of many rivers in the American Southwest, with large and sustained flows driven by montane snowmelt in the spring and early summer, followed by lower baseflows in summer, autumn, and winter. The occurrence of monsoonal rains in late summer and autumn can lead to short-duration, high flow events, occasionally of considerable magnitude. Coincident with an array of nonnative fishes, six native fish species currently exist in the SJR in our study area, including two federally listed species, the Colorado pikeminnow *Ptychocheilus lucius* and razorback sucker *Xyrauchen texanus*, and three species listed as a conservation priority by a multistate agreement (UDWR 2006). Populations of the two federally listed species are sustained through stocking of hatchery-reared fish. Without continued stocking, these populations would decline towards extirpation (USFWS 2018, 2020). Hypothesized constraints limiting juvenile recruitment in the SJR are high emigration, few spawning adults, predation by nonnative fishes, and a lack of rearing habitat (Brandenburg and Gido 1999; Diver et al. 2021; USFWS 2018, 2020).

Closure of Navajo Dam in 1962 altered the flow regime and resulted in dramatically dampened springtime flows (61% of pre-dam) along with elevated baseflows in summer, autumn, and winter (Propst and Gido 2004). The ongoing megadrought in the American Southwest has also contributed to diminished flows in the SJR, primarily through reduced springtime runoff (Williams et al. 2020). Beginning in 1993, releases from Navajo Dam were elevated in the spring to mimic the timing, duration, and magnitude of high flows resulting from montane snowmelt runoff from the unimpounded Animas River. The goal of this effort was to increase abundance of important habitat types, particularly low velocity habitats, for native fishes while disadvantaging nonnative fishes (Gido and Propst 2012); however, dam releases are limited to 140 m^3/s (5000 cfs) due to infrastructure constraints (Holden 1999; Bliesner and Lamarra 2000; BOR 2006). Flow targets have not been met in most years because consumptive water use has been prioritized over environmental flows (Pennock et al. 2022a). In addition to an altered flow regime, establishment of nonnative Tamarisk and Russian olive in riparian areas of the SJR has contributed to declines in active channel width and in-stream habitat complexity via bank armoring, resulting in a stabilized channel with limited lateral movement; a phenomenon that has been well documented in other rivers in the region (e.g., Fortney et al. 2011, Dean and Schmidt 2011). Overall, the SJR has experienced a substantial decline in habitat complexity since being impounded, as evidenced by channel narrowing, a lack of floodplain connectivity, and a scarcity of quality low-velocity habitats, ultimately hindering the recovery of endangered fish species (Bliesner and Lamarra 2000; Hansen 2023).

Experimental design

Our experimental design consisted of river reaches equally partitioned into paired reference and treatment subreaches (range: 50 – 100 m, Figure 2). In 2021 and 2022, we established multiple (2021: n = 12, 2022; n =7) reference-treatment pairs (hereafter sites) throughout the study area (~ 80 river km, Figure 1), located in southeast Utah and northwest New Mexico and within the borders of the Navajo Nation. River managers have identified eight distinct river reaches on the SJR based on quantitative geomorphological differences (Bliesner and Lamarra 2000); we concentrated sites in two distinct geomorphic reaches of the SJR (3 and 4; sensu Bliesner and Lamarra 2000) where juvenile (age–0 and age–1) Colorado pikeminnow are most consistently captured (Zeigler et al 2018). We selected site locations within these geomorphic reaches based on accessibility and habitat homogeneity between reference and treatment subreaches.

In September of each year, we collected baseline samples of fishes, macroinvertebrates, and habitat (depth, velocity, dominant substrate size, and in the second year, geomorphic features) at all sites prior to wood addition. To prevent treatment subreaches affecting reference subreaches (e.g., downstream movement of added wood), reference subreaches were located upstream of treatment subreaches. Immediately after baseline sampling, we added woody structures (width x length: approximately 2m x 4m) to treatment subreaches consisting of cut Russian olive trees (approximately 1 – 3 m branches/trunks). In 2021, we added 10 structures to each treatment subreach. In this first year of our study, we noticed extensive evidence of beaver dismantling wood piles at some sites and variable flows left some piles stranded near active channel margins. Thus, we adapted our design in 2022 by adding 5 structures of larger size to each treatment subreach, enabling the placement of structures in deeper water and preventing the complete dismantling of structures by beaver. We maintained wood structure position for the duration of the experiment by driving untreated wooden posts (~10 cm diameter) into the riverbed within the woody structures (*n* = 4 - 6) using a gas-powered, hand-held post pounder. Following wood addition, we resampled both reference and treatment subreaches on a nearly monthly basis throughout the fall and winter (October, November, December), and again in March or April the following spring.

Fish and macroinvertebrate sampling

We sampled fishes using a straight seine (one pass per subreach; 1.8 m x 4.6 m, 3 mm mesh) and a backpack electrofisher (in and around wood structures present in treatment subreaches; Smith-Root LR24). In the field, we identified and measured total length (mm) of all captured fishes. We sampled benthic macroinvertebrates using a D-framed kick net (500 µm mesh) in both subreaches and wood scrubs in treatment subreaches. We sampled benthic macroinvertebrates at three equally-spaced points along three transects perpendicular to shore and distributed longitudinally (top, middle, and bottom) within each subreach (*n* = 9). We also collected wood scrub samples from submerged branches of woody structures in treatment subreaches (*n* = 3). We measured the dimensions (length x diameter) of each wood section to calculate area sampled. Each kick net sample was approximately 0.1 m^2. We combined all kick net samples and wood scrubs from a subreach into respective composite samples. We elutriated samples in a bucket to separate macroinvertebrates from substrate, poured the elutriated samples through a sieve (500 µm mesh), and preserved samples in 95% ethanol. In the laboratory, we identified macroinvertebrates to order or family and counted all individuals from each taxonomic group. Taxonomic groups that constituted less than 1% of all macroinvertebrates encountered were grouped as “other” and oligochaetes were counted in year 1 only. We estimated macroinvertebrate biomass by measuring bulk dry mass (dried for 24 hours at 60°C) of all macroinvertebrates from each sample. All sampling was performed under the auspices of the USU IACUC protocol No. 12145.

Habitat assessments

We measured water velocity (Marsh McBirney Flo-Mate 2000), water depth, and dominant substrate particle size (Wentworth 1922) immediately downstream and within each woody structure (hereafter near-structure; $n = 2$ per structure) as well as at five equally-spaced points along three transects within each subreach ($n = 15$). Habitat characteristics were measured along the same three transects where benthic macroinvertebrate samples were collected. In 2022-2023, we assessed geomorphic responses induced by woody structures by conducting on-site assessments of subreaches where we identified and enumerated geomorphic features. Also in 2022-2023, we took aerial photographs of subreaches with a drone (DGI Mavic 2) to track geomorphic responses over time. We imported aerial drone imagery into a GIS where geomorphic features were manually digitized and represented as polygons to enable calculation of the proportion of subreach area occupied by each geomorphic feature. We classified geomorphic features into five categories: bed scour, chute, forced bar, woody debris, and run (sensu Wheaton et al. 2015).

Data analysis

All data were processed in R version 4.30 (R Core Team 2023).

Fish and macroinvertebrate abundance

To assess the impact of wood addition on fish abundance, we compared total native and non-native fish densities (fish/m^2) between reference and treatment subreaches using a before-after/control-impact (BACI) design which included the additive and interactive effects of before-after and control-impact (i.e., reference-treatment). We used a generalized linear mixed-effects model (GLMM) using the glmmTMB R package (Brookes et al. 2017). We used a Tweedie distribution with a log-link function because data were positive and continuous and included zeroes. Fish densities vary longitudinally in the San Juan River (Franssen et al. 2015), and our experimental reaches were spread across two geomorphic reaches. Therefore, to account for potential spatial variation, we included geomorphic reach (categorical) as a fixed effect in the model. We also included study year (categorical) as a fixed effect to account for differences between years and included sampling month as a random effect to account for repeated sampling over time. To compare total macroinvertebrate biomass (mg/m^2) between reference and treatment subreaches, we used a linear mixed-effects model (LMM) with the same model structure as described above. We combined data from kick net and wood samples to represent macroinvertebrate abundances in treatment subreaches. For both models, we inspected residual plots to determine if model assumptions were reasonably met. We assessed statistical significance ($\alpha = 0.05$) of fixed effects using Wald tests with the *Anova* function in the car package (Fox and Weisberg 2019). Finally, we used the performance package (Lüdecke et al. 2021) to calculate marginal R^2 and conditional R^2 for mixed effects models, which represent the variance explained by fixed effects alone and by both fixed and random effects combined, respectively (Nakagawa et al. 2017).

Habitat

We used habitat heterogeneity (coefficient of variation; CV) and counts of geomorphic features as measures of habitat complexity within treatment and reference subreaches. To test for differences in habitat heterogeneity between reference and treatment subreaches, we used a LMM with the CV of depth, velocity, and dominant substrate size as response variables. We used the same fixed effect structure as described above and again included sampling month as a random effect to account for repeated measures. To evaluate our hypothesis that wood addition would lower water velocities, we also fit a GLMM for velocity data and assumed a Tweedie distribution with a log-link function because data were positive and continuous and included zeroes. All habitat models incorporated data from transect and near-structure measurements to represent conditions within treatment subreaches. For each model, we assessed residual plots and calculated marginal and conditional R^2 as described above.

Results

The data that support the findings of this study are available in the DigitalCommons@USU repository at https://doi.org/10.26078/mtdx-fz41.

Fish response

In total, we captured 4,489 fishes across all sampling events in both years (Table 2). Notably, captures of all species were substantially lower during the second year of the study (2022-2023; Table 2). Native fishes comprised 11% of the total catch; flannelmouth sucker *Catostomous latipinnis* (*n* = 250) was the most abundant native species, followed by speckled dace (*n* = 172). Captures of nonnative fish were dominated by red shiner *Cyprinella lutrensis* (*n* = 1806) followed by channel catfish *Ictalurus punctatus* (*n* = 329).

Native fishes responded positively to wood addition in treatment reaches, while nonnative fishes demonstrated no response. For native fishes, the BACI interaction was statistically significant (GLMM: $p = 0.02$; Table 3). Before wood addition, native fish densities were variable among sites but similar between reference and treatment subreaches (Figure 3). After wood addition, native fish densities declined and were less variable among reference subreaches (mean ± SE; 0.005 ± 0.001 fish/m^2) but remained higher in treatment subreaches (0.011 ± 0.002; Figure 3). Conversely, the BACI interaction term was not significant for nonnative fishes ($p = 0.14$; Table 3), and densities in both reference (0.047 ± 0.014 fish/m^2) and treatment (0.048 ± 0.010) subreaches declined and became less variable among subreaches over time (Figure 3).

Macroinvertebrate response

Diptera, namely chironomidae and simuliidae, was the most abundant group encountered, followed by ephemeroptera, oligochaeta, trichoptera, and plecoptera (Table 4). As observed with fishes, macroinvertebrate biomass was generally lower in the second year of the study, particularly for diptera and ephemeroptera (Table 4).

Additionally, wood addition demonstrated a strong positive effect on macroinvertebrate biomass as indicated by a statistically significant BACI interaction (LMM: $p < 0.001$; Table 3, Figure 3). After the addition of wood, average macroinvertebrate biomass in treatment subreaches was 6.8x higher than reference subreaches (mean ± SE; 219 ± 45 and 32 ± 12 mg/m^2, respectively). This result was driven by high macroinvertebrate colonization of wood structures in treatment subreaches (244 ± 51 mg/m^2) compared to benthic samples (30 ± 6).

Habitat response

Habitat heterogeneity and geomorphic feature count responded positively to wood addition in treatment reaches, whereas these measures either increased marginally, remained unchanged, or declined in reference subreaches. The CV of all three habitat characteristics (depth, velocity, and dominant substrate particle size) exhibited a significant BACI interaction (LMM: depth $p = 0.001$; velocity $p < 0.001$; substrate $p = 0.04$; Table 3, Figure 4), with higher CV values observed in treatment subreaches compared to reference subreaches, indicating higher habitat heterogeneity induced by wood addition. Overall water velocities (i.e., combined transect and near–structure measurements) were significantly lower in treatment subreaches after the addition of wood, but increased over time in reference subreaches due to general increases in discharge over the study period (GLMM: $p < 0.001$; Table 3, Figure 4). The number of geomorphic features in treatment subreaches (not including wood structures) increased from 1 (run) to a maximum of 11 two months after wood addition (Figure 5). This effect was relatively consistent across sites (7.9 ± 0.4) and was maintained into the spring. Conversely, in reference reaches, no additional geomorphic features formed over the study period. The formation of geomorphic features in treatment subreaches primarily occurred during periods of increased discharge and sediment mobility associated with monsoonal activity, facilitated by the presence of woody structures that appeared to induce diverse hydraulic conditions. These conditions led to variable sediment aggradation and degradation, ultimately resulting in the development of sand/silt bars, chutes, and bed scours (Figures 2 and 5).

Discussion

Our findings provide experimental evidence demonstrating nonnative wood addition in a simplified, large dryland river led to rapid localized increases in habitat complexity and abundances of macroinvertebrates and native fishes. While the positive effects of wood addition in rivers are well-documented (e.g., Angermeier and Karr 1984; Brooks et al. 2004; Schneider and Winemiller 2008), these techniques to enhance instream habitat have not been thoroughly tested and adapted in dryland rivers where instream wood was not as historically abundant as forested rivers in wetter climates, but likely still held ecological significance (Minckley and Rinne 1985, Wohl et al. 2018). Furthermore, wood that is now available consists almost entirely of nonnative species and given the pervasive habitat simplification from flow reduction and riparian vegetation encroachment, there is an opportunity for adding woody vegetation to rivers to enhance in-stream habitat for native biodiversity in rivers of differing sizes and landscape settings. Identification of non-flow alternatives to restore and maintain instream habitat is particularly important in river systems where the amount of water available for adequate environmental flows is limited by water availability, infrastructure, and societal demands (Bruckerhoff et al. 2022; Pennock et al. 2022a; Wineland et al. 2022).

The higher abundance of native fishes in the treatment subreaches can likely be attributed to the enhanced habitat complexity and increased availability of food resources in those areas, both of which were facilitated by the addition of woody structures. Wood addition resulted in a variety of geomorphic features and hydraulic conditions such as sand/silt bars, chutes, bed scours, and a wide range of flow velocities, depths, and substrate particle sizes. We frequently captured flannelmouth sucker along edge habitats near woody structures, where areas of low-velocity flow and fine sediments were in close proximity to areas of higher velocity and coarse substrates. These edge habitats contrasted to the relatively homogenous habitat conditions observed in the reference subreaches, where no fish response was observed. High habitat complexity has been widely demonstrated to promote greater fish abundances (reviewed by Smokorowski and Pratt 2007; Cornell et al. 2022). The fundamental drivers behind this phenomenon is that high habitat complexity can promote higher food production, provide refuges from predators and high flows, lead to stabile predator-prey interactions, and offer diverse microhabitats; thus, creating opportunities for more individuals, and potentially more species, to inhabit a specific area through habitat and niche partitioning (Holt 1984; Soukup et al. 2022; Scholl et al. 2023). In addition to high habitat complexity, the observed high densities of macroinvertebrates within the woody structures likely provided a food source for fishes in treatment subreaches. The bed material in experimental reaches was primarily unstable fine sediments, which is known to have lower algal and macroinvertebrate production (e.g., Way et al. 1995; Rier and King 1996; Benke 2018). As such, woody structures likely served as colonization surfaces and provided energy sources for macroinvertebrates in the form of wood and entrapped leaf litter, fostering periphyton growth and subsequent colonization by macroinvertebrates (Entrekin et al. 2009; Flores et al. 2011).

While we expected both native and nonnative fishes to respond positively to the complex habitat facilitated by wood addition treatments, we were surprised by the lack of response by nonnative fishes which may be attributed to species-specific habitat selection. Our results for nonnative fishes were predominantly driven by channel catfish and, particularly, red shiner, which is a widespread habitat generalist (Matthews 1985; Archdeacon et al. 2022). An analysis of red shiner across a large portion of its geographic range determined that neither environmental variables nor measures of habitat complexity explained patterns in relative abundance (Marsh-Matthews and Matthews 2000). As such, the lack of response by red shiner to the increase in local habitat complexity is likely due to the species' highly generalist nature. In contrast to red shiner, channel catfish densities were somewhat higher in treatment subreaches (1.5x on average), which suggests wood addition might benefit this species to some degree, a finding that aligns with prior research indicating channel catfish prefer habitats with low water velocities and woody cover (e.g., Paragamian 1990; Kelsch and Wendel 2004). Negative interactions with nonnative fishes are one of the top hypothesized factors contributing to native fish declines in the CRB (Tyus and Saunders 2000; Clarkson et al. 2005; Propst et al. 2021). Although some nonnative fish might have responded somewhat positively to wood addition, the strong positive response demonstrated by native fishes to increased habitat complexity and food availability remains, even when sharing these resources with non-native fishes.

Differences in hydrology and monsoon activity among years likely contributed to some of the patterns we observed in fish and macroinvertebrate abundance. We observed a general decline in fish (all species) and macroinvertebrate abundance over the course of our experiment. This pattern aligns with observations made by other researchers conducting concurrent fish sampling throughout the SJR in 2021-2022 as part of other monitoring and research (e.g., Hansen 2023), as well as long-term declines in fish densities coinciding with a failure to achieve recommended environmental flows (Pennock et al. 2022a). Legacies of poor water quality following a large monsoon event in 2021 might be one potential explanation. For instance, a fish kill was observed in July 2021 upstream of our experimental reaches (Whitney et al., In Press). Researchers observed dead fish of multiple species and sizes, including crayfish and other macroinvertebrates (e.g., hellgrammites) on sand bars following recession of flood waters; although the specific aspects of water quality impacted by this large monsoon flood are unknown, this event corresponded with generally low fish densities that lingered into 2022 throughout the SJR (Whitney et al., In Press). There were also more monsoonal floods in 2022 relative to 2021, which could have contributed to generally lower abundances in the second year (Figure 1). Both years in our experiment had relatively active monsoon seasons and small magnitude and duration snowmelt floods with peak annual daily flows occurring in August 2021 and September 2022. These high magnitude monsoonal floods could have killed or displaced smaller fishes and macroinvertebrates prior to our experiment beginning in each year.

Our experiment was designed as a first step to assess potential benefits of wood addition using abundant invasive vegetation in a large dryland river to enhance instream habitat, and consequently, our results were localized in terms of fish and macroinvertebrate abundance, as well as habitat complexity. To achieve broader-scale changes in habitat complexity or population-level responses by fishes (i.e., production vs attraction), this type of habitat enhancement would likely need to take place and be tested over larger reaches of river (1-10 km) and over longer periods of time (i.e., multiple years). Fish responses to habitat enhancement efforts are scale-dependent, mirroring the scale-dependence of their ecology across various life stages and behaviors (Durance et al. 2006; Keller 2023). Hydrologic and geomorphic processes can also respond to restoration efforts differently based on the scale at which they are implemented (Polvi et al. 2020). Further research is needed to assess potential reach-scale fish, macroinvertebrate, and hydrogeomorphic responses and longer-term effects, as the localized effects demonstrated here are likely not fully representative of the outcomes of wood addition at broader spatiotemporal scales.

Conclusion

Our finding of increased abundances of native fishes following wood addition contribute to a substantial body of literature indicating wood addition typically leads to higher fish densities; however, most of these studies were conducted in small and medium-sized rivers and focused on salmonids (reviewed by Nagayama and Nakamura 2010). Due to anthropogenic stressors such as climate change, land use alteration, and flow reduction from water abstraction and the construction of dams, large dryland rivers are experiencing habitat degradation worldwide (e.g., Barmuta 2003; García et al. 2010; Gozlan et al. 2019). While flow management has been the primary tool used by managers to improve habitat conditions for native fishes in large dryland rivers, this approach is increasingly less effective with chronic water overallocation and increased aridity (Chen et al. 2020; Ryan et al. 2021). Given the daunting scale of river habitat degradation and the typically limited options available to managers, there is a need to consider a diversity of mitigation techniques for addressing this challenge more effectively (e.g., Valdez et al. 2023). Our results suggest that wood addition has the potential to ameliorate simplified habitat conditions in large dryland rivers by instigating natural riverine processes.

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Tables and Figures

Table 2-1. Model structure used to test effects of experimental wood addition for fish captures in the San Juan River, NM & UT 2021-2023.

Response	Model type	Distribution	Link	Fixed effects	Random effects
Native fish density Nonnative fish density	GLMM	Tweedie	Log	Geomorphic reach Study year Before-after Control impact BA:CI interaction term	Sampling month
Macroinvertebrate density	LMM	Gaussian	Identity	Geomorphic reach Study year Before-after Control impact BA:CI interaction term	Sampling month
Depth CV Velocity CV Substrate size CV	LMM	Gaussian	Identity	Before-after Control impact BA:CI interaction term	Sampling month
Velocity	GLMM	Tweedie	Log	Before-after Control impact BA:CI interaction term	Sampling month

Table 2-2. Number of fishes captured in reference and treatment subreaches and overall lengths (mm, TL) across all sampling, September 2021 - April 2023 in the San Juan River, NM & UT.

	Year 1 (fall 2021 - spring 2022)		Year 2 (fall 2022 - spring 2023)			
Species	Reference	Treatment	Reference	Treatment	Mean TL (range)	Proportion of total catch
Red Shiner *Cyprinella lutrensis*	1662	1385	27	14	49 (14-85)	0.69
Channel Catfish *Ictalurus punctatus*	357	397	56	60	67 (27-520)	0.19
Flannelmouth Sucker* *Catostomus latipinnis*	90	138	3	19	153 (44-490)	0.06
Speckled Dace* *Rhinichthys osculus*	59	68	9	36	65 (33-98)	0.04
Fathead Minnow *Pimephales promelas*	19	14	0	12	52 (28-73)	0.01
Bluehead Sucker* *Catostomus discobolus*	10	12	0	0	142 (52-288)	< 0.01
Western Mosquitofish *Gambusia affinis*	3	13	0	0	28 (22-37)	< 0.01
Colorado Pikeminnow* *Ptychocheilus lucius*	9	5	0	1	165 (115-222)	< 0.01
Black Bullhead *Ameirus melas*	4	2	0	2	63 (41-152)	< 0.01
Razorback Sucker* *Xyrauchen texanus*	0	1	0	1	436 (378-493)	< 0.01
Common Carp *Cyprinus carpio*	0	1	0	0	145	< 0.01

*denotes native species

Table 2-3. Output from linear mixed effects models (LMM) and generalized linear mixed effects models (GLMM) testing fixed effects used in wood addition experiment in the San Juan River NM & UT, 2021-2023.

Response	Model type	Fixed effects	χ^2	*df*	*p*	Marginal R^2	Conditional R^2
Native fish density	GLMM	Geomorphic reach: 4	11.22	1	< 0.001	0.23	0.45
		Study year: 2	1.22	1	0.27		
		Before-after: after	0.59	1	0.44		
		Control-impact: impact	11.45	1	< 0.001		
		Before-after: after*Control-impact: impact	5.50	1	0.02		
Nonnative fish density	GLMM	Geomorphic reach: 4	23.33	1	< 0.001	0.45	0.74
		Study year: 2	40.91	1	< 0.001		
		Before-after: after	2.07	1	0.15		
		Control-impact: impact	0.09	1	0.76		
		Before-after: after*Control-impact: impact	2.21	1	0.14		
Macro-invertebrate density	LMM	Geomorphic reach: 4	3.02	1	0.22	0.34	0.45
		Study year: 2	2.66	1	0.10		
		Before-after: after	2.98	1	0.08		
		Control-impact: impact	33.32	1	< 0.001		
		Before-after: after*Control-impact: impact	14.33	1	< 0.001		

Table 2-3. (cont.)

Depth CV	LMM	Before-after: after	0.16	1	0.69	0.10	0.48
		Control-impact: impact	13.99	1	< 0.001		
		Before-after: after*Control-impact: impact	10.23	1	0.001		
Velocity CV	LMM	Before-after: after	0.02	1	0.89	0.40	0.54
		Control-impact: impact	81.71	1	< 0.001		
		Before-after: after*Control-impact: impact	41.70	1	< 0.001		
Substrate size CV	LMM	Before-after: after	13.38	1	< 0.001	0.13	0.13
		Control-impact: impact	2.42	1	0.12		
		Before-after: after*Control-impact: impact	4.10	1	0.04		
Velocity	GLMM	Before-after: after	0.12	1	0.72	0.06	0.10
		Control-impact: impact	90.72	1	< 0.001		
		Before-after: after*Control-impact: impact	40.83	1	< 0.001		

Table 2-4. Total estimated counts of macroinvertebrates sampled in reference and treatment subreaches across all sampling, San Juan River NM & UT, September 2021 - April 2023.

	Year 1 (fall 2021 - spring 2022)		Year 2 (fall 2022 - spring 2023)		
Order or Family	Reference	Treatment	Reference	Treatment	Proportion of total
Chironomidae	2852	6289	29	149	0.54
Ephemeroptera	618	1264	202	490	0.15
Simuliidae	721	819	203	305	0.12
Oligochaeta	501	601	NA*	NA*	0.06
Trichoptera	183	257	85	261	0.05
Plecoptera	128	228	76	250	0.04
Coleoptera	87	64	36	48	0.01
Diptera	88	67	23	81	0.01
Odonata	41	43	6	10	0.01
Other	44	58	16	39	0.01

“Other” group represents rare taxa: amphipoda, araneae, decapoda, trombidiformes, hirudinea, hymenoptera, lepidoptera, megaloptera, mollusca, and nematoda.
*Oligochaetes were counted in year 1 only

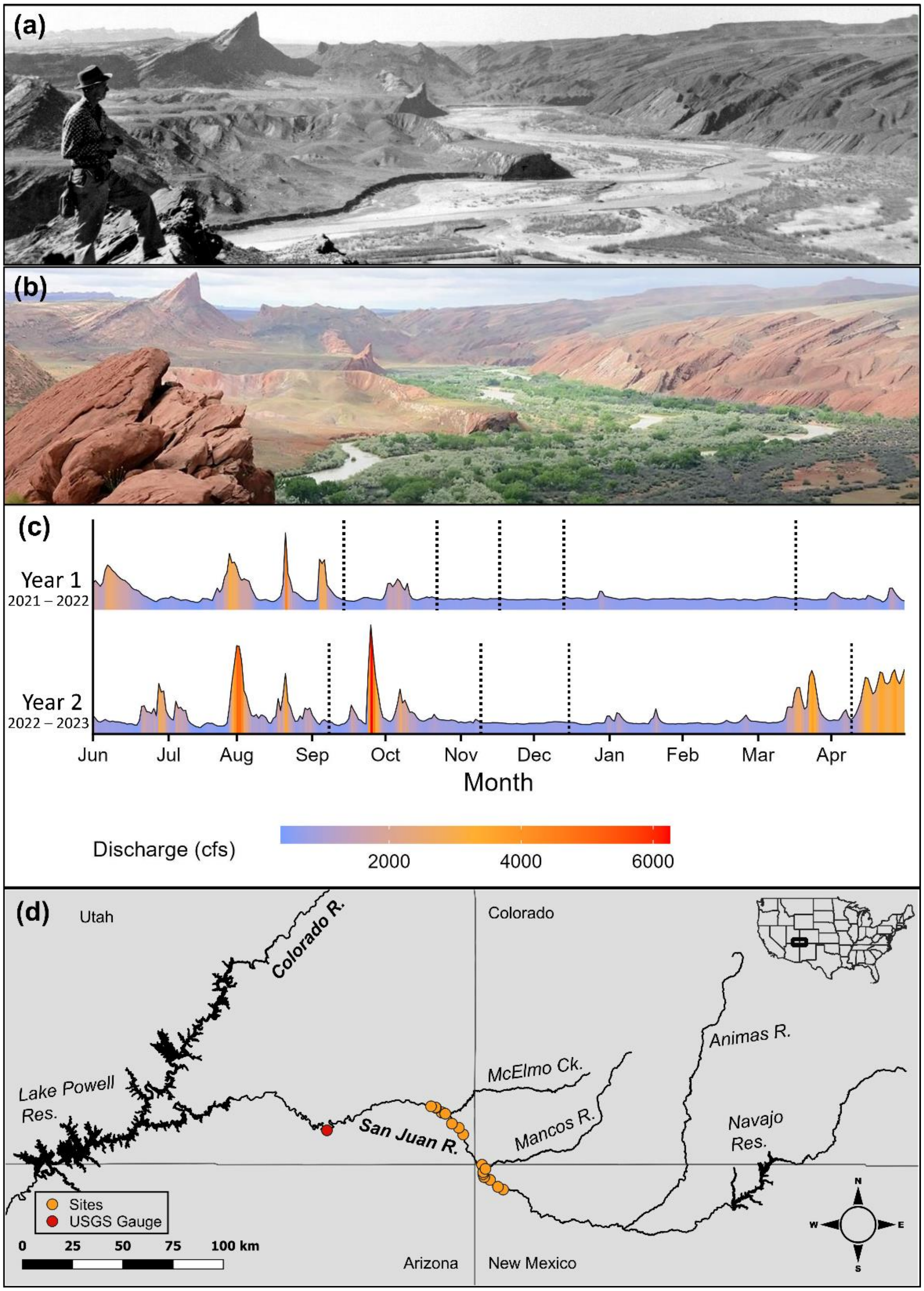

Figure 2-1. View of the San Juan River from San Juan Hill in 1954 (a) and 2017 (b), daily discharge at the USGS gage 09379500 (San Juan River near Bluff) throughout study period with sampling events indicated by dashed vertical lines (c), and map of the SJR showing study sites and USGS gage (San Juan River near Bluff, 09379500) (d). Historical photo: Gregory C. Crampton PO197:52:1:36, courtesy of the University of Utah Marriott Library.

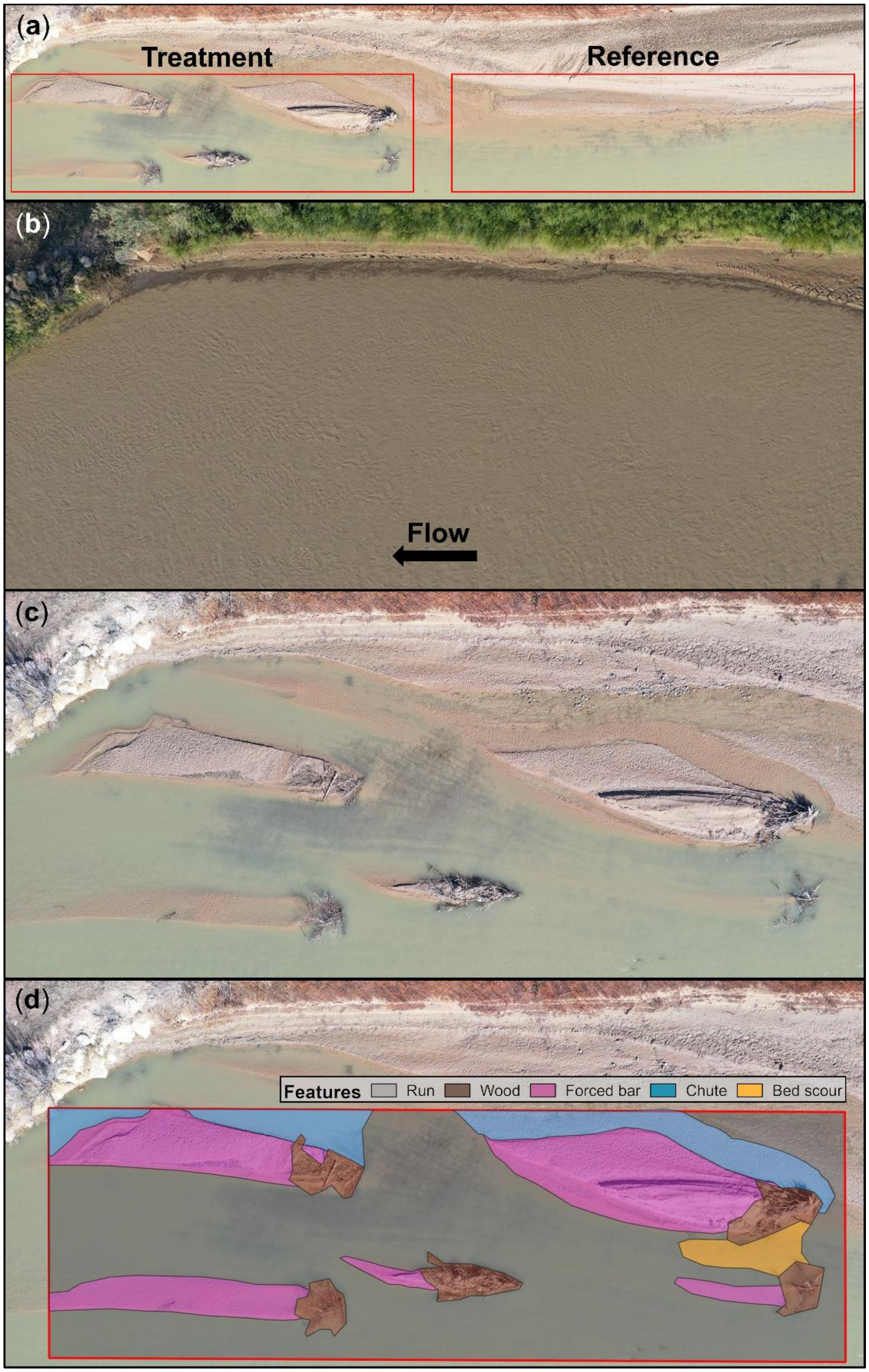

Figure 2-2. Wood addition at site 7 on the San Juan River. Full subreach showing treatment and reference subreaches (November 2022; a), treatment subreach before wood addition (September 2022; b) and two months after wood addition (November 2022; c), and delineation of geomorphic and structural features (d).

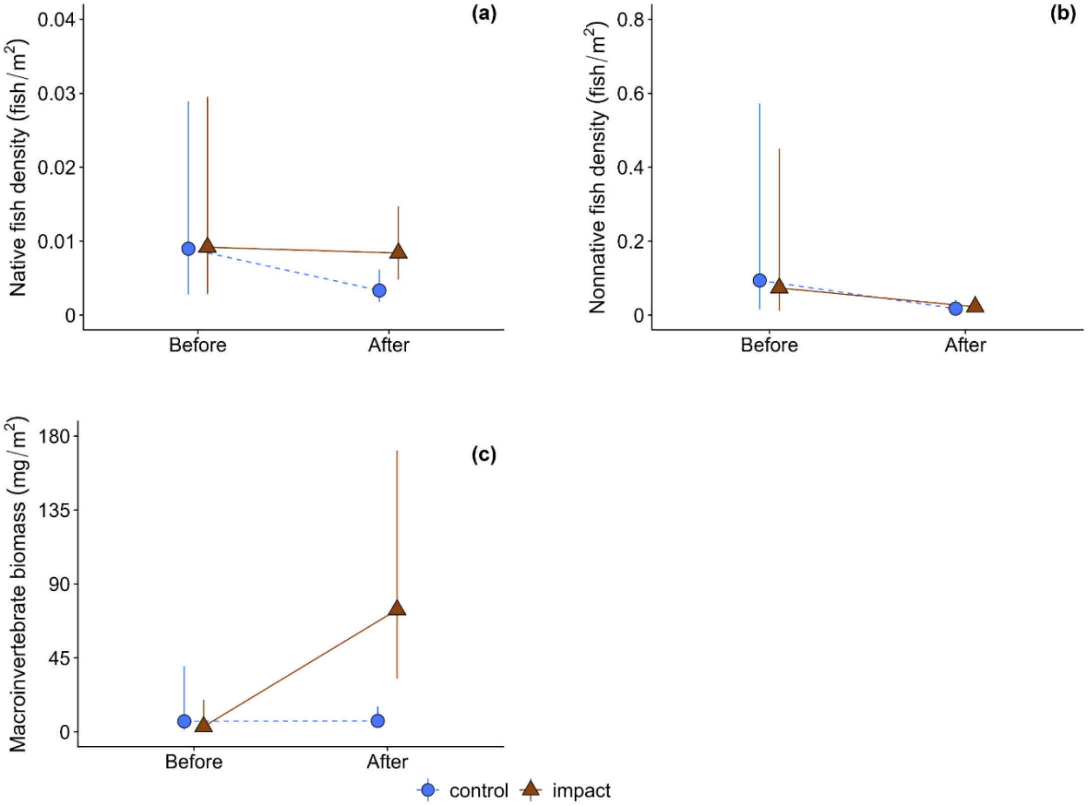

Figure 2-3. Interaction plots showing native fish (**a**) and nonnative fish (**b**), and macroinvertebrate densities (**c**) in reference (control) and treatment (impact) reaches before and after woody structure addition in the San Juan River NM & UT 2021-2023. Values are marginal means from generalized linear mixed effects models. Error bars are 95% CI.

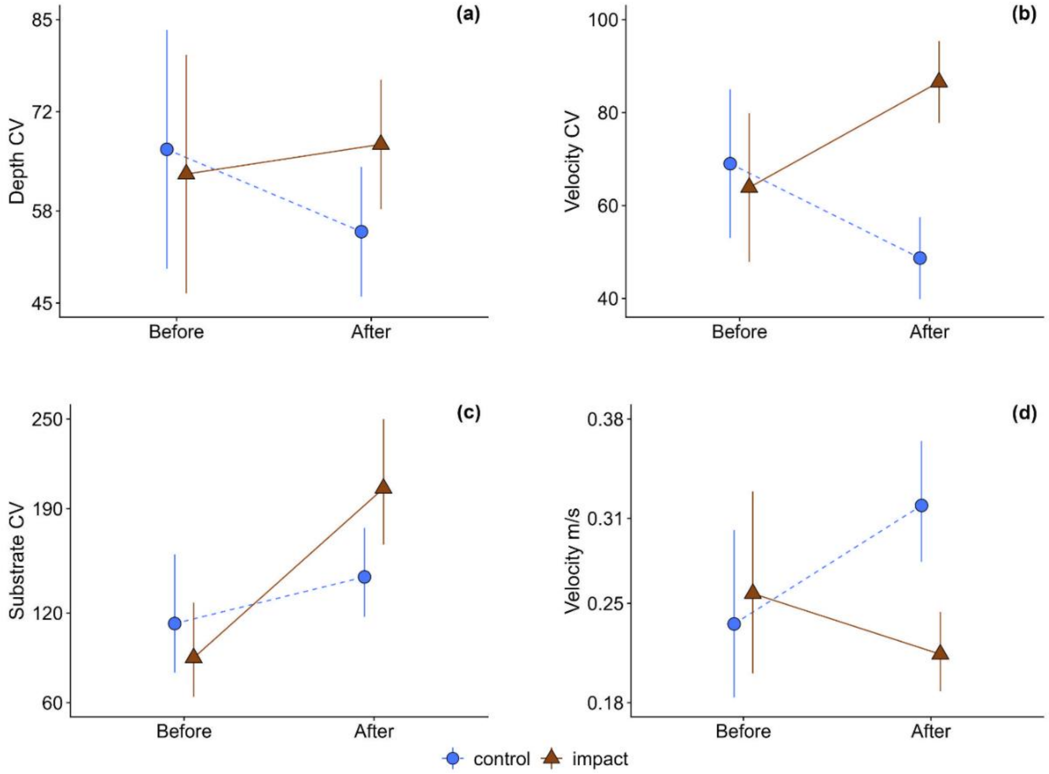

Figure 2-4. Interaction plots showing coefficient of variation (CV) of depth (**a**), dominate substrate size (**b**), velocity (**c**), as well as velocity values (**d**) in reference (control) and treatment (impact) reaches before and after woody structure addition in the San Juan River NM & UT 2021-2023. Values are marginal means from linear and generalized mixed effects models. Error bars are 95% CI.

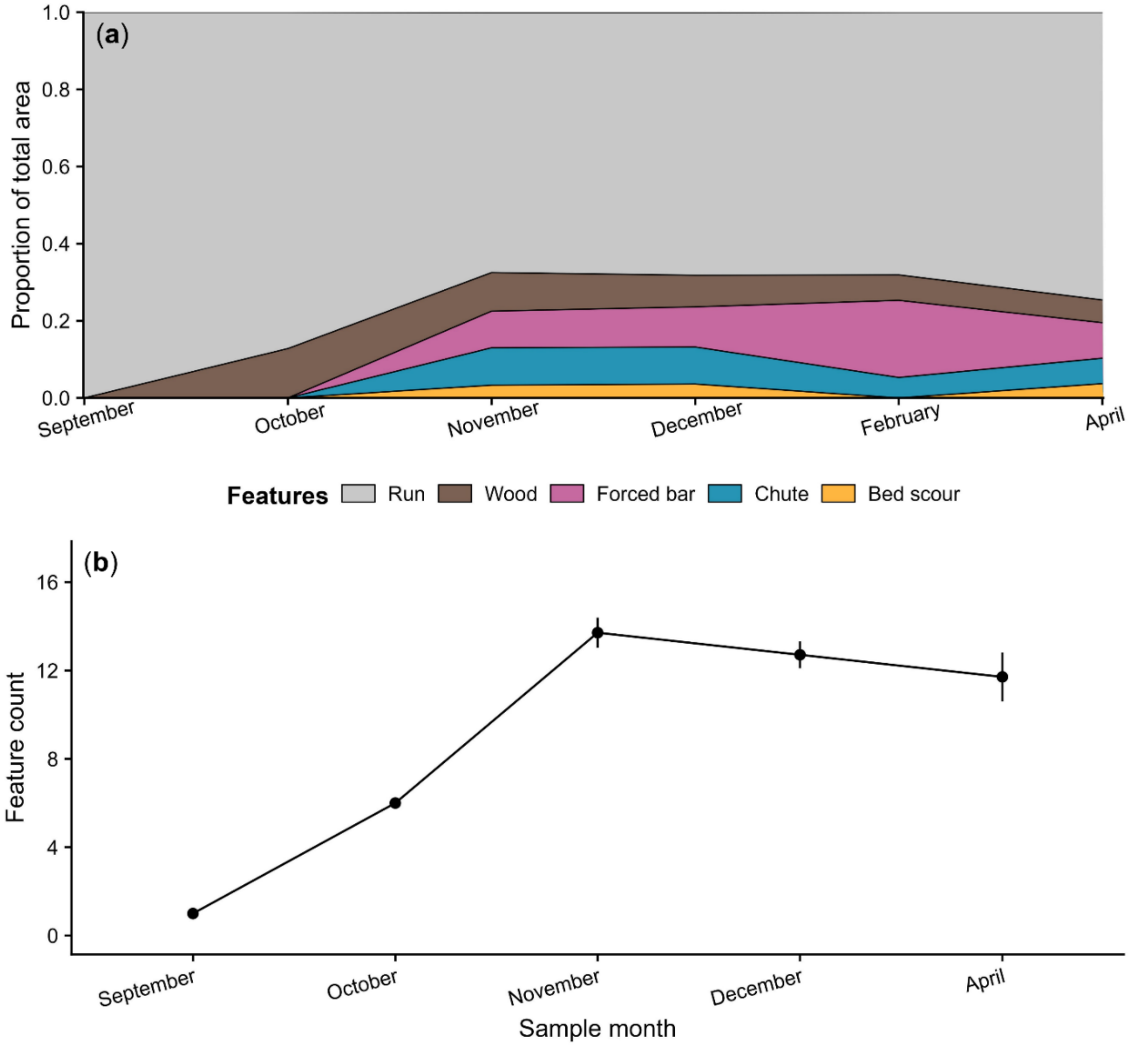

Figure 2-5. Mean proportion of total area of geomorphic and structural features over time across all treatment subreaches (**a**) and mean (± SE) feature count (including woody structures) over time **(b)** in treatment subreaches during the second year of the experimental wood addition in the San Juan River 2022 –2023.

CHAPTER 3

RIVER ALTERATIONS: CHANNEL NARROWING AND NONNATIVE VEGETATION ENCROACHMENT IN THREE DRYLAND RIVERS[2]

Abstract

Water development and the proliferation of invasive riparian vegetation has led to widespread habitat loss and simplification of rivers in the western United States, contributing to the imperilment of native fishes. Here, we quantify channel narrowing and vegetation encroachment, which are conspicuous indicators of riverine habitat alteration, along approximately 400 km of three dryland tributaries of the upper Colorado River. To accomplish this, we conducted a comparative analysis of aerial photographs from historical (1930s) and contemporary (2010s or 2020s) time periods and utilized Light Detection and Ranging (LiDAR) data and Object-Based Image Analysis (OBIA) to determine contemporary canopy cover of woody riparian species. Coinciding with a general decrease in flows over time, all three rivers underwent substantial channel narrowing, although the degree of narrowing varied among rivers (78%, 73%, and 29%). The magnitude of channel narrowing generally matched the deviation from historical spring (i.e., peak) flows, with large decreases in spring flows corresponding to substantially more pronounced channel narrowing. In contrast to patterns of channel narrowing, contemporary woody cover was similarly high among all three rivers (39%, 41%, and 36% of valley bottom area), and a woody vegetation change analysis conducted for one river indicated a substantial increase in woody vegetation along the active

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[2] Co-Authored by Casey Pennock, Phaedra Budy, Wally MacFarlane, and Steven Bassett

channel compared to historical conditions (4% to 74%). These findings underscore a common pattern observed in rivers throughout the basin, where river channels often undergo narrowing and encroachment by invasive vegetation, ultimately leading to habitat simplification. Our findings also emphasize that, when possible, preserving or restoring large magnitude and long duration floods, should be prioritized for the effective conservation of dryland rivers.

Introduction

Habitat loss and degradation is a major driver of riverine biodiversity decline, and is largely the result of water overallocation, land use perturbations, and water control infrastructure such as dams and levees that alter flow regimes (Dudgeon et al. 2006, Vörösmarty et al. 2010). A reduction in the magnitude and duration of floods from flow regime alteration results in the loss of stream power, typically leading to instream habitat simplification through processes such as channel width reduction, valley alluviation or channel incision, and a shift from a complex to simple channel form (i.e., planform simplification; see Benke 1990; Fortney 2015; Grams et al. 2020). Simplified rivers contain relatively few habitat types with long stretches of homogenous, low-quality habitat. Habitat simplification due to flow alteration is exacerbated by the encroachment of invasive riparian vegetation, such as tamarisk *Tamarix spp.* and Russian olive *Elaeagnus angustifolia*, onto formerly active channel surfaces (e.g., Laub et al. 2015; West et al. 2020). Due to long-standing anthropogenic alterations that have led to the widespread prevalence of simple, single-threaded meandering rivers, widely held misconceptions exist regarding the constitution of a healthy river channel form (Kondolf 2006; Cluer and Thorne 2014). A heightened awareness of river channel and riparian vegetation changes can empower natural resource managers, providing them with a more accurate perception and improved context for making informed decisions, thus potentially enhancing conservation efforts for imperiled species.

The habitat available for fishes and other aquatic organisms in rivers is primarily determined by its geomorphic structure, which is influenced by valley setting (slope and width), the magnitude, duration, timing, and frequency of floods (Poff et al. 1997), and the amount and particle size of sediment in the system (Thomson et al. 2001). For example, habitat simplification can result from a reduction of the upstream sediment supply (e.g., entrapment behind dams), which generally leads to a sediment deficit and progressive downward erosion (Skylar and Dietrich 1998). Diminished floods due to factors such as water abstraction, prolonged drought, and dams typically result in decreases in bank erosion and lateral channel migration rates, and reduced or absent overbanking flows (e.g., Shields et al. 2000). Flow alteration in dryland rivers has exacerbated the expansion of invasive riparian vegetation (e.g., Dean and Schmidt 2011; Wieting et al. 2023), and through its interaction with fluxes of water and sediment, can exert strong influences on channel and geomorphic structure (Dean and Topping 2019; Dean et al. 2020). Increased bank material cohesion by invasive vegetation root systems can lead to bank armoring and further reduce lateral channel migration rates (e.g., Pollen-Bankhead et al. 2009). Hydraulic roughness of invasive riparian vegetation stems above ground can also decelerate floodwaters, leading to sediment deposition and progressive aggradation of channel margins, resulting in natural levees that further preclude overbanking flows and reduce lateral connectivity (Webb et al. 2007). These mechanisms of habitat simplification ultimately result in degraded rivers and negatively impact fishes and other aquatic organisms, underscoring the importance of evaluating long-term habitat changes in riverine ecosystems.

Rivers in the Colorado River basin (CRB), draining predominantly arid portions of the American Southwest and Northern Mexico, are negatively affected by flow alteration as well as invasion of riparian woody species such as tamarisk and Russian olive (Stromberg et al. 2007b; Macfarlane et al. 2017; Scott et al. 2018). Flow alteration due to chronic overallocation (Wheeler et al. 2022) and more recent encroachment of nonnative vegetation have contributed to habitat simplification throughout the CRB. Widespread habitat simplification and loss has contributed to declines in both the distribution and abundance of native fish populations, many of which remain imperiled despite intensive management efforts (Minckley and Deacon 1968, 1991; Propst et al. 2021; Comte et al. 2022). While habitat restoration efforts have been undertaken, such as the restoration of secondary and off-channel habitats (e.g., Caruso et al. 2019; Lamarra et al. 2018), many of these initiatives are confined to relatively small spatial extents. This raises concerns about a likely mismatch between small-scale interventions and the landscape-scale magnitude of stressors responsible for habitat degradation.

The mechanisms of riverine habitat (i.e., geomorphic) simplification are often complex and difficult to ascertain, given longitudinal variability in valley settings, typically extended time frames required for observable changes, and interactions among multiple, simultaneously occurring processes. Adding another layer of complexity, patterns of channel and vegetation change following human alterations to flow and sediment supply are also dependent on historical conditions of a given river, specifically, its position on the braided – meandering continuum (Friedman et al. 1998; Johnson

1998). Given these challenges, studies aiming to comprehensively characterize changes in geomorphic condition and riparian vegetation typically require substantial effort, even when focusing on a single system. Such studies conventionally employ methods such as topographic and cross-sectional surveys, analysis of sedimentological, stratigraphic, and dendrogeomorphic data, in addition to inclusion of remote data sources such as aerial imagery and digital elevation models (Grabowski et al. 2014). Comprehensive studies describing channel and concurrent riparian vegetation change have been carried out in some rivers within the CRB, including the Green (e.g., Allred and Schmidt 1999; Grams et al. 2020), Yampa (Manners et al. 2014), San Rafael (Fortney 2015), Little Colorado (Dean and Topping 2019), and Escalante rivers (Scott et al. 2018). While these studies are valuable for better understanding the mechanisms underlying geomorphic alterations, they also emphasize that changes in channel and riparian vegetation can serve as straightforward and readily noticeable indicators of habitat simplification. In this study, we aimed to quantify the magnitude of channel and riparian vegetation change over large reaches of three tributary rivers in the CRB: the Price, San Juan, and White rivers, while comparing variations in the context of both substantial and modest flow regime alterations. These rivers demonstrate how interactions between flow alteration and riparian vegetation encroachment can lead to in-stream habitat simplification, a pervasive phenomenon throughout the CRB (and elsewhere) that continues to threaten vulnerable native fish populations.

Methods

Study area and background

The Price, San Juan, and White rivers in the upper CRB (i.e., upstream of Glen Canyon Dam) drain portions Utah, Colorado, and New Mexico (Figure 3-1). Historically, these three rivers exhibited large inter- and intra-annual variability in discharge, a characteristic of many rivers in the American Southwest, with large and sustained flows in the spring and early summer driven by montane snowmelt, followed by low flows in summer, autumn, and winter (Figure 3-1). The occurrence of monsoonal rains starting in late summer and continuing through autumn can lead to sporadic high flow events, occasionally of considerable magnitude but typically short duration (Figure 3-1). The contemporary native fish assemblage in these rivers includes the federally protected Colorado pikeminnow *Ptychocheilus lucius* and razorback sucker *Xyrauchen texanus* as well as the flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *Catostomus discobolus*, and roundtail chub *Gila robusta* which are listed as a conservation priority by a multistate conservation agreement, and collectively referred to as the “three species” (UDWR 2006).

The Price River begins in the Wasatch plateau of central Utah and runs generally southeast for approximately 220 km before its confluence with the Green River. Our study area constitutes the lower 150 km of the Price River (Figure 3-1). Water development in the Price River basin began in the late 1800’s and has continued to grow to meet increasing societal needs. About 50% of annual flow volumes are now depleted (Chart and Mohrman 2012). Scofield Dam was completed in 1945 in the mountainous headwaters of the river, and several major agricultural water diversions exist in the vicinity of Price, UT. The contemporary (2000 - 2021) median spring (March - June) flow of the Price River is 59% of the historical flow between 1945 - 1949 (Pennock et al. 2022a), primarily a result of intensive water abstraction for agriculture irrigation. The Price River is considered a high priority for native fish conservation (Chart and Mohrman 2012; Laub et al. 2018).

The San Juan River originates in the San Juan Mountains of southwest Colorado and flows for approximately 600 km through portions of Colorado, New Mexico and Utah before joining the Colorado River, now inundated by Lake Powell (Figure 3-1). Our study area encompassed approximately 200 km of river. We excluded the lowest reaches due to the canyon-bound nature of the river and inundation by Lake Powell. We also did not consider reaches immediately downstream of Navajo Dam, as these areas are significantly affected by dam releases, and channel banks are reinforced to control lateral channel movement (Bliesner and Lammarra 2000). Closure of Navajo Dam in 1962 altered the flow regime and resulted in dramatically dampened springtime flows along with elevated baseflows in summer, autumn, and winter (Propst and Gido 2004; Figure 3-1). From 1993 onward, efforts were made to implement environmental flows, with elevated releases from Navajo Dam during the spring in attempts to mimic the timing, duration, and magnitude of natural flows from the unimpounded Animas River (Propst and Gido 2004). However, the magnitude of historical spring floods has not been reproduced, as dam releases are capped at 140 $m^3/2$ (5,000 cfs) due to infrastructure constraints (BOR 2006). Consequently, complex habitat in the San Juan River remains limited (Bliesner and Lamarra 2000; Hansen 2023). The contemporary (2000 - 2021) median spring (March - June) flow of the San Juan River is only 30% of the historical flow (1929 - 1949; Pennock et al. 2022a). The San Juan River mainstem is designated as critical habitat for the federally endangered Colorado pikeminnow and razorback sucker (USFWS 2018; 2020).

The White River begins in western Colorado, flows westward into Utah and travels approximately 300 km before reaching its confluence with the Green River (Figure 3-1). Our study area encompassed 77 km of river beginning at the Colorado/Utah border and ending at the Uintah and Ouray reservation boundary (Figure 3-1). In contrast to the Price and San Juan rivers, the White River has experienced less flow regime alteration, retaining 75% of its historical (1929 - 1949) median spring flow in contemporary times (2000 - 2021; Pennock et al. 2022a). This is primarily due to less water abstraction, and to its sole major impoundment, Taylor Draw Dam, being operated as a "run of the river" structure where reservoir inflows generally equal outflows. As a result, this is one of the few major tributary rivers in the CRB regularly experiencing relatively unaltered spring snowmelt floods. These floods contribute to geomorphically effective flows where complex habitat is created and maintained by processes such as channel movement and widening, flushing of fine sediments, scouring of encroaching woody vegetation, lateral interactions with the floodplain, and the recruitment of woody debris (O’Brien et al. 2018). Owing to its less altered flow regime and the resulting high-quality, complex in-stream habitat, the White River is considered a critical stronghold for native fishes in the region (Pennock et al. 2022b).

Channel change

To quantify channel change between historical and contemporary time periods, we delineated and compared active channel area between the 1930s and 2010s or 2020s using aerial imagery. Historical aerial imagery for the upper Colorado River basin is generally available starting in the mid-1930s. For our study, we obtained historical aerial imagery through either the deprecated Mapserv imagery server provided by the Utah Geospatial Resource Center (UGRC; Price and White rivers), or from scanning physical historical aerial photographs and georeferencing them with contemporary high-resolution aerial imagery from the National Agricultural Imagery Program (NAIP) in a geographic information systems (GIS) program (San Juan River). For contemporary time periods, NAIP aerial imagery was utilized for active channel delineation, which has a 0.60 - 1m resolution and 4m - 6m horizontal accuracy depending on the flight year. The years of aerial imagery included in our channel change analysis were 1934/1935 and 2020/2021 for the San Juan River; 1938 and 2014 for the Price River; and 1936 and 2016 for the White River. We considered the active channel as the zone representing the extent of high-discharge events which have the most pronounced impact on erosion, deposition, and reshaping of the channel (i.e., bankfull; O’Brien et al. 2019). In dryland rivers, active channel boundaries can be identified by recent fluvial erosion or deposition (i.e., exposed alluvium) and the general absence of terrestrial vegetation (Lichvar and McColley 2008). In a GIS, we digitized active channel boundaries as polygon features at the interface between active and non-active channel features. This delineation was carried out at a scale of 1:5,000 for each river and time period. Channel change between time periods was determined by calculating the percent change in total active channel area within the study area for each river.

Contemporary woody vegetation cover

Price and White rivers

To describe the current overall extent and species composition of woody vegetation along the study rivers, we evaluated contemporary woody vegetation cover as a percentage of the valley bottom area. The valley bottom is used because it roughly represents the maximum possible extent of riparian vegetation (Ilhardt et al. 2000), and we used the Valley Bottom Extraction Tool (V-BET) with manual editing to delineate valley bottoms (Gilbert et al. 2016). For the Price and White rivers, vegetation classification was accomplished through the combination of field data, Object Based Image Analysis (OBIA) land cover classification, and overflight data. A brief overview of this methodology is presented here but see Macfarlane et al. (2017) and Urbanczyk et al. (2020) for a comprehensive detailing of this approach. First, 1m 2014 NAIP (Price River) and 1m 2016/0.60 m 2018 NAIP (White River) aerial imagery were obtained. Second, overflights were conducted in manned fixed-wing aircraft in 2015 (Price River) and 2020 (White River) over the entire study area to capture oblique aerial photography for determination of existing land cover types and verification of OBIA classification results. Third, field data points were collected for OBIA training and validation in 2016 (Price; n = 274) and 2020 (White; n = 1,165). Fourth, classification of vegetation classes was accomplished using OBIA capability of Trimble eCognition software on the NAIP aerial imagery. Woody vegetation classes included Russian olive, tamarisk, cottonwood *Populus fremontii*, and willow *Salix spp./Phragmites spp.* (OBIA was unable to differentiate these two species), all of which were grouped to obtain total woody cover. Finally, an accuracy assessment was carried out in the eCognition software using validation points from the field data. Overall classification accuracy was 95% for the Price River and 77% for the White River.

San Juan river

We quantified total woody cover for the San Juan River by using bare-earth and first-return lidar data from the Utah Geospatial Resource Center (UGRC). Lidar data was collected in 2020 (Utah) and 2018 (New Mexico) and has a resolution of 1m, a vertical accuracy of 18.1cm at the 95% confidence interval, and a point density between 2 and 8 per m^2. To identify woody vegetation, we clipped lidar data to the valley bottom extent, and the bare-earth layer elevations were subtracted from the first-return layer (i.e., tops of vegetation). We then filtered the resultant values to only include cells from 1m to 20m in height, which represents the approximate height range of woody vegetation species present (i.e., Russian olive, tamarisk, cottonwood, and willow) while excluding non-woody species such as grasses and forbs. We excluded the approximately 65 km of river valley downstream of Farmington, NM dominated by agricultural fields. Accuracy was assessed by comparison to 100 randomly selected points that were manually interpreted for the presence of woody vegetation using 2020/2021 NAIP imagery which indicated an overall accuracy of 88%. In our assessment of the San Juan River, we did not quantify the proportions of native and nonnative species; however, according to Bliesner and Lamarra (2000), less than 15% of the woody riparian vegetation was reported to be native.

Woody vegetation change

To quantify changes in woody riparian vegetation between historical and contemporary time periods in the San Juan River, we carried out a presence/absence analysis along the active channel, utilizing the historical aerial imagery previously described for the channel change analysis, but utilizing 2011 NAIP imagery (1m resolution) to represent contemporary conditions. Due to the lower resolution and absence of color bands in historical aerial imagery, automated techniques for identifying woody vegetation were unavailable. As a result, we employed manual interpretation of woody vegetation for both historical and contemporary aerial photographs, maximizing consistency between the two time periods. In a GIS, we designated continuous sampling transects parallel to the digitized active channel margin. We placed sampling points every 40m along the transects and recorded the presence or absence of woody vegetation at each point at a scale of 1:5,000. This method of sampling tends to overestimate actual canopy cover because it fails to account for small gaps in vegetation below the photo resolution and shadows cast by the canopy (Frescino and Moisen 2012). The estimates from this analysis should therefore be considered as an index to changes in woody vegetation cover over time, rather than a direct reflection of true canopy cover.

Flood analysis

To better evaluate flow patterns among the three rivers, we conducted a comparative analysis of annual peak floods and riparian vegetation density through time. To account for differences in flow volumes among rivers, we scaled the annual max mean daily discharge by calculating the ratio of annual max daily mean discharge to the overall mean discharge of the available record. Flow data was derived from the following USGS gages: Price River; #09314500, San Juan River; #09379500, and White River; #09306500. Small gaps in the flow record for the Price River (1993 – 1999) and White River (1982 – 1984) were interpolated via simple linear regression of scaled peak annual floods from nearby gages. The San Rafael River, gage #09328500 was used for Price River interpolation ($R^2 = 0.31$, $p < 0.001$) and the White River, gage #09306290 was used for White River interpolation ($R^2 = 0.78$, $p < 0.001$). Floods were broadly categorized as originating from either snowmelt (February – June) or monsoonal rainfall (July – November). Flood patterns were assessed alongside aerial imagery illustrating riparian vegetation densities from the 1930s, 1970s, and 2020s.

Results

The data that support the findings of this study are available in the DigitalCommons@USU repository at https://doi.org/10.26078/zd75-va03.

Channel change

Coinciding with a general decrease in flows over time (Figure 3-1), the Price, San Juan, and White rivers have undergone substantial channel narrowing over the past century; although, the degree of narrowing varied among rivers. Between the 1930s and 2010s, total channel area (across the entire study extent) of the Price River decreased by 78% (Figure 3-2), and between the 1930s and 2020s the San Juan River experienced a 73% reduction (Figure 3-2). In contrast, the total channel area of the White River decreased by only 29% between the 1930s and 2010s (Figure 3-3). As expected, the magnitude of channel narrowing generally matched the deviation from historical median spring discharge, with large decreases in spring discharge corresponding with substantially more pronounced channel narrowing, as seen for the Price and San Juan rivers (Figure 3-4).

Contemporary woody cover and vegetation change

In contrast to patterns of channel narrowing, contemporary total woody cover was similar among all three rivers (Figure 3-5). In the Price, San Juan, and White rivers, woody vegetation canopy (i.e., Russian olive, tamarisk, cottonwood, and willow) covered 39%, 41%, and 36% of the valley bottom, respectively (Figure 3-5). Vegetation composition analysis completed for the Price and White rivers revealed that nonnative vegetation, i.e., Russian olive and tamarisk, dominated the riparian woody community. Specifically, 81% of all woody cover in the Price River and 67% in the White River consisted of nonnative species. In the Price River, tamarisk was the predominant contributor to nonnative woody cover, representing 92%, while Russian olive was less common (8%). In the White River, the abundance of tamarisk and Russian olive was roughly equal, accounting for 53% and 47% of nonnative woody cover, respectively. The woody vegetation presence/absence analysis conducted for the San Juan River further confirmed a substantial increase in woody vegetation along the active channel compared to historical conditions. Between the 1930s and 2010s, woody vegetation presence along the active channel of the San Juan River increased from 4% to 74% (e.g., Figure 3-6).

Flood analysis

The flood history and vegetation patterns of the Price and San Juan rivers exhibited multiple similarities, in contrast to the White River, which presented a distinctive profile (Figure 3-7). Historical (i.e., early to middle 20th century) scaled floods were substantially larger for the Price and San Juan rivers in comparison to the White River. The White River largely maintained flood magnitudes over time, whereas the Price and San Juan rivers generally experienced a decline in flood magnitudes. Floods were predominantly of monsoonal origin for the Price River, while those in the White River were of snowmelt origin, and the San Juan River experienced a combination of snowmelt and monsoonal floods. In the 1930s, the Price and San Juan rivers exhibited sparse riparian vegetation while the White River exhibited higher levels of vegetation (see Appendix A for example aerial imagery).

Discussion

Covering over 400 km of river, we provide spatially robust results indicating that the Price, San Juan, and White rivers have undergone substantial changes in channel form since the 1930s, and that these riverscapes presently host dense populations of primarily invasive woody riparian species. Notably, the Price and San Juan rivers exhibited pronounced channel narrowing coinciding with large declines in spring flows, while the White River, with its relatively less altered spring flows, has maintained much of its historical channel area despite hosting similarly high woody vegetation densities. These results contribute to a growing body of literature on the importance of natural flows to maintain complex channel forms, and the need to preserve or restore natural flows for dryland river conservation (e.g., Arthington and Pusey 2003; Stromberg et al. 2007a; Pennock et al. 2022a,b). Given the prevalence and scale of riverine habitat degradation, as well as the escalating threat of increased consumptive water use and diminishing regional runoff (Wheeler et al. 2021), it is increasingly important to develop a broad awareness of the extensive riverscape alteration that has occurred over the past century, as well as the primary drivers behind these changes. While most riverine restoration efforts occur at small spatial and temporal extents, there is a continued need to pursue strategies that target and mitigate the root causes of riverine habitat degradation.

The smaller degree of channel narrowing observed in the White River is likely attributable to the preservation of its flow regime, namely, large magnitude, long duration snowmelt floods (Figures 3-1 and 3-7). In general, large floods maintain habitat complexity and facilitate topographically complex rivers which are indicative of high habitat quality, and include specific features such as deep pools, confluences and diffluences, bars, islands, and low-velocity habitat (Cluer and Thorne 2014). While we did not ascertain the magnitude that climate, water abstraction, and riparian vegetation have played in channel narrowing for the White River, it is likely that water removals and riparian vegetation encroachment are the main drivers. The White River basin borders that of the Yampa River, which similar to the White River, retains a largely natural flow regime and therefore serves as a useful means of comparison. Manners et al. (2014) concluded that the observed 6% reduction in channel width for the Yampa River in their study area was primarily attributable to tamarisk establishment rather than reductions in annual flows, which they determined remained relatively unchanged from 1923 to 2011. Specifically, they determined that the recent occurrence of clusters of low-flow years enabled the establishment of tamarisk within the previously active channel which, in turn, contributed to sediment aggradation during wet periods. Given that the White and Yampa rivers are more closely hydrologically related to one another than to other rivers in the CRB (Salehabadi et al. 2020), it is possible that vegetation encroachment and channel narrowing on the White River has followed a similar process. While increased riparian vegetation density is a likely contributor to channel narrowing on the White River, our results suggest that habitat complexity, as represented by total channel area, can be sustained despite woody vegetation encroachment, if spring flow magnitude and duration are similar to historical patterns (Figure 3-4). Considering that vegetation, which establishes in the active channel during low-flow years, is resistant to removal by subsequent flows (Smith 1976; Manners et al. 2014), and given the unclear relationship between the magnitude of natural flows required to maintain channel form in riverscapes experiencing woody vegetation encroachment, it is imperative to safeguard the relatively natural flow regime of the White River and similarly intact systems from potential future water development.

The substantial channel narrowing experienced by the Price and San Juan rivers is likely attributable to the attenuation of flows and the compounding effects of invasive riparian vegetation. In this scenario, diminished peak flows are unable to maintain channel form, a phenomenon that has been revealed by geomorphological studies across the region (e.g., Fortney 2015; Dean and Topping 2019; Grams et al. 2020). The largest annual floods in these river systems frequently result from monsoonal activity, especially in the case of the Price River, standing in contrast to the largest floods on the White River, which consistently originate from snowmelt (Figure 3-7). In the Price and San Juan Rivers, short duration sediment-laden monsoonal floods can deposit large quantities of fine sediment that diminished snowmelt floods, which are generally erosional, are unable to transport out of the system. Monsoonal sediments therefore aggrade over time along river margins and within secondary channels, providing colonization surfaces for invasive vegetation and ultimately contributing to planform simplification (Laub et al. 2020; Hansen 2023). Although hosting similar densities of woody vegetation as the White River, the Price and San Juan rivers likely lack sufficient stream power to effectively counteract the increased bank cohesion and hydraulic roughness created by the presence of riparian vegetation. The White River suggests a contrasting model; that maintenance of flood flows reduces, but likely does not eliminate, the negative impacts of invasive vegetation encroachment. This hypothesis is supported by the precept that alterations in flow are the main driver of channel narrowing, with riparian vegetation encroachment being a secondary, partially dependent mechanism (e.g., Manners et al 2014; Walker et al. 2020). During the vegetation change analysis conducted for the San Juan River, we observed active channel surfaces (i.e., bare alluvium with scattered cottonwood and willow) become colonized with dense stands of nonnative vegetation, primarily Russian olive, thereby contributing to channel narrowing. Although it is clear the Price and San Juan rivers would benefit from restoration of natural flows, the existence of water infrastructure, such as dams and diversions, and the increasing demands of consumptive water use pose formidable obstacles (Pennock et al. 2022d). Instead, mitigating habitat simplification in rivers facing challenges akin to those of the Price and San Juan rivers will require pairing strategies aimed at increasing peak flows with non-flow alternatives such as process-based instream addition of woody debris.

While the Price, San Juan, and White rivers share the commonality of being tributaries to the Colorado River within its upper basin, it is important to recognize that inherent differences among these rivers are likely to influence responses to human-induced changes in flow and sediment dynamics. A dissimilarity in flood history emerges as a potential, if partial, explanation for the differing channel narrowing patterns observed between the Price and San Juan rivers versus the White River. Additionally, it may provide insights into the seemingly paradoxical occurrence of high contemporary vegetation densities along the White River. Analyzing the historical flood context reveals that, when scaled to the overall mean discharge, peak floods exhibited greater magnitudes on the San Juan and Price rivers compared to the White River during the early to middle 20th century (Figure 3-7). Although the flow record is limited for the Price River, floods were still relatively large during the middle 20th century and were likely of large magnitude in the early 20th century as well (Salehabadi et al. 2020). In contrast, the White River experienced less-extreme floods during the early to middle 20th century but has largely maintained consistent flood magnitudes over the entire flow record (Figure 3-7). The early 20th century was a period of unusually high precipitation in the western United States, known as the "20th century pluvial" (Woodhouse et al. 2005). The resultant large floods in the early 20th century are widely recognized as the cause of riparian vegetation denudation along rivers in the region (e.g., Webb et al. 2007). This led to the formation of wide, alluvial, and sparsely vegetated active channels observed for the Price and San Juan rivers in the 1930s, subsequently colonized by primarily invasive vegetation over the ensuing decades. In contrast, the 1930s White River presents a different scenario, distinguished by less exposed alluvium and considerably denser riparian vegetation, a characterization that, in rough terms, persists to the present day (see Appendix A for example aerial imagery). It is logical that a consistent flow regime would be associated with a consistent riparian vegetation density, although the presence of invasive tamarisk and more recently Russian olive has likely contributed to an increase in vegetation densities over time (Pennock et al. 2022c). In summary, maintaining a natural flow regime, as demonstrated by the White River, sustains consistent flood magnitudes that, in turn, maintain relatively consistent riparian and in-stream conditions that are favorable to imperiled species.

While we achieved our objectives of documenting the magnitude of channel change and status of contemporary woody cover in the study rivers, it is important to note that we did not establish quantitative mechanistic explanations for the observed alterations in these riverscapes. Despite the somewhat limited comparison among three rivers, our analyses covering over 400 km of watercourses provide spatially robust information on the past and current state of these rivers. We contend that, although the complete story is likely highly complex and system-dependent, anthropogenic reductions in flow and subsequent invasions by nonnative vegetation are a primary driver of habitat simplification for many western rivers, a notion shared by numerous studies (e.g., Fortney 2015; Dean and Topping 2019; Dean et al. 2020). Continued monitoring of channel form and vegetation dynamics in these rivers, including the amount and composition of vegetation, is crucial to provide insights on habitat form and quality for conservation efforts aimed at recovering imperiled species.

Conclusion

Change is a natural component of river behavior, but interactions among human alterations, such as flow alteration and invasive tree introductions, have negatively affected native fish populations across the CRB and other dryland river basins. Our findings of channel narrowing, increased prevalence of riparian vegetation, and high contemporary densities of woody riparian species for the Price, San Juan, and White rivers add to an already quite clear story of rivers in the west. Today’s riverscapes are characterized by simple, static channels, often reduced to mere water conveyance pathways, flanked by dense stands of riparian vegetation, bearing little semblance to historical conditions (e.g., Figure 3-6). Although efforts to remove riparian vegetation have demonstrated some positive outcomes locally, it is important to bear in mind that invasive vegetation is an issue ancillary to that of anthropogenically diminished river flows (*see* Stromberg et al. 2007b; Jaeger and Wohl 2011). It is evident that flow regime alteration precedes the full realization of the negative impacts caused by invasive vegetation and that the mere presence of invasive riparian vegetation, as demonstrated here for the White River, does not necessarily imply a highly degraded ecosystem. Indeed, rivers commonly exhibit increased abundances of native vegetation following flow alteration, for reasons similar to those that contribute to the proliferation of nonnative species (e.g., Scott and Miller 2017; Grams et al. 2020). However, most western rivers lack sufficient flows due to anthropogenic alterations to counteract the adverse effects of invasive vegetation. Invasive vegetation removal efforts alone are likely not enough to rehabilitate degraded rivers, as they present formidable challenges, such as regrowth, reestablishment, and the extensive scale of removal required. Our results emphasize that, when possible, preserving or restoring natural, particularly peak snowmelt floods, should be prioritized for the effective conservation of dryland rivers.

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Figures

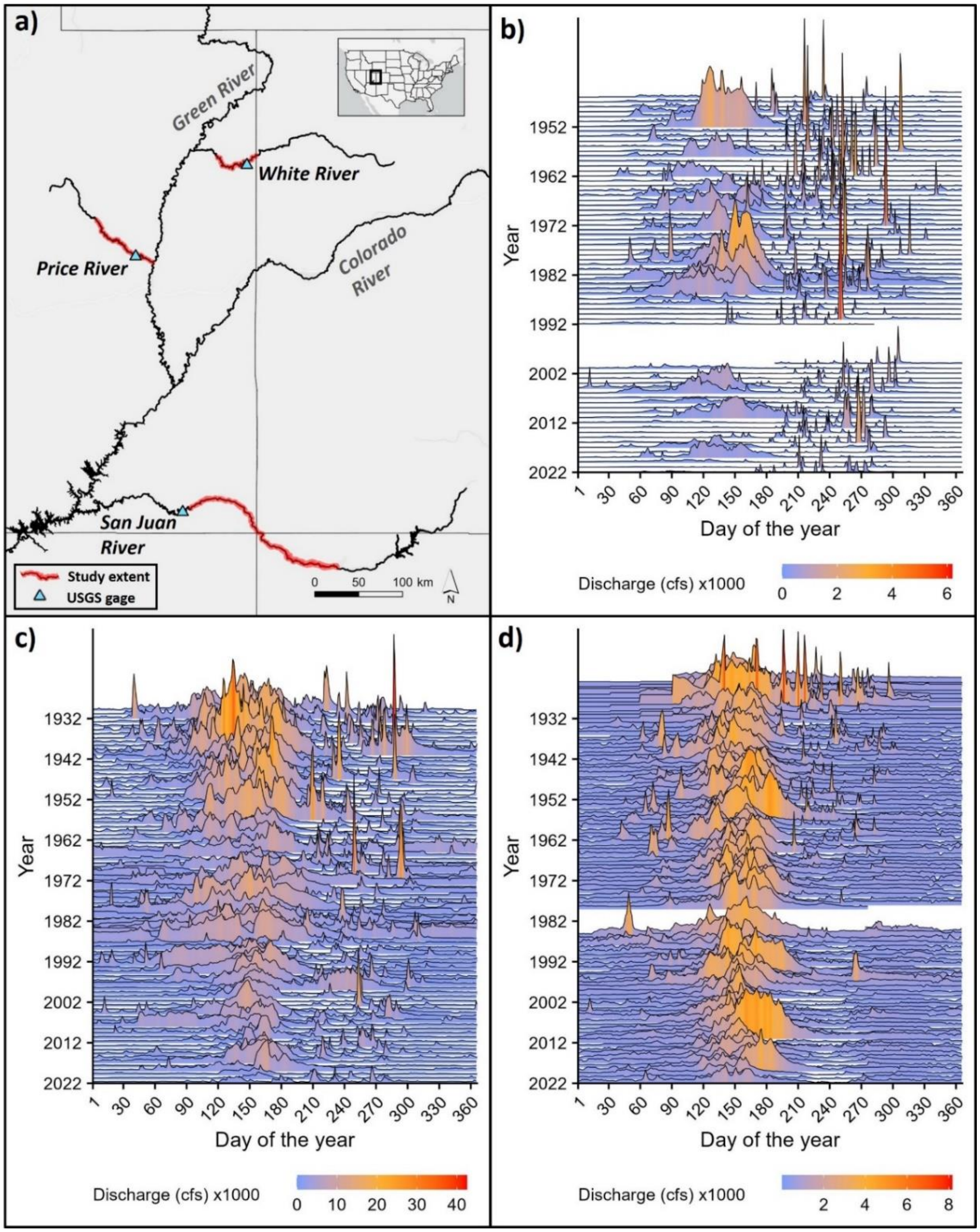

Figure 3-1. Study area extent (a) and flow regimes over time (mean daily discharge) for the Price; gage #09314500 (b), San Juan; gage #09379500 (c), and White rivers; gage #09306500, (d). Note the flow magnitude legend differs. among panels.

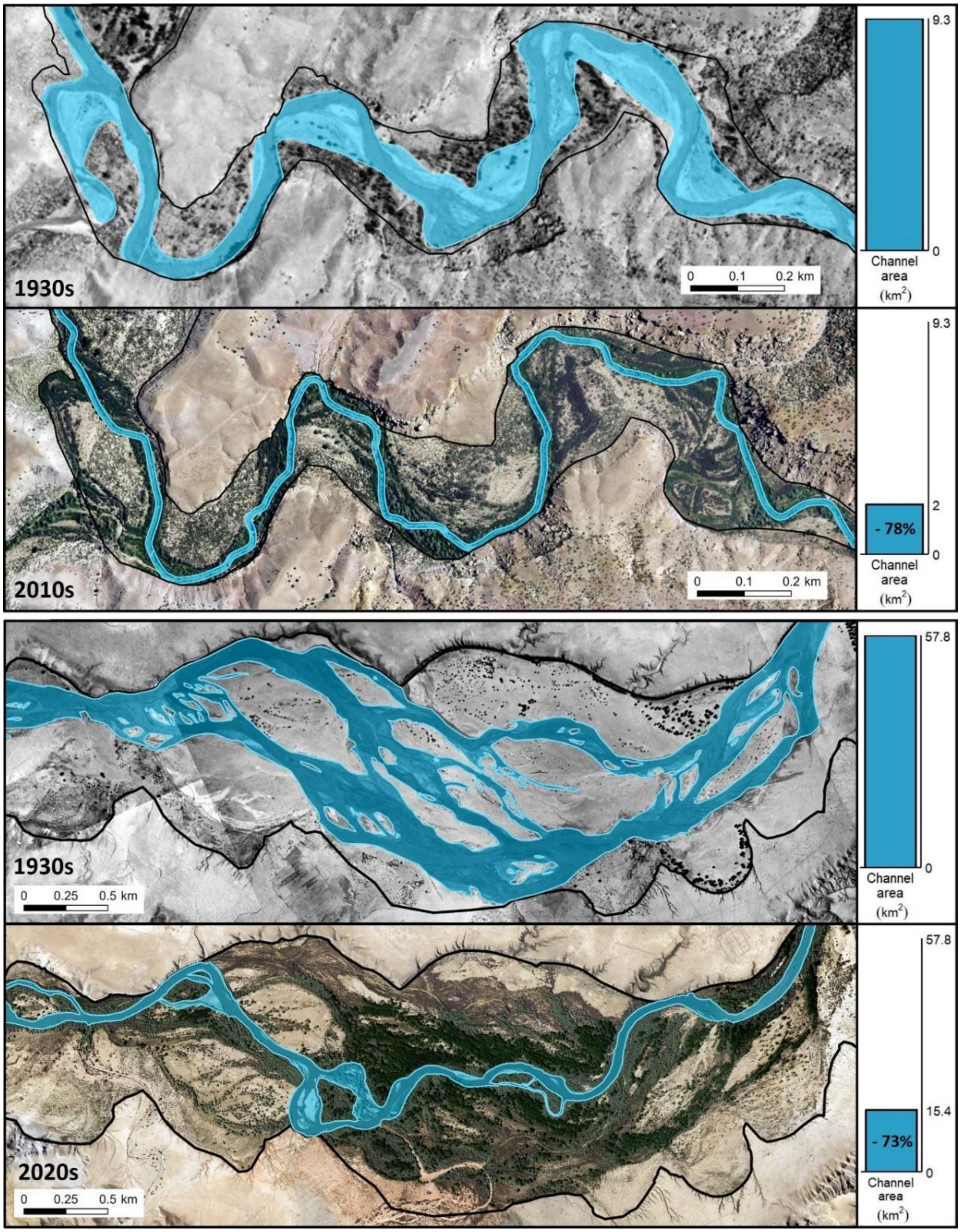

Figure 3-2. Example aerial imagery of the Price (top) and San Juan (bottom) rivers demonstrating substantial channel narrowing between the 1930s and 2010s or 2020s. Blue polygons indicate the active channel (flow is from right to left) and black lines indicate the valley margins.

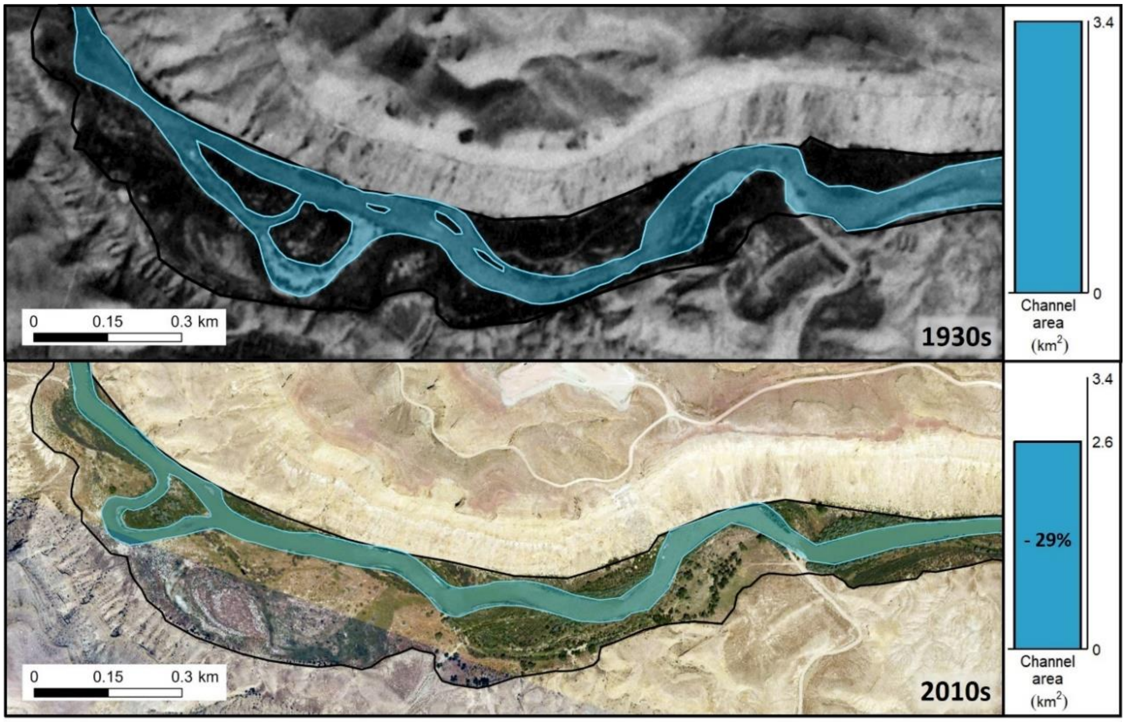

Figure 3-3. Example aerial imagery of the White River demonstrating relatively minor channel narrowing between the 1930s and 2010s. Blue polygons indicate the active channel (flow is from right to left) and black lines indicate the valley margins.

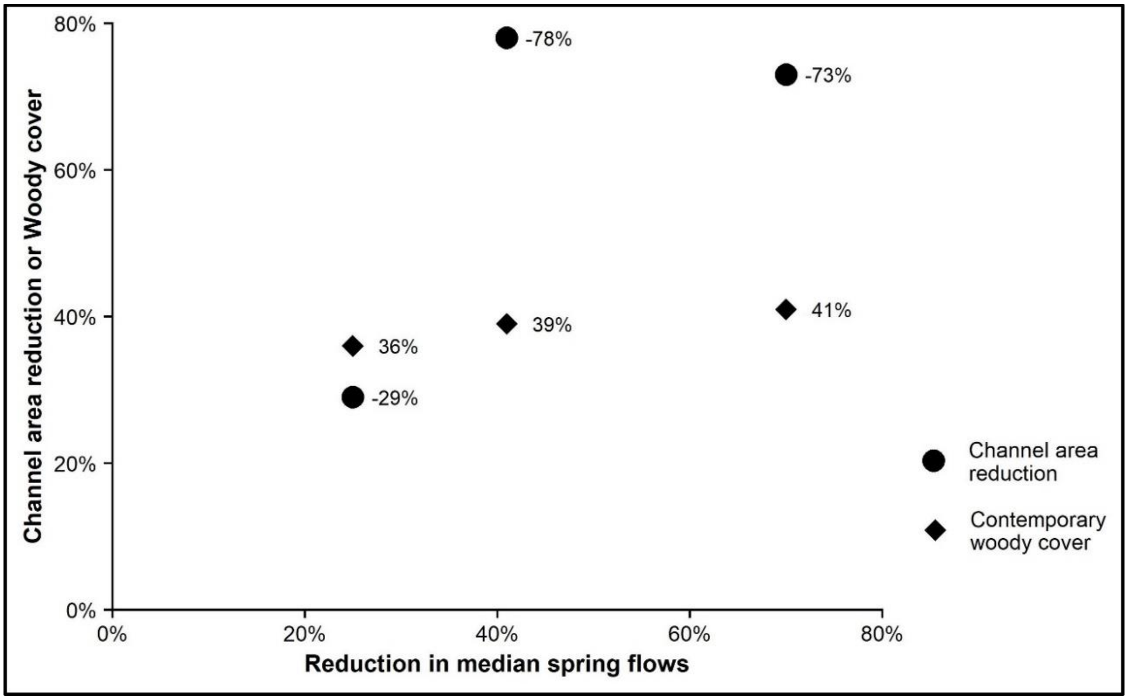

Figure 3-4. Channel area reduction and contemporary valley bottom woody cover as a function of change in median spring flows (March – June) between historical (all: 1930s) and contemporary (Price and White: 2010s; San Juan 2020s) time periods. Period of historical flows varies; Price: 1945 – 1949, San Juan and White: 1929 -1949 while contemporary flows are for the period 2000 – 2021.

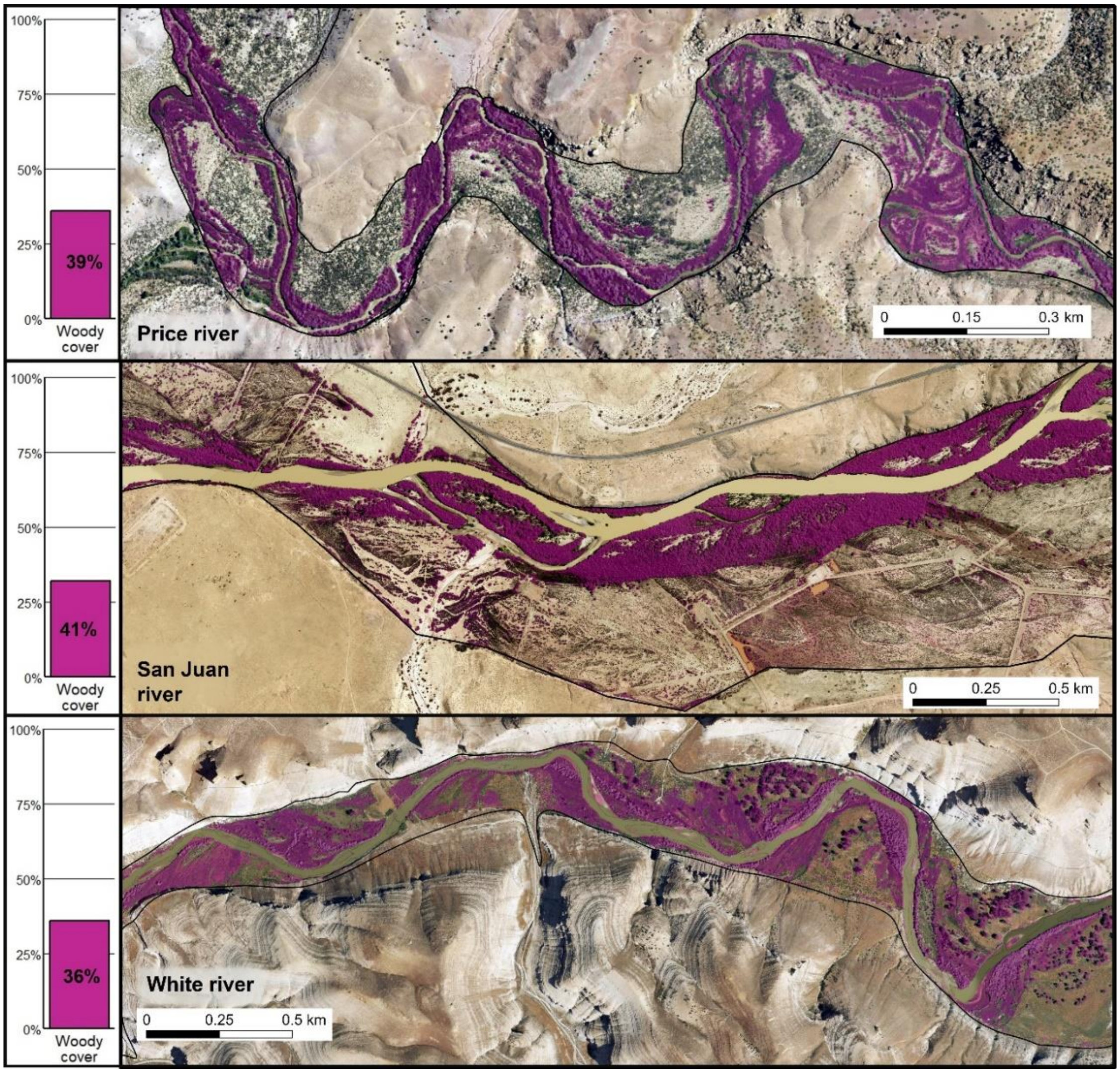

Figure 3-5. Example aerial imagery demonstrating contemporary total woody vegetation canopy cover for the 2010s (Price and White rivers) and 2020s (San Juan River). Bar plots indicate the percentage of valley bottom canopy cover of woody riparian species across the entire study area.

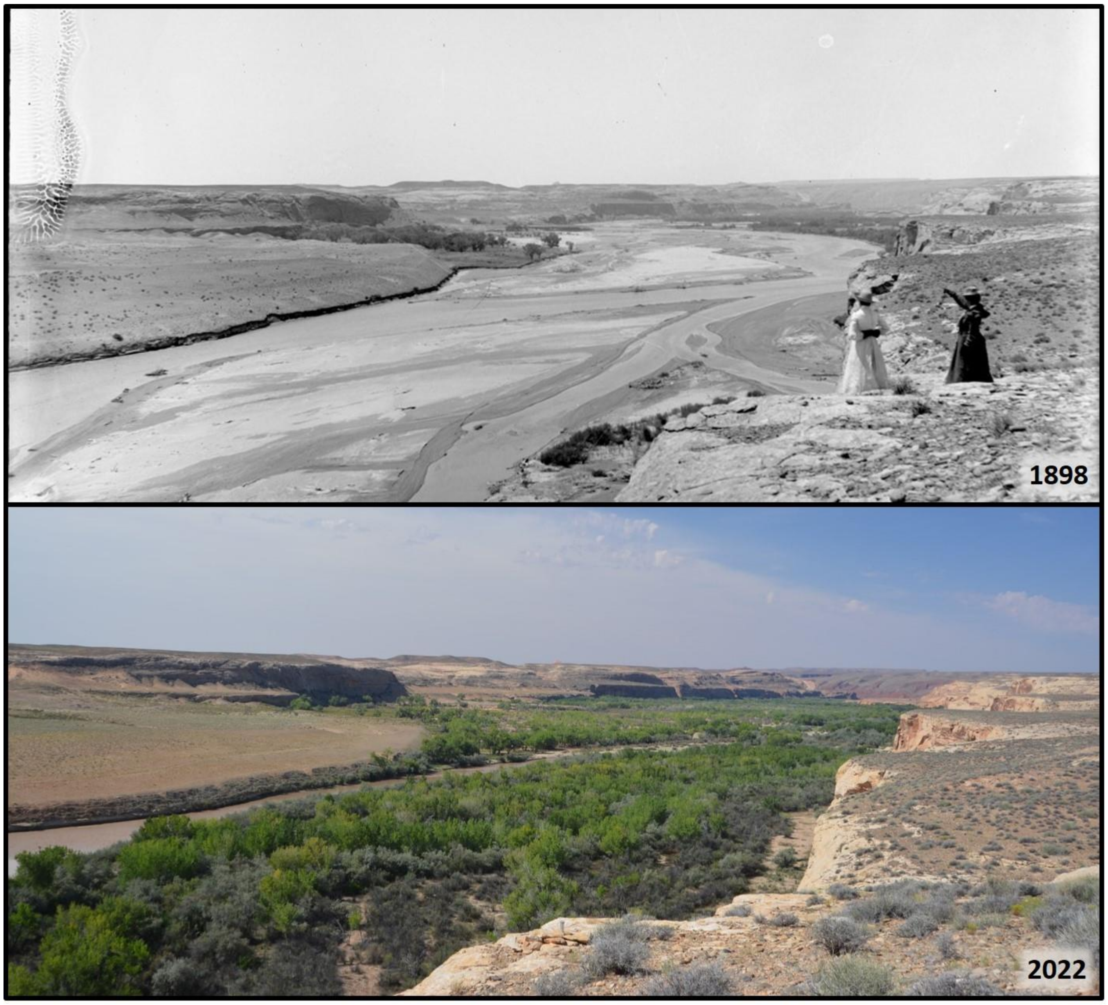

Figure 3-6. Repeat photography near Bluff, UT (37.246102, -109.637504) between 1898 and 2022 demonstrating dramatic channel narrowing and vegetation encroachment. In 1898, the channel form was wide and complex, featuring braided or anastomosing channels, large areas of exposed alluvium, and sparse riparian vegetation. In 2022, channel form is simplified with dense stands of riparian vegetation throughout the valley bottom. 1898 photo by Charles Goodman, available at https://collections.lib.utah.edu/ark:/87278/s6zd1qcb.

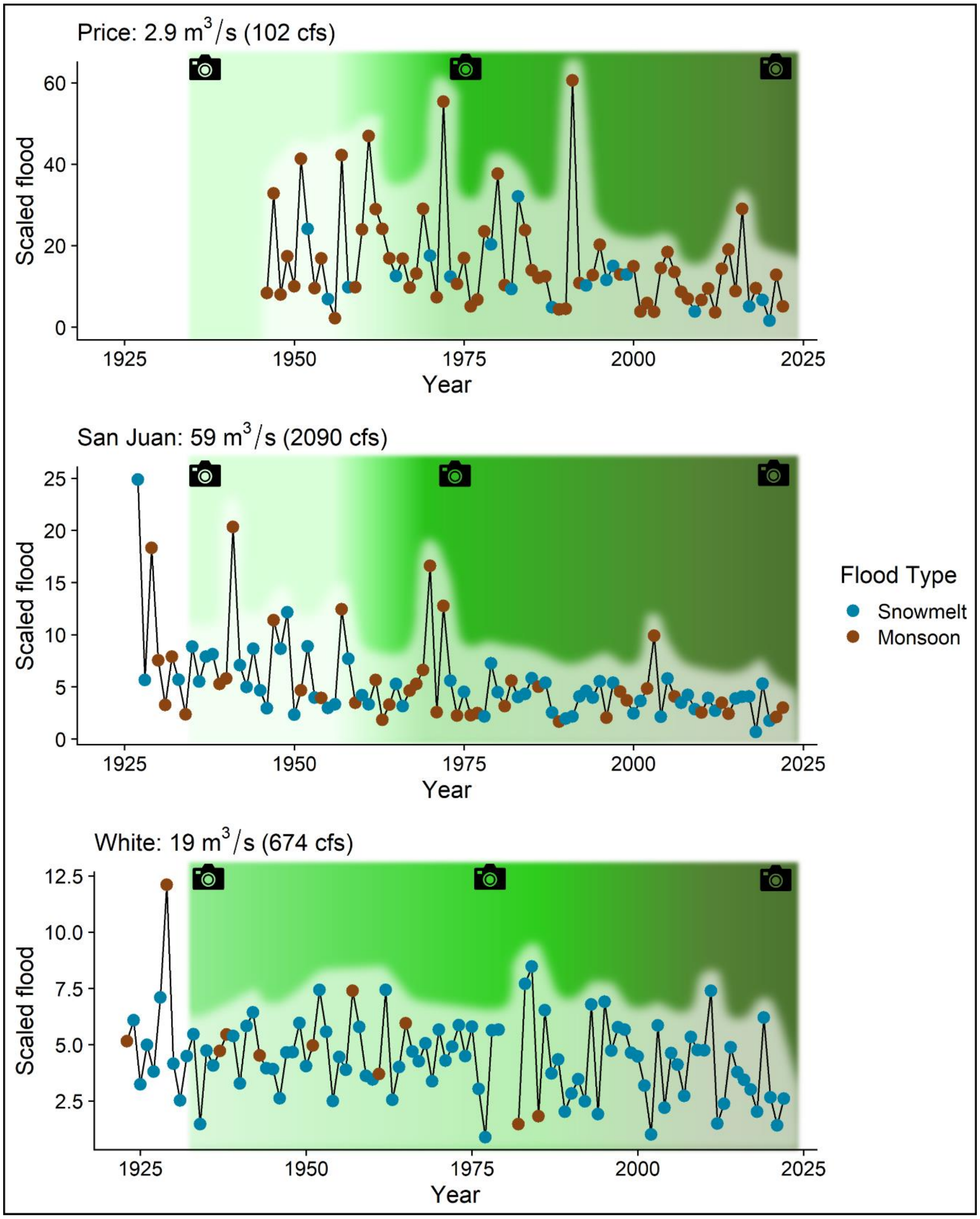

Figure 3-7. Scaled flood discharge (annual max mean daily flow / overall mean flow) for the Price (gage #09314500), San Juan (gage #09379500), and White (gage #09306500) rivers for the available flow record; note that y-axes are of different magnitude. Values by river names represents the mean flow for the entire flow record. Green shading indicates riparian vegetation establishment and camera icons indicate year of aerial photographs provided in Appendix A. Snowmelt floods represent months Feb. – June, and monsoon floods July – Nov.

CHAPTER 4

CONCLUSIONS

We assessed the use of nonnative vegetation for enhancing simplified in-stream habitat for native fishes in a dryland river, and then investigated river alterations, specifically channel narrowing and vegetation encroachment, across three dryland rivers in the Colorado River Basin (CRB). Our results underscore the magnitude of riverine alterations in the region and suggest that nonnative wood addition can be an effective approach to enhance habitat for native fishes in dryland rivers. Additionally, restoring or maintaining large magnitude, long duration spring floods is likely critical for creating complex habitat and mitigating the negative effects of riparian vegetation encroachment. Because restoring flows often poses a significant and sometime insurmountable challenge due to competing ecological and societal needs, approaches that directly enhance habitat for imperiled native fishes are likely required.

In Chapter 2, we conducted a field experiment to assess the effectiveness of enhancing native fish habitat in a large dryland river by utilizing an abundant resource, Russian olive (*Elaeagnus angustifolia*). To evaluate responses to wood addition, we repeatedly sampled fishes and macroinvertebrates, and assessed habitat characteristics (depth, velocity, dominant substrate size, and geomorphic features). Following the addition of wood, average native fish densities were 2.2x higher in treatment subreaches compared to reference subreaches, whereas nonnative fish densities exhibited no response. Additionally, treatment subreaches exhibited significantly higher macroinvertebrate densities as well as increased hydraulic and geomorphic complexity. Our results suggest nonnative wood addition is an effective management action for enhancing native fish habitat by increasing available food sources and facilitating hydraulic and geomorphic heterogeneity. While flow management has been the primary tool used by managers to improve habitat conditions for native fishes in large dryland rivers, this approach is increasingly less effective due to water overallocation, increased aridity, and riparian vegetation encroachment (Chen et al. 2020; Ryan et al. 2021). Managers might consider pairing flow management with non-flow physical habitat improvement alternatives, such as simple wood addition, to improve degraded habitat for native fishes.

In Chapter 3, we quantified channel narrowing and vegetation encroachment, which are conspicuous indicators of riverine habitat alteration, along approximately 400 km of three dryland tributaries of the upper Colorado River. To accomplish this, we conducted a comparative analysis of aerial photographs from historical and contemporary time periods and utilized Light Detection and Ranging (LiDAR) data and Object-Based Image Analysis (OBIA) to determine contemporary canopy cover of woody riparian species. The White River experienced the smallest amount of flow alteration and exhibited the smallest degree of channel narrowing (29%) while hosting similar densities of riparian vegetation to the Price and San Juan rivers, both of which experienced drastic losses in both flood magnitude and channel area (78% and 73%) over time. The White River and other relatively intact systems stand as a testament to the concept that if historical flow magnitudes and duration are largely maintained that complex channel planforms can persist, even in the presence of high densities of invasive riparian vegetation.

Despite decades of dedicated conservation efforts, many native fish populations in the CRB remain imperiled or threatened (Propst et al 2021). Most rivers in the CRB are in a highly degraded state due to anthropogenic alterations, namely habitat loss due to water development and the proliferation of nonnative species. Our results add to an increasingly clear story of rivers in the West: that healthy rivers facilitate healthy fish populations. Due to deep-rooted societal practices, it is unlikely for many rivers to be returned to a state resembling historical conditions in the foreseeable future. Nevertheless, as demonstrated here, modest initiatives can lead to strong responses in habitat and native fish abundance, even in a highly altered river. Scaling up physical habitat improvement approaches has the potential to yield broader responses in habitat quality and fish abundances. We assert that striving for improved conservation perspectives and healthier river ecosystems remain causes worth advocating for. Achieving the goal of healthier rivers in the CRB will likely involve efforts to directly enhance habitat conditions alongside prioritizing large-magnitude, prolonged floods to instigate natural riverine processes for the native biota reliant upon them.

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Appendices

Appendix A: Riparian vegetation density: 1930s, 1970s, and 2020s

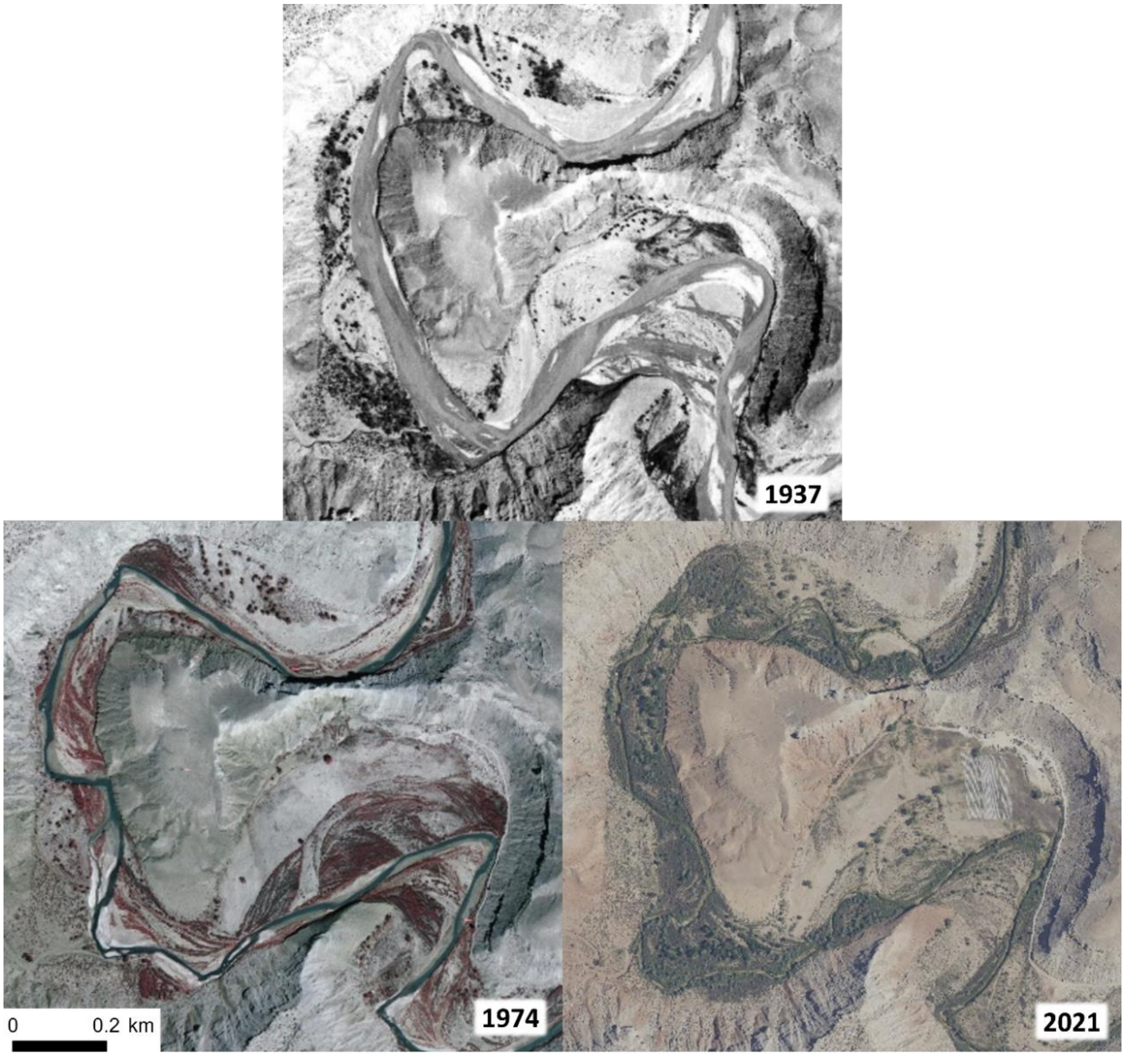

Figure A-1. Example aerial imagery of the Price River illustrating substantial increase in riparian vegetation density over time: sparse in 1935, moderate in 1974, and dense in 2021. Red hue of vegetation in 1974 is an artifact of the original photograph.

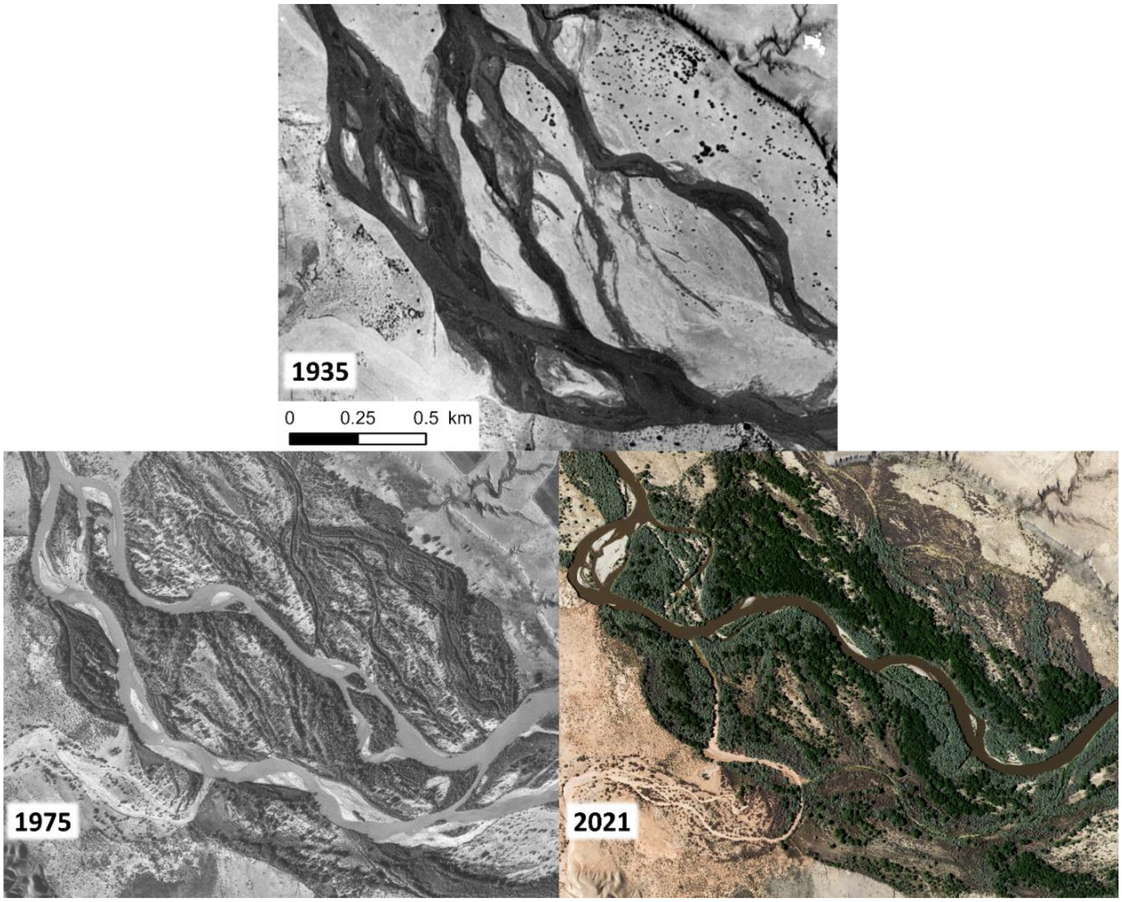

Figure A-2. Example aerial imagery of the San Juan River illustrating substantial increase in riparian vegetation density over time: sparse in 1935, moderate in 1975, and dense in 2021.

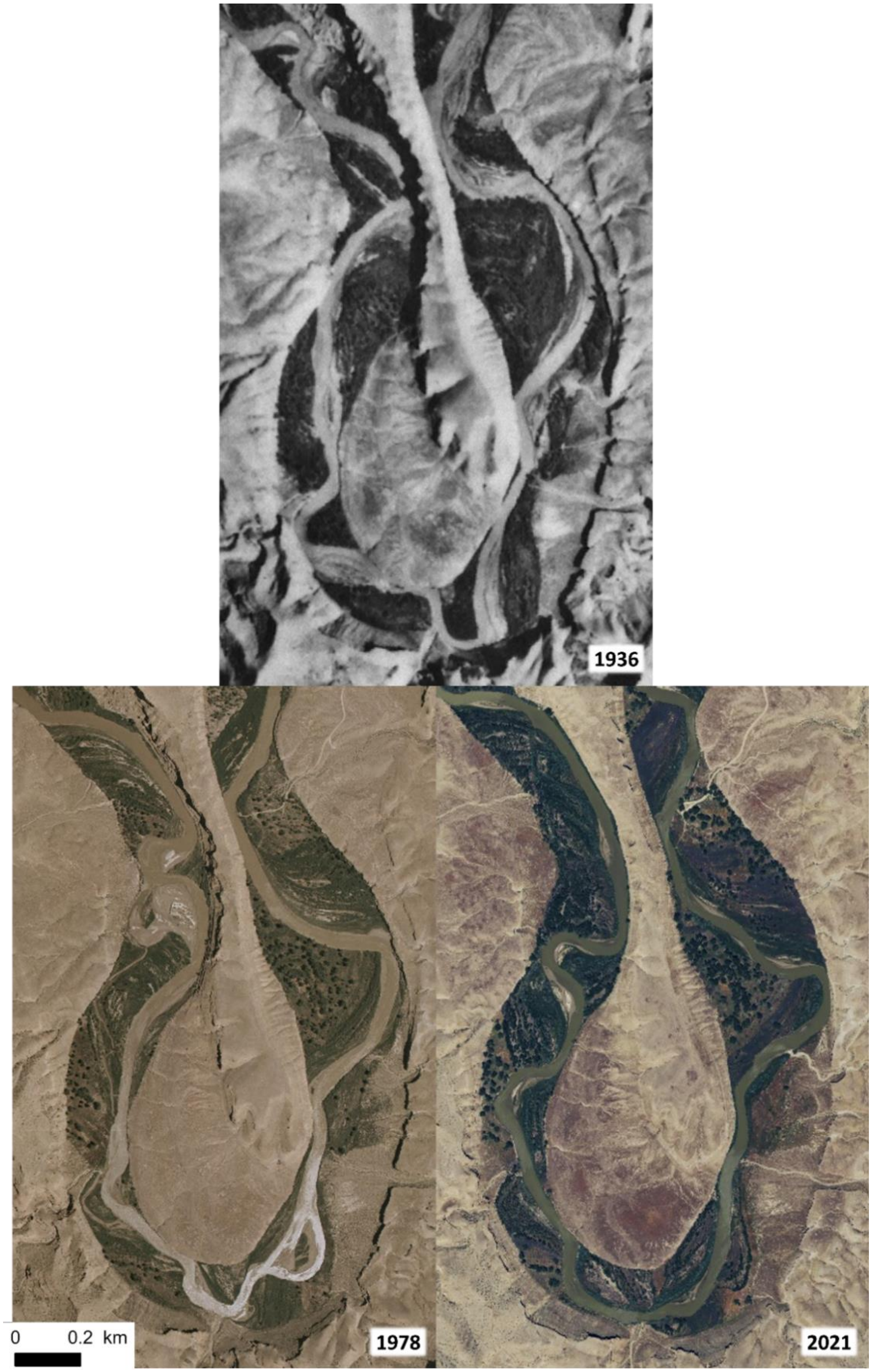

Figure A-3. Example aerial imagery of the White River illustrating relatively modest increase in riparian vegetation density over time: moderate in 1936, moderate in 1978, and dense in 2021.

Appendix B: Co-author permission letters

3/05/2024
Steven Bassett
The Nature Conservancy
1613 Paseo de Peralta, Suite 200
Santa Fe, NM

Dear Steven Bassett:

I am in the process of preparing my (report, thesis, dissertation) in the department at Utah State University.

I am requesting your permission to include the attached material as shown. I will include acknowledgments and/or appropriate citations to your work as shown. Please advise me of any changes you require.

Please indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you charge a reprint fee for use of your material, please indicate that as well. If you have any questions, please call me at the number below.

I hope you will be able to reply immediately. If you are not the copyright holder, please forward my request to the appropriate person or institution.

Thank you for your collaboration,
Benjamin Miller

I hereby give permission to (your name) to reprint the following material in his/her thesis/dissertation:

- Historical channel area data and riparian vegetation change data for the San Juan River.

Fee: $0.00

Signed: ______________________________

3/09/2024

Wally Macfarlane
ETAL Lab
5275 Old Main Hill
Logan, UT 84322

Dear Wally Macfarlane:

I am in the process of preparing my (report, thesis, dissertation) in the department at Utah State University.

I am requesting your permission to include the attached material as shown. I will include acknowledgments and/or appropriate citations to your work as shown. Please advise me of any changes you require.

Please indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you charge a reprint fee for use of your material, please indicate that as well. If you have any questions, please call me at the number below.

I hope you will be able to reply immediately. If you are not the copyright holder, please forward my request to the appropriate person or institution.

Thank you for your collaboration,
Benjamin Miller

I hereby give permission to (your name) to reprint the following material in his/her thesis/dissertation:

- OBIA riparian vegetation data for the Price and White rivers
- Channel change data for the Price and White rivers

Fee: $0.00

Signed:

3/05/2024