Designing and transferring environmental flows

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Abstract

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Societal and environmental water needs are increasingly in conflict due to rising water demands from growing global human populations and climate-change-induced intensification of hydrologic drought. The last couple of decades have seen a blossoming of research in environmental flows – the provisioning of water within rivers to sustain freshwater ecosystems while maintaining societal water needs – to resolve these water conflicts. The unfortunate reality, however, is that societal water needs are outpacing our ability to utilize prevailing methodology for prescribing in-stream flows based on natural flow restoration and develop rigorous environmental flow recommendations on an individual river basis.

My thesis addresses these challenges by first presenting in Chapter 1 a framework for designing environmental flows to balance the conflicting goals of meeting human water needs and benefiting native fish species over nonnative fish species, using novel holistic methods to quantify species' flow-ecology relationships and multi-objective optimization to determine efficient flow recommendations for the San Juan River, NM. Flow designs were predicted to lead to greater gains in native fishes and losses in nonnative fishes as compared to natural flow mimicry. Moreover, flow designs minimized or circumvented conflicts between human and environmental water needs, even during periods of hydrological drought. The scope of these designs illustrated an encouraging future for ecosystem sustainability in regulated rivers.

In Chapter 2, I address the gap between the desire to prescribe regional-scale environmental flows and the dearth of research that quantifies the transferability of flow-ecology knowledge meant to support environmental flow recommendations. Building on the flow-ecology modeling framework developed in Chapter 1, I elucidate the relationships of freshwater fish species with streamflow across five river basins in southwestern United States to quantify the transferability of flow-ecology relationships across space, time, and taxonomy. Species' flow-ecology relationships transferred similarly well across different river basins as compared to within a river basin, though species in regulated rivers saw less transferability than those in free-flowing rivers. Species' flow-ecology relationships transferred through time just as well as across space. Finally, fluvial dependence and life-history trait guilds proved to be strong conduits for transferring flow-ecology knowledge across taxonomy.

Together, these chapters present crucial insights into and encouraging opportunities for the use of environmental flows to meet the goals of sustainable water use and freshwater species conservation in contemporary rivers around the globe.

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DEDICATION

To Rachel Minji Lee, who made these last few years brighter than I could have ever imagined.

1 Designing flows to resolve human and environmental water needs in a dam-regulated river

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Contributions

WC and JDO designed research, performed research, analyzed data, and wrote the paper.

Keywords

environmental flows, dam operations, freshwater biodiversity, nonnative species, optimization

1.1 Abstract

Navigating complex trade-offs between meeting societal water needs and supporting functioning ecosystems is integral to river management and policy priorities. Emerging frameworks provide the opportunity to consider multiple river uses explicitly, but balancing multiple ecological objectives remains challenging. Here, we apply multi-objective optimization to design below-dam environmental flows that would simultaneously balance human water needs with the dual conservation targets of benefiting native fishes while disadvantaging nonnative fishes in a large, dryland river basin. We predict that flow designs would lead to greater gains in native fishes and losses in nonnative fishes when compared to natural flow mimicry. Flow designs rarely, if ever, encroached on human water needs, and the predicted benefits for favoring native over nonnative fishes increasingly surpassed those generated by natural flow mimicry across periods of heightened hydrological drought. We provide a quantitative illustration of theoretical predictions that designer flows offer greater ecosystem sustainability in human-altered rivers.

1.2 Introduction

Human societies are grappling with the need to supply reliable and affordable water to growing populations, while at the same time not degrading freshwater ecosystems nor disrupting important ecosystem goods and services. Climate change is intensifying this challenge as droughts increase in both frequency and severity in many parts of the world, leading to greater risk of water supply deficits[1,2]. Innovative strategies are now needed to account for, and assess trade-offs among, multiple potential river uses, taking into consideration the need for water security and the protection of critical ecosystem functions[3,4].

One of the most promising approaches to integrating human uses into the larger scope of ecological sustainability is the concept of environmental flows, or the provision of water within rivers to support positive ecological outcomes while maintaining the water needs of human society[5]. Recent decades have witnessed significant advances in the science underpinning environmental flow management, particularly in relation to prescribing water releases from large dams[6], which now number in the tens of thousands globally and growing[7]. These efforts, as well as most traditional water management practices, are founded on the fundamental principle that native plants and animals are adapted to natural (unaltered) flow regimes and will therefore benefit from dam operations that seek to emulate historical flow conditions[8,9]. Indeed, streamflow alteration is a primary threat to freshwater ecosystems[10]. However, the human enterprise has already drastically changed how hydrology regulates riverine processes[11,12], thus raising the question of whether natural flow mimicry remains the most appropriate management goal for conserving freshwater biodiversity and ensuring functioning ecosystems.

The designer flow concept is an emerging paradigm to address the challenge of environmental flow management in human-altered rivers. Extensive reliance on rivers to produce hydropower, reduce flood risk, and store water for consumptive use cannot be avoided, therefore the traditional approach where natural flow regimes are the target for environmental flow management may only be feasible for the least-regulated ecosystems[13]. Building from previous advancements in "holistic" approaches to water management[6], the designer flow concept seeks to define the hydrologic conditions – which may deviate from natural flow conditions – that promote key ecosystem processes or biological outcomes of interest while navigating the increasingly-competing, societal demands for water and flow[13,14,15]. Although dams alter the natural flow of rivers and threaten freshwater biodiversity, they also provide the prospect to design flows through their downstream release of water. Thus, designer flows have the potential to support freshwater conservation goals by mitigating dam-related impacts, while also striving to provide multiple social and economic benefits.

Designing environmental flows for rivers is hampered by the lack of robust models that explicitly account for multiple human and ecosystem needs[4,16], particularly with respect to contrasting ecological targets. Water management practices that balance multiple ecological objectives is challenging. Dams and their regulation of downstream hydrology have allowed many invasive species to thrive in rivers where natural flow regimes previously hindered their establishment[17]. Invasive fish species are a leading threat in freshwater ecosystems[18], and thus are an increasingly important consideration when defining dam-related environmental flow prescriptions. Although ecological knowledge suggests that a natural flow regime should simultaneously benefit native species and disadvantage nonnative species[8], the reality is that fishes show a variety of responses to flow regimes that do not necessarily align with their status of origin (e.g., refs. 19, 20). Thus, efforts to manage river flows to mimic historical flow conditions may unintentionally assist nonnative species and even fail to achieve the full benefit to native species[8,9,17].

Here, we apply multi-objective optimization to narrow the knowledge gap between the designer flow concept and the science needed to support this approach for sustainable water management when confronted with multiple ecological considerations. Using a large, dam-regulated, dryland river in southwestern United States (Fig. 1.1) as an epitome of water resource challenges in a changing climate, we forecast the trade-offs among allocating water for three objectives: (1) ensure sufficient water for agricultural, domestic, and industrial supply (hereafter, termed human water needs), (2) benefit populations of native fishes, and (3) inhibit populations of nonnative fishes. We first examine the contemporary relationship between annual hydrographs and the relative abundance of multiple native and nonnative fishes using functional regression models. Second, we incorporate the resultant flow-ecology relationships along with a dam operations model into a multi-objective optimization framework. Finally, we use this optimization model to identify facets of the designer flow regime that are predicted to efficiently meet both human and ecosystem water needs and support explicit and actionable prescriptions for daily dam releases. We consider multiple climatic scenarios that encompass the range of water availability in the region (including hydrologic drought conditions), and we evaluate the potential of designer flows to promote native fish biodiversity in comparison to attempts to mimic natural flow regimes.

1.3 Results

Designer flows consistently outperformed natural flow mimicry in simultaneously meeting human water needs and promoting ecological goals (Fig. 1.2). For illustrative purposes, we focused on one of several flow designs that heavily prioritized human water security and concurrently sought to balance the objectives of native abundance gains versus nonnative abundance losses equally (i.e. minimal human water deficit, moderate native abundance gains, and moderate nonnative abundance losses). Most striking was that designer flows were predicted to lead to over 200% greater nonnative abundance losses when compared to natural flow mimicry (Table 1.1). In addition, designer flows were always predicted to benefit native species, whereas flow prescriptions that mimicked natural flow regimes led to small losses in native fish abundance during periods of average or low water availability and only small gains in high-flow years. These predictions were generated from flow-ecology models where streamflow explained on average 35% of the variance in fish densities across years and locations (Supplementary Table 1.1).

The benefit of designer flows for favoring native over nonnative fishes further surpassed those generated by natural flow mimicry during periods of heightened hydrological drought. Predicted improvement to native fish abundances from our example designer flows versus natural flow mimicry grew by nearly 100% when comparing the low-flow, dry (below-average annual river discharge) climate scenario to the high-flow, wet (above-average annual river discharge) scenario (Table 1.1). Meanwhile, improvement in nonnative abundance losses for this same comparison increased by nearly 40%.

These comparisons represent but one set of priorities for flow designs. Our optimization procedure identified many possible flow prescriptions as leading to simultaneous benefits to fish conservation goals (i.e., native fish abundance gains, nonnative fish abundance losses) and to society by meeting water needs for agricultural, domestic, and industrial use, even during drought conditions (Fig. 1.2). Flow designs rarely, if ever, encroached on human water needs, and perhaps most importantly, opportunities for achieving multiple benefits did not disappear during periods of limited water availability. Only the dry climatic scenario saw flow designs that resulted in major deficits to human water needs, and then only when disproportionately prioritizing ecological objectives.

Designer flows achieve this balance by capitalizing on empirically-based, predicted differences between native and nonnative responses to river flow (Supplementary Fig. 1.1). In general, high late-winter (February) flows simultaneously benefited native flannelmouth sucker (*Catostomus latipinnis*) and speckled dace (*Rhinichthys osculus*) while disadvantaging nonnative red shiner (*Cyprinella lutrensis*), fathead minnow (*Pimephales promelas*), and channel catfish (*Ictalurus punctatus*). On the other hand, native and nonnative fishes both benefited from increased mid-spring (April) flow magnitudes and both responded negatively to increased mid-autumn (October) flow magnitudes. Higher flow releases late-summer demonstrated a strong negative influence on nonnative species, with negligible effects on native species. Consequently, our predictions suggest that flow designs that favor native over nonnative fishes in the San Juan River could involve large dam releases in late-winter to benefit native species at the expense of nonnative species, carefully-managed releases in the mid- and late-spring months to consider relative benefits to both native and nonnative species, and additional releases in late-summer to the detriment of nonnative species (Fig. 1.3, 1.4). Flow designs also tracked changing water availability, reserving water when unregulated Animas River flow could readily provide for societal water diversions in order to maximize ecological benefit of dam releases at other times of the year.

Despite these overall trends in flow designs, we found individual predicted species' responses to flow designs did not necessarily align along nativity groupings (Fig. 1.5). Across climatic scenarios, flow designs simultaneously benefited both native fish species while greatly decreasing abundances of the two small-bodied, nonnative competitors – red shiner (*Cyprinella lutrensis*) and fathead minnow (*Pimephales promelas*). By contrast, the large-bodied, nonnative channel catfish (*Ictalurus punctatus*) consistently showed weak positive responses to optimal flow designs, thus demonstrating the unavoidable trade-offs associated with managing dam releases for entire assemblages of species.

1.4 Discussion

The past decade has seen considerable empirical and methodological advancements in understanding the functional flows required to support ecosystems (e.g. refs. 14, 21), thus providing the foundation for the multi-objective optimization framework implemented here. We found that designer flows provide greater potential for disadvantaging nonnative species compared to natural flow mimicry, and that dam release schedules informed solely by historical flow conditions may fail to achieve native species conservation goals fully (Table 1.1). This trend in native fish responses is not predicted by the ecological literature[8,9], and instead likely suggests that the response of native fishes to flow regimes within our study system may be mediated by the presence of nonnative fishes or influenced by other environmental drivers[12]. Previous studies have shown the potential of introduced fishes to affect native fishes' behavior and habitat use[22], which can modify native flow responses[23]. Building on theoretical frameworks that propose greater opportunities for ecosystem sustainability resulting from designer flows[13,14], we provide a quantitative illustration for these predictions in a human-altered river.

A suite of dam operation strategies that simultaneously met both societal and environmental water needs underscored the potential benefits provided by designer flows (Fig.

1.2). Ensuring human water security versus supporting ecosystems services via natural hydrology have long been considered conflicting objectives in water resource management[24], a perspective that has been reinforced by previous optimization studies[25,26]. Most multi-objective optimization studies have focused on balancing human water needs with the goal of releasing environmental flows to mimic a natural flow regime or of solely benefiting native fishes[27,28]. By contrast, our approach looks beyond the natural flow paradigm and considers multiple native and nonnative species explicitly in the design of environmental flows. The notions that societal water use inherently precludes the ability to achieve positive conservation outcomes, and that the severity of trade-offs between these two goals only intensifies as water availability continues to decrease, is pervasive among scientists, practitioners, and the public[4,29]. Our results suggest that these trade-offs can be overcome through multi-objective optimization and careful planning.

Despite mounting pleas and accumulating science to define environmental flows for freshwater ecosystems, previous efforts have overwhelmingly focused on single species or ecosystem surrogates for river restoration (e.g. refs. 30, 31, 32) with little consideration of explicit targets for biological communities[33]. By incorporating multiple species associations with the entire hydrologic regime, we demonstrate that designer flows may be engineered to meet human water demands and take advantage of mismatches between native and nonnative species responses to flow. These mismatches create small, but powerful, windows of opportunity to allocate water for dam releases that deliver multiple ecological outcomes; in this case supporting native species conservation and nonnative species control. Capitalizing on such opportunities are admittedly challenging and require interdisciplinary collaborations among researchers, engineers, watershed planners and policy makers, just to name a few.

The sheer prevalence of nonnative fishes in dam-impacted rivers and the considerable similarities in life histories exhibited by native and nonnative fishes[20] necessitate a multi-species approach to water management. Native and nonnative fishes did not always demonstrate contrasting responses to high flows (Fig. 1.3, 1.4), which is indicative of ecological and flow-preference similarities[19]. Flow responses varied within nativity groupings, as seen with the channel catfish (*Ictalurus punctatus*), which responded to flow designs more similarly to native species compared to other nonnative species[19]. The fact that flow designs may have a net negative effect on nonnative fish communities, but that a spectrum of species-specific responses are possible, reinforces multi-faceted strategies to nonnative species management. For example, whereas populations of small-bodied fish species are infeasible to control physically in river systems, opportunities for active mechanical removal efforts for larger species exist[34]. Given that predation and competition from introduced species are major threats to native biodiversity and are exacerbated by human alteration of rivers[18], it is critical to quantify the trade-offs inherent in environmental flow prescriptions that seek to disfavor multiple nonnative species.

Most dam release experiments – while founded on a robust understanding of species' responses to natural flow conditions – have predominantly implemented only simple flow recommendations based on single flow events[33]. We found that isolated flow events often failed to simultaneously bolster native species and deter nonnative species (Fig. 1.3). Indeed, flood manipulations in other southwestern rivers of the United States have benefited some native fishes but with limited to no effect on nonnative fishes[35,36]. Increased flooding in the Murray-Darling River Basin, Australia, showed similar inconsistency in responses of native and nonnative fishes[37]. By contrast, environmental flow prescriptions that were motivated by multiple ecological processes created more opportunities for native fishes to flourish over nonnative fishes[32]. Evaluating trade-offs and informing flow management in human-altered rivers require identifying the manifold facets of the flow regime that support desired ecological structure and function[14]. Our study quantifies this knowledge and integrates regime-wide flow ecology for multiple species into environmental flow prescriptions; this foundation is readily transferable to other river systems across the world and could be prioritized towards dams where benefits to river biodiversity are likely to be maximized[38].

Environmental flow management is often overlooked during years with below-average flow because of the perceived scarcity of water available to meet ecological objectives after human demands have been satisfied. We assert that this represents a potential lost opportunity. Although low water availability creates challenges for prescribing the flood pulses that often form the basis of natural flow mimicry, our results demonstrate considerable scope for achieving ecological outcomes using designer flows of all magnitudes and timing. Specifically, hypothetical flow designs that prioritized dam releases in late-winter, late-summer, and mid-autumn were predicted to favor native over nonnative fish populations, even in drought conditions (Fig. 1.4). Here, flow designs depended on the unregulated inflow of water from the Animas River into the San Juan River. During high-flow years, Animas inflow provided water for societal water diversions, whereas drought conditions placed greater weight on environmental flows relative to unregulated flow for meeting ecological and societal water needs. Low-flow hydrology is critical for fish movement, spawning, and recruitment[39], and environmental flow management has shown some success in reversing the impact of human alteration on low-flow events[40]. Elevating the value of targeted environmental flow management under water scarcity will reveal new and unexpected opportunities for freshwater conservation in an increasingly drought-stricken future[41,42].

Quantitative models that support more diversified options for utilizing environmental flows to target multiple species and ecological processes provide exciting opportunities to tailor prescriptions for entire ecosystems. For example, experimental floods have successfully restored native riparian vegetation[43], returned aquatic macroinvertebrate communities to pre-dam conditions[44], and invoked food web responses in river ecosystems[45]. Moreover, environmental flows have the potential to reverse the detrimental effects of dams on riverine thermal regimes[12,46] and sediment transport[47]. A central challenge for the adoption of designer flows will be the explicit consideration of desired physical and biological outcomes, leading to a truly holistic or ecosystem approach. Not meeting this challenge will ultimately impede the translation of flow designs from theory to practice. Our study suggests how we might accomplish this integration via multi-objective optimization to inform dam operations.

Considerable scope also exists for designing environmental flows that are informed by multiple social and economic objectives, while still supporting functioning freshwater ecosystems. For example, designer flows are equally pertinent to managing potential conflicts between hydropeaking operations and biodiversity conservation[48], a particularly relevant challenge given the thousands of existing and new hydropower dams planned for construction around the world[49]. Optimizing flow designs around minimizing operational costs creates opportunities for evaluating the economic value of ecosystem goals and increasing potential ecological benefits per dollar spent[15]. Furthermore, dams provide opportunities to manage, and thus optimize, downstream water temperature regimes[12], leading to discussions on whether dam operations can mitigate warming effects from climate change[50]. Finally, the modular nature of multi-objective optimization allows for evaluating additional societal dimensions, such as accounting for lake-level fluctuations and thermal structures that influence greenhouse gas (carbon dioxide and methane) emissions from reservoirs[51].

The science on flow-ecology relationships is now substantial[21], yet we acknowledge that it is often not complete or universally available to provide stakeholder-relevant information necessary to inform management decisions[16,52]. Furthermore, the interactive effects of streamflow, water quality, and physical habitat characteristics on ecological responses are widely recognized, but rarely incorporated into flow-ecology relationships[12]. Whether it is broad flow-management frameworks[31] or quantitative optimization approaches (this study), environmental flow designs are inextricably linked to the robustness of underlying flow-ecology models. Here, we leveraged recent statistical advances in functional data analysis to enable a more holistic characterization of the flow regime and its relation to fish species density[53], but we recognize that predictions arising from our study are only as strong as the validity of the modeled flow-ecology relationships. Because the designer flow approach relaxes the assumption of adhering to a natural flow regime, flow designs may fall outside the range of hydrological conditions used to inform flow-ecology models. Additionally, response metrics, such as fish biomass, may advance flow-ecology models by capturing differences in individuals’ ecological influence in the ecosystem. Greater scrutiny into flow-ecology associations, particularly accounting for non-linear variable relationships[54], non-stationarity in hydro-climatic and ecological processes[55], and variable flow responses across ecological metrics[56], remains a critical research frontier.

How multiple benefits from designer environmental flows are realized across different groups in society depends on the physical and social structures, as well as the political economy from which access and entitlements to these benefits are mediated[4,57]. Successful environmental flow implementation requires diverse and authentic stakeholder involvement to define and refine desired social and biological outcomes[4,58]. We have illustrated how particular flow designs may best promote native fish conservation after accounting for human water needs, but these decisions ultimately depend on the shifting values that stakeholders place on a whole suite of competing objectives. These values are also likely to morph in response to changes in water availability, human water needs, and natural resource management goals[1,15]. Region-wide planning and consensus building remains essential to achieving multiple benefits from environmental flow management, and there is no denying that many water-resource decisions are made in contentious contexts constrained by political, legal, social, and economic realities.

Despite the oft-cited headlines of mounting conflicts between human and ecosystem needs for water, we predict that such trade-offs can be creatively navigated and potentially avoided by using multi-objective optimization[59]. This approach allows for the discovery of efficient solutions that minimize conflict among competing water needs when trade-offs cannot be avoided. In human-altered rivers facing multiple stressors that include invasive species, mimicking natural flow regimes below dams may be just one of many options for conserving freshwater diversity. Designer flows have been suggested as a means to enable ecosystem design and support adaptation to environmental change, and here we provide a quantitative, albeit untested, illustration of how this emerging paradigm can be realized to ensure both societal and environmental benefits of dam operations. Further advancements in the development of multi-species functional flow-ecology models and the incorporation of environmental, social and political stochasticity in flow design prescriptions will increase consensus on designer flows as the operating standard for human-altered rivers.

1.5 Methods

1.5.1 Study System

The San Juan River Basin (SJRB) is in an arid to semi-arid region of southwestern United States (Fig. 1.1). Regulated releases from Navajo Dam on the mainstem and unregulated inflow from the Animas River tributary largely determines its hydrology. The SJRB exhibits high mean daily spring discharge and low mean daily summer discharge (Supplementary Fig. 1.2, Supplementary Fig. 1.3), though the Navajo Dam has greatly decreased spring discharge magnitude and interannual summer discharge variation[36,60]. This dynamic, snowmelt-fed system led us to consider multiple climatic scenarios: periods of wet high-flow, normal average-flow, and dry low-flow conditions. We used the Discrete Fast Fourier Transform to extract the seasonal component of logarithmic-transformed, normalized stream flow records at the USGS flow gage station near Four Corners, CO (USGS 09371010) from 1985-2014[61]. We then calculated the total annual deviation from this seasonal component to characterize water availability in each year (Supplementary Fig. 1.4). Based on this analysis, we identified three-year periods that represented: (1) positive anomalies indicating higher-than-average flow conditions (water years 1993-1995; water years start in October); (2) minimal anomalies indicating average flow conditions, (water years 1999-2001), and (3) negative anomalies indicating lower-than-average flow conditions (water years 2002-2004). A year of average flow conditions preceded each period. We used three-year periods to match general planning periods for Navajo Dam operation rules, though other planning periods could be investigated. These periods represent wet, normal, and dry flow conditions, respectively, and reflect historical differences in Navajo Dam water releases, inflow into the Navajo Reservoir, and inflow from the Animas River tributary (Supplementary Table 1.2).

The Navajo Reservoir primarily serves as a water storage facility for agricultural, domestic, and industrial use within the SJRB. The Navajo Indian Irrigation Project (NIIP) comprises the largest portion of the water needs in the SJRB, which draws water directly from the reservoir, while other water diversions occur at numerous locations below Navajo Reservoir. These diversions, which were similar across the three climatic scenarios, are concentrated in March through October, and peak during June and July. We modeled human water use needs within the SJRB using United States Bureau of Reclamation (USBR) water depletion data (Supplementary Fig. 1.5). Although there are return flows from water diversions within SJRB, we made the conservative and simplifying assumption that return flows from river diversions were negligible relative to channel flow[62].

The SJRB supports numerous native and nonnative fishes and is a critical stronghold for several threatened fish species[36]. Dam-related flow regime alterations have led to considerable spatial overlap of native and nonnative populations[63]. Management actively seeks to increase the abundance of desired native fishes while concurrently depressing the populations of nonnative fishes[64]. We collated time series of native and nonnative fish abundances in San Juan River secondary channels (river kilometers 110-248) collected once a year between mid-September and mid-October (hereafter "Fall") from 1993 to 2010 per standardized shore seining protocols from the San Juan River Basin Recovery Implementation Program[36,60]. Surveyors used a 2.2 m x 1.9 m x 3.0 mm mesh drag seine, made at least five hauls per secondary channel to sample all distinct habitats, with additional hauls for secondary channels with greater habitat diversity, and estimated the area of each haul. Fish surveys targeted a range of habitats (backwaters, pools, riffles, runs, and shoals) in 200-meter long secondary channels (characterized as <25% of the main channel discharge). We focused on two native (*Rhinichthys osculus* speckled dace and

Catostomus latipinnis flannelmouth sucker) and three nonnative (*Cyprinella lutrensis* red shiner, *Pimephales promelas* fathead minnow, and *Ictalurus punctatus* channel catfish) fish species. These species span a range of flow and mesohabitat preferences, are sufficiently abundant in the San Juan River to be effectively sampled, and exhibit similar life histories to species that were not included in our study[19,36].

1.5.2 Modeling Fish-flow Relationships

We used historical discharge data (in m^3/s) from three USGS flow gaging stations to examine the daily influence of flow magnitude on focal species' Fall abundance: Shiprock, NM (USGS 09368000), Four Corners, CO (USGS 09371010) and Mexican Hat, UT (USGS 09379500). Discharge was similar across all three points of the river, spanned a wide range of hydrologic conditions, and is representative of hydrologic conditions that persist in the San Juan River Basin after the construction of Navajo Dam (Supplementary Fig. 1.3). We calculated the density of focal species (individuals per m^2 seined) within corresponding geomorphic reaches: Red Wash, NM to Shiprock, NM, river kilometers 211-248; Aneth, UT to Red Wash, NM, river kilometers 173-211; and Chinle Creek to Aneth, UT, river kilometers 110-173. By considering flow responses across three reaches, we minimized the risk that hydrological or species density idiosyncrasies would affect the analysis. Both densities and river discharges were logarithmic-transformed to reduce the influence of disproportionately large values in our analyses.

We implemented functional regression models to estimate the influence of local daily discharge on native and nonnative fish abundances throughout the San Juan River. Functional data analysis is more appropriate than traditional regression analysis for data that take the form of functions rather than single values[65], and is considered to provide a more holistic characterization of flow regimes than traditional hydrologic metric approaches to fish-flow relationships[53]. Rather than using hydrological summary statistics, functional regression uses annual hydrographs as the environmental covariate to predict fish abundances. The basic (discrete) form of the regression model is:

$$y_i = \beta_0 + \sum_t \beta_1(t) f_i(t) + \epsilon_i \, , \qquad [1.1]$$

where t spans the days of the year, y_i is the fish abundance in year i, $f_i(t)$ is the log-transformed flow magnitude in year i on day t, β_0 is the average fish abundance, $\beta_1(t)$ is the regression coefficient indicating the daily influence of flow on fish abundance, and ε_i accounts for unexplained variation in fish abundance. We extended this approach by adopting a methodology – termed functional regression that is interpretable (FLiRTI) – that preserves the desired, smooth function estimation of the basic functional regression approach, but improves the interpretability of the estimate by constraining nonzero effects of predictor variables to only the most relevant parts of the function's domain[62]. While we acknowledge that hydrograph idiosyncrasies could skew interpretations of flow-ecology relationships, such effects also manifest in hydrological statistics.

Using the FLiRTI approach, we determined the daily influence of antecedent flows (prior year) on annual Fall abundances of each species within each reach, assessed model fit via five iterations of 6-fold cross-validation, and selected models that exhibited the smallest median cross-validated error, to avoid overfitting to our data[66] (Supplementary Table 1.1). From these models, we obtained regression coefficients $\beta_{xr}(t)$ for species x in reach r on each day t, which we used to predict the cumulative effect of flow M_{xry} on a species x in reach r during year y given different hypothetical discharges $Q_{G,r}(y,t)$:

$$M_{xry} = \sum_t \beta_{xr}(t) \log Q_{G,r}(y,t) \, , \qquad [1.2]$$

Each individual species' responses to potential flow regimes were calculated by averaging M_{xry} across all reaches and years for that species.

1.5.3 Establishing Efficient Flow Designs via Multi-objective Optimization

We modeled daily dam operations, human water use diversions, and SJRB hydrology over each three-year climatic scenario using mass-balance equations to elucidate daily dam water releases and water use diversions that led to optimal flow designs. See Supplementary Table 1.3 for a summary of all parameters and variables used in our modeling framework, and see Supplementary Fig. 1.6 for a schematic of our study system.

We evaluated flow designs based on their efficiency at balancing trade-offs among three objectives: (1) minimizing the proportional deficit between prescribed water diversions and SJRB water needs, (2) maximizing SJRB native fish abundance gains, and (3) minimizing nonnative fish abundance gains. To quantify the degree to which a flow design satisfied human water use needs in the SJRB, we calculated the total proportional deficit between the amount of water diverted $Q_{D,r}$ and the amount required d_r over all reaches r, years y, and days t:

$$WD = \frac{\sum_{r,y,t}\left[d_r(y,t) - Q_{D,r}(y,t)\right]}{\sum_{r,y,t} d_r(y,t)}. \qquad [1.3]$$

Native and nonnative fish abundance gains (*NF* and *NNF*, respectively) were designated as the aggregated effects of flow estimated from functional regression M_{xry} averaged over each reach, year, and species within native and nonnative groupings.

To meet these objectives, we must decide the Navajo Dam water release rate $Q_R(y,t)$ on each day t of each year y. We must also decide the water withdrawal rate from Navajo Reservoir $Q_{D,0}(y,t)$, and the water diversion rate from each of our channel reaches: between Navajo Reservoir and Shiprock $Q_{D,1}(y,t)$, Shiprock and Four Corners $Q_{D,2}(y,t)$, and Four Corners and

Mexican Hat $Q_{D,3}(y,t)$. These decisions are constrained by the physical and operational limits of Navajo Reservoir. The volume of water in the reservoir must be small enough to avoid overtopping the dam (S_{max}) and large enough to ensure that the Navajo Indian Irrigation Project can draw water from the reservoir (S_{min}):

$$S_{min} \leq S(y,t) \leq S_{max} \,. \qquad [1.4]$$

We additionally constrained the reservoir volume on the first and last days of each simulation to be equivalent to actual, historical reservoir storage on the corresponding days. Alternatively, reservoir volume on the first day of each simulation could be constrained to be equal to that of the last day, but we deemed this constraint unrealistic during drought conditions. Dam releases $Q_R(y,t)$ from the reservoir are operatively limited by minimum ($Q_{R,min}$) and maximum flows ($Q_{R,max}$):

$$Q_{R,min} \leq Q_R(y,t) \leq Q_{R,max} \,. \qquad [1.5]$$

In addition, daily dam releases cannot change by more than a limit $\delta_{R,max}$:

$$|Q_R(y,t+1) - Q_R(y,t)| \leq \ \delta_{R,max} \,. \qquad [1.6]$$

Finally, we restrict diversions $Q_{D,r}(y,t)$ in each region r to be nonnegative and no more than the water demand for that region $d_r(y,t)$:

$$0 \leq Q_{D,r}(y,t) \leq d_r(y,t) \ . \qquad [1.7]$$

SJRB hydrology is subsequently constrained by our water diversion and dam release decisions, and vice versa. Water flows into the Navajo Reservoir from the San Juan River and its tributaries upstream of the Navajo Dam at a rate of $Q_{I,SJ}$; we considered direct precipitation on the reservoir surface and groundwater contributions to be negligible based on available evidence[67]. The main outflows from the Navajo Reservoir are releases from the Navajo Dam, Q_R, water diversions directly from the reservoir for the Navajo Indian Irrigation Project (NIIP), $Q_{D,0}$, and evaporative water loss from the reservoir, E. Consequently, the amount of water in the reservoir $S(y, t)$ on day t of year y is a function of the amount of water stored on the previous day $t - 1$ and the inflows and outflows on the current day:

$$S(y,t) = S(y,t-1) - E(y,t) + \gamma\left[\, Q_{I,SJ}(y,t) - Q_R(y,t) - Q_{D,0}(y,t) \,\right], \tag{1.8}$$

where γ is a constant that extrapolates flow rates into daily volumes, assuming a constant flow within each day. The discharge at each USGS flow gaging station $Q_{G,r}(y,t)$ can then be predicted using mass-balance equations (flow into and out of a point must be equivalent):

$$Q_{G,1}(y,t) = Q_R(y,t) - Q_{D,1}(y,t) + Q_{I,A}(y,t)\,, \tag{1.9}$$

$$Q_{G,2}(y,t) = Q_{G,1}(y,t) - Q_{D,2}(y,t)\,, \tag{1.10}$$

$$Q_{G,3}(y,t) = Q_{G,2}(y,t) - Q_{D,3}(y,t)\,, \tag{1.11}$$

where $Q_{I,A}(y,t)$ is the rate of inflow from the Animas River into the San Juan River. We assumed that evaporation and transpiration processes are negligible along the San Juan River. Although there are some return flows from the non-consumptive portion of diversions in SJRB, we omitted them for the sake of tractability.

Confronted with multiple, likely conflicting objectives, it would be impossible to create a single dam release schedule that met all objectives perfectly. Thus, our goal was to find the set of efficient flow designs (i.e. the Pareto frontier) that adhered to dam operation requirements and water availability, and were not strictly outclassed by any other possible flow design[68]. We established this set by maximizing a weighted average F of our three objectives and changing the relative weights to obtain designs with different prioritizations[69]:

$$F = w_1 WD + w_2 NF + w_3 NNF\,, \tag{1.12}$$

where w_1, w_2, and w_3 are weights that must sum to one, and the three objectives – human water needs WD, native fish gains NF, and nonnative fish losses NNF – are scaled to lie between zero and one for their worst and best possible values, respectively.

Optimization models and routines were carried out using AIMMS 4.10.2[70].

1.5.4 Comparing Flow Designs and Natural Flows

We evaluated the strength of the designer flow approach for simultaneously maximizing native and minimizing nonnative fish abundances for each of the three climatic scenarios by comparing flow designs to a natural flow mimicry baseline. For each scenario, we collated the historical, daily inflow into Navajo Reservoir (i.e. upstream from the dam) to ascertain the hypothetical flow patterns of an unregulated San Juan River (Supplementary Fig. 1.5). We then extracted the total amount of water released during our prescribed three-year flow designs, and distributed that amount per the unregulated inflow patterns to obtain a hypothetical reconstruction of dam operations that would mimic natural flows whilst fully meeting human water needs. Thus, we could compare the predicted response of native and nonnative fishes to the same volume of water allocated using designer flows versus natural flow mimicry.

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1.8 Tables and Figures

Table 1.1 Predicted average* native and nonnative abundance gains (+) and losses (-) resulting from designer flows (left) versus natural flow mimicry (right) for three climatic scenarios of decreasing river discharge (flow).

Water Availability	Designer Flows †		Natural Flow Mimicry	
	Native	Nonnative	Native	Nonnative
Wet (high-flow)	2.11	-20.00	0.29	-9.27
Normal	1.13	-25.67	-0.42	-9.12
Dry (low-flow)	3.29	-21.61	-0.26	-6.77

* Abundances (individual/m^2) are on the log-scale averaged across all years, river reaches, and species within each scenario

† Sample flow designs that heavily prioritized human water needs and otherwise focused equally on native abundance gains and nonnative abundance losses (90%/5%/5% respective priority split).

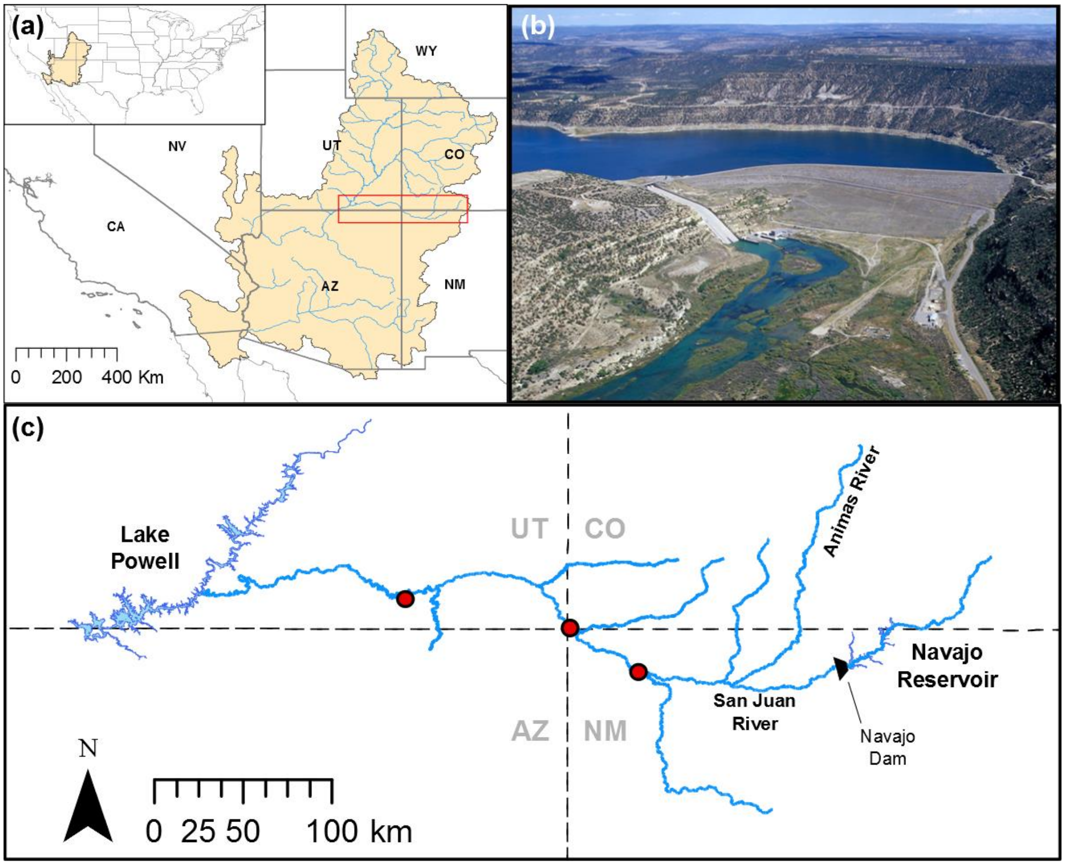


Figure 1.1 Map of study region. (a) The San Juan River Basin (red box) is a major tributary of the Colorado River Basin, located in southwestern United States. (b) The Navajo Dam is an earthen dam on the San Juan River that creates the Navajo Reservoir. (c) Our case study focused on the region from Navajo Reservoir (river kilometer 360) to Lake Powell (river kilometer 0). Red circles indicate the USGS flow gage stations used in the study. Photo credit: United States Bureau of Reclamation.

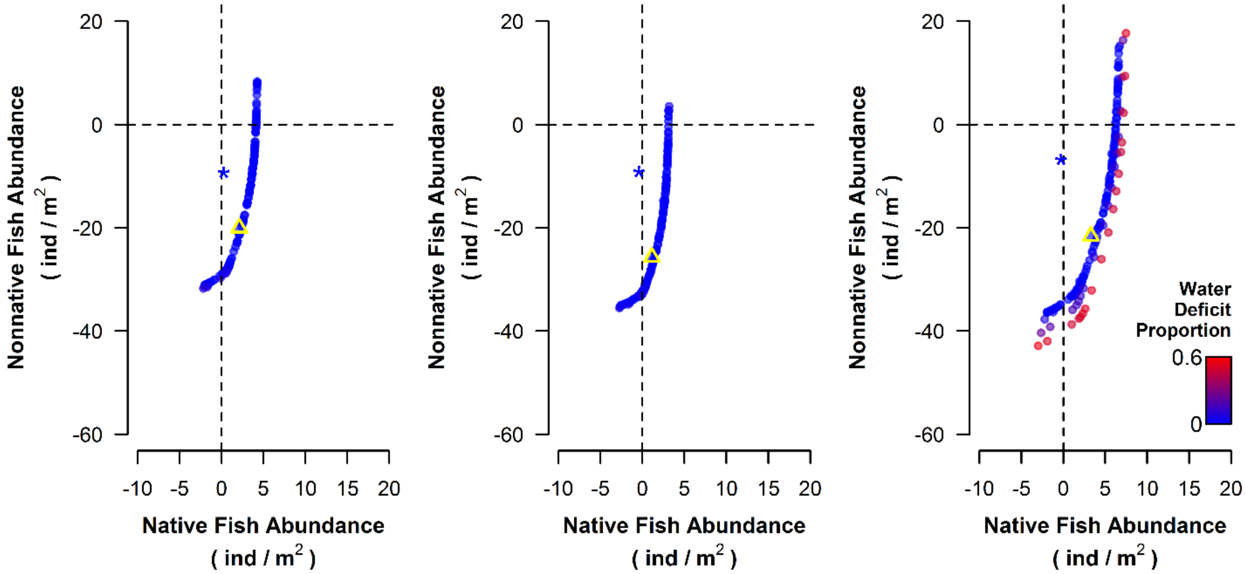


Figure 1.2 Efficient (Pareto) frontiers showing various flow designs that differentially prioritized human water needs, average native fish abundance gains, and average nonnative fish abundance losses during the (a) wet (high-flow) period, (b) normal (average-flow), and (c) dry (low-flow) period. Predicted effects on abundances (individual/m^2) are on the log-scale averaged across all years, river reaches, and species within each scenario. Each point represents a different flow design. The triangle symbol in each panel designates sample flow design used for discussion of designer flow approach in main text. The star symbol in each panel indicates the outcomes of hypothetical natural flow mimicry during the same periods with no deficit to human water needs.

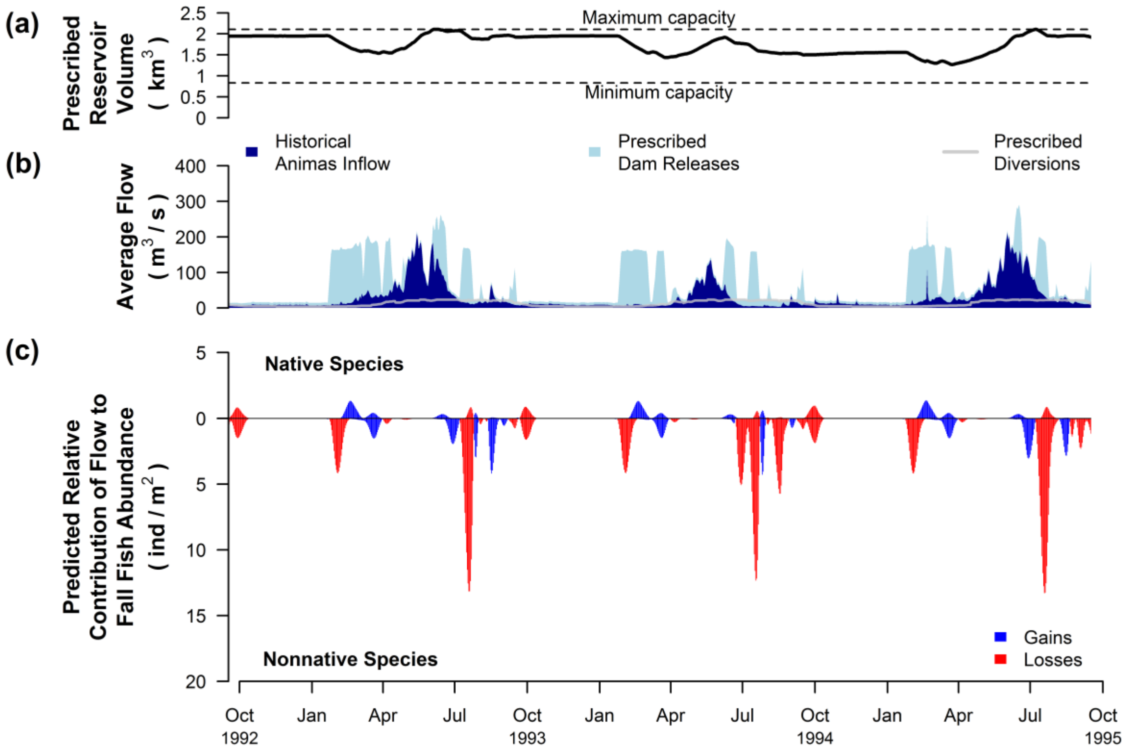


Figure 1.3 Designer flow prescription (triangle symbol in Fig. 1.2a) that heavily prioritized human water needs and focused equally on native species abundance gains and nonnative species abundance losses (90%/5%/5% respective priority split) per a wet (high-flow) scenario. (a) Prescribed reservoir volume; (b) Cumulative plot of historical Animas inflow (dark blue) and prescribed dam releases (light blue), with prescribed water diversions downstream of Navajo Reservoir overlaid (gray); (c) Predicted relative abundance gains (blue) or losses (red) of native (above zero axis) and nonnative (below zero axis) fishes in response to flow designs (individual/m^2 on log scale).

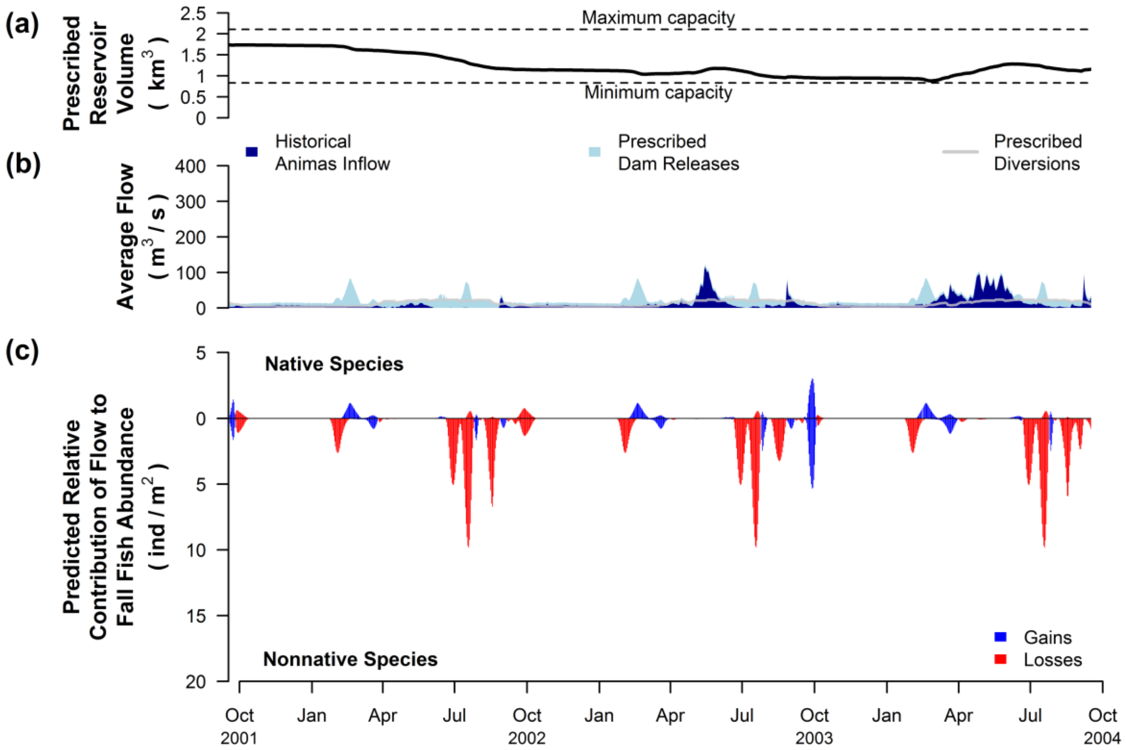


Figure 1.4 Designer flow prescription (triangle symbol in Fig. 1.2b) that heavily prioritized human water needs and focused equally on native species abundance gains and nonnative species abundance losses (90%/5%/5% respective priority split) per a dry (low-flow) scenario. (a) Prescribed reservoir volume; (b) Cumulative plot of historical Animas inflow (dark blue) and prescribed dam releases (light blue), with prescribed water diversions downstream of Navajo Reservoir overlaid (gray); (c) Predicted relative abundance gains (blue) or losses (red) of native (above zero axis) and nonnative (below zero axis) fishes in response to flow designs (individual/m^2 on log scale).

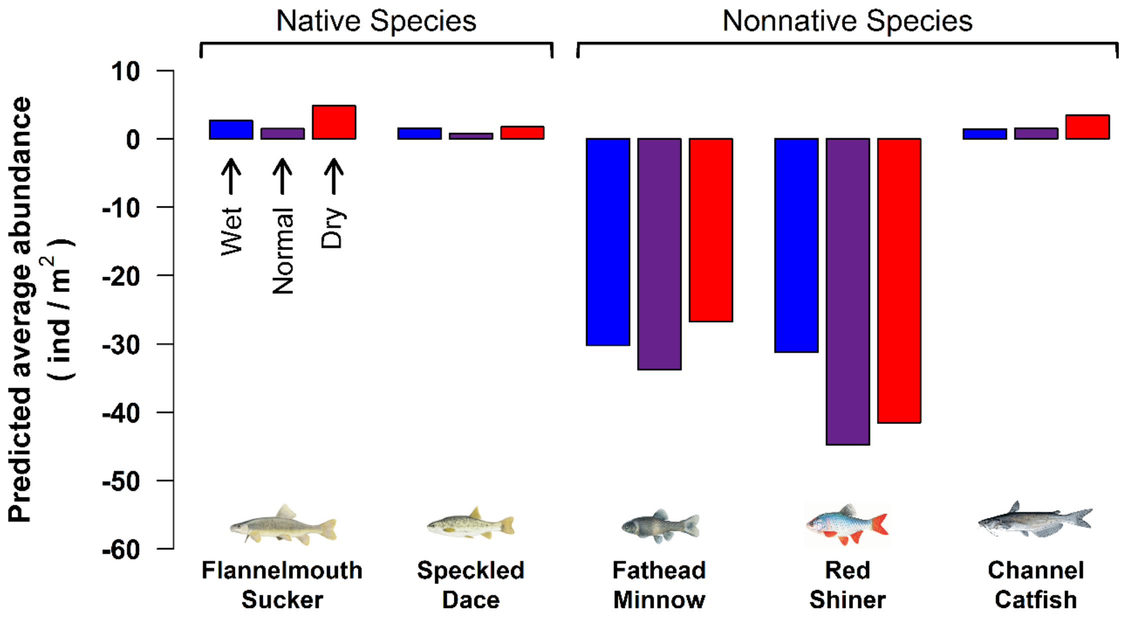


Figure 1.5 Relative individual species abundance gains or losses averaged across three-year periods under wet (blue fill), normal (purple fill), and dry (red fill) climatic scenarios. Species responses are based on flow designs (triangles in Fig. 1.2) that heavily prioritized human water needs and gave equal consideration to native fish benefit (*Rhinichthys osculus* and *Catostomus latipinnis*) and nonnative fish detriment (*Cyprinella lutrensis*, *Pimephales promelas*, and *Ictalurus punctatus*).

1.9 Supplementary Tables and Figures

Supplementary Table 1.1. Model diagnostics of selected flow-ecology model for each species and USGS gage combination.

Species	USGS Gage	Median CV Error*		NRMSE †	R^2
		Min	Max		
Native					
Catostomus latipinnis flannelmouth sucker	Mexican Hat	20.90	44.04	0.23	0.04
	Four Corners	22.08	64.66	0.20	0.27
	Shiprock	26.02	49.28	0.17	0.50
Rhinichthys osculus speckled dace	Mexican Hat	8.22	16.35	0.29	0
	Four Corners	13.73	20.58	0.26	0
	Shiprock	13.50	20.95	0.27	0.42
Nonnative					
Cyprinella lutrensis red shiner	Mexican Hat	53.06	87.43	0.19	0.55
	Four Corners	23.95	50.19	0.19	0.50
	Shiprock	79.60	149.86	0.14	0.62
Ictalurus punctatus channel catfish	Mexican Hat	25.06	38.43	0.13	0.58
	Four Corners	10.55	17.60	0.26	0
	Shiprock	23.82	47.63	0.28	0
Pimephales promelas fathead minnow	Mexican Hat	89.89	153.36	0.16	0.70
	Four Corners	77.66	197.17	0.25	0.34
	Shiprock	64.95	122.26	0.13	0.71

***** Minimum median cross-validation error was used to select models; maximum median cross-validation errors were derived from all considered models

† Root-mean squared error, normalized by the range of the response, log-transformed species density

Supplementary Table 1.2. Summary of historical data within each climatic scenario.*

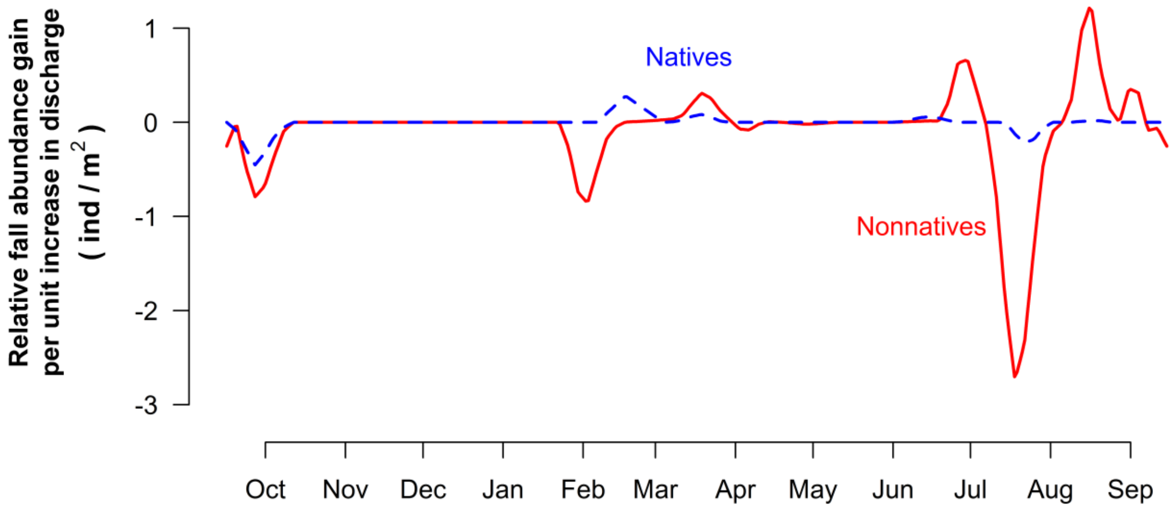
Characteristic	Period†		
	Wet 1993-1995	Normal 1999-2001	Dry 2002-2004
Hydrology Totals			
Reservoir Inflow (km^3)	4.782	3.142	1.536
Reservoir Evaporation (km^3)	0.113	0.100	0.073
Animas River Inflow (km^3)	2.859	2.276	1.206
Precipitation (mm)	1013	877	797
Reservoir Operations			
Initial Reservoir Capacity (km^3)	1.947	1.705	1.737
Final Reservoir Capacity (km^3)	1.919	1.738	1.153
Dam Release Total (km^3)	4.043	2.515	1.360
Water Diversion Totals			
Navajo Reservoir (km^3)	0.656	0.491	0.688
Downstream San Juan (km^3)	1.191	1.178	1.190

*Precipitation data collated from PRISM Climate Group. All other data collated from United States Bureau of Reclamation.

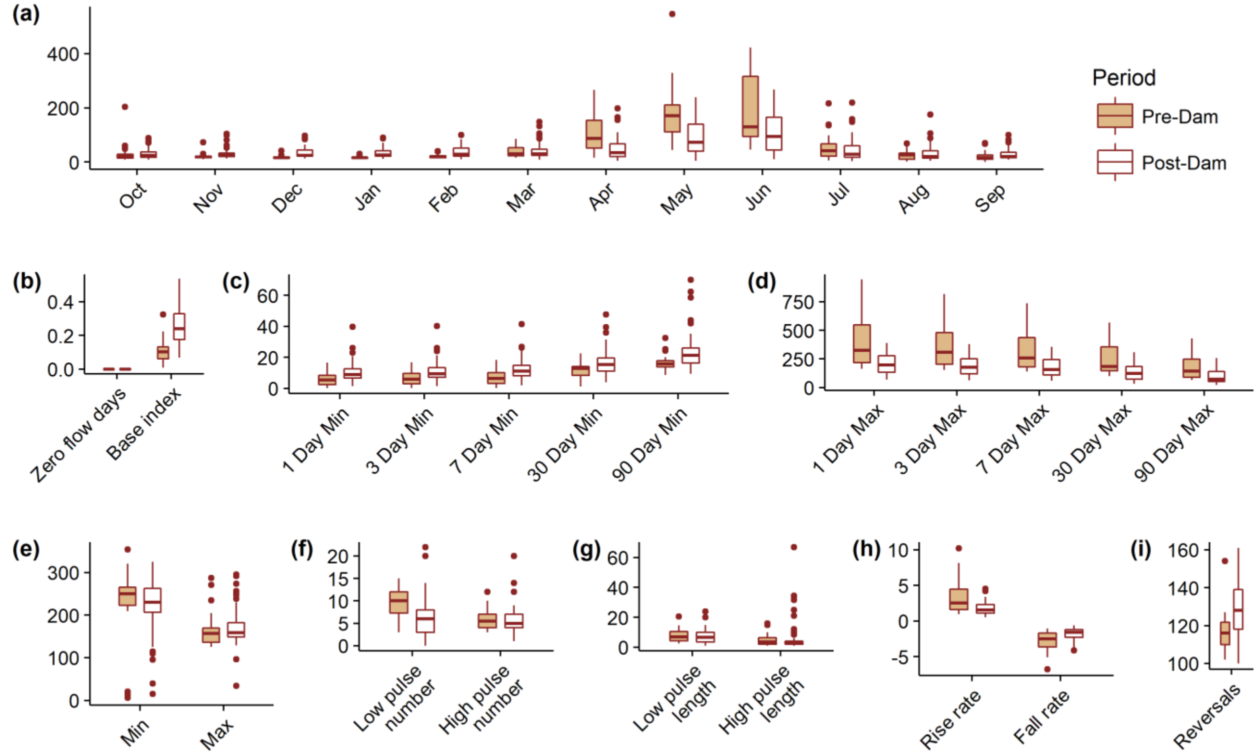
†Periods are based on water years (October - September)

Supplementary Table 1.3. Description [and units] of parameters and variables used in optimization model.

Known inflows, depletions, and demands	
$Q_{I,SJ}$	Inflow of water from the San Juan River to Navajo Reservoir [m^3/s]
$Q_{I,A}$	Inflow of water from the Animas River to the San Juan River [m^3/s]
E	Daily volume of water evaporation from the Navajo Reservoir [m^3]
d_0	Flow required by the Navajo Indian Irrigation Project [m^3/s]
d_1	Flow required by users downstream of Navajo Reservoir and upstream of the USGS gage near Shiprock, NM [m^3/s]
d_2	Flow required by users downstream of the Shiprock gage and above the USGS gage near Four Corners, CO [m^3/s]
d_3	Flow required by users downstream of the Four Corners gage and above the USGS gage near Mexican Hat, UT [m^3/s]
Known reservoir capacities and requirements	
S_{min}	Minimum volume of water that must be stored in Navajo Reservoir for it to be active [m^3]
S_{max}	Maximum volume of water that the Navajo Reservoir can hold [m^3]
$Q_{R,min}$	Minimum release flow from the Navajo Reservoir required by the US Bureau of Reclamation [m^3/s]
$Q_{R,max}$	Maximum release flow through the Navajo Dam outlet [m^3/s]
$\delta_{R,max}$	Maximum absolute amount that Navajo releases can change by per time step [m^3/s]
γ	Conversion factor between flow in m^3/s to volume per day in m^3
Decision Variables	
Q_R	Flow released through the Navajo Dam [m^3/s]
$Q_{D,0}$	Flow diverted from Navajo Reservoir for the Navajo Indian Irrigation Project [m^3/s]
$Q_{D,1}$	Flow diverted between Navajo Reservoir and the USGS gage near Shiprock, NM [m^3/s]
$Q_{D,2}$	Flow diverted between the Shiprock and Four Corners USGS gages [m^3/s]
$Q_{D,3}$	Flow diverted between the Four Corners and Mexican Hat USGS gages [m^3/s]
$Q_{G,1}$	Discharge at the USGS gage near Shiprock [m^3/s]
$Q_{G,2}$	Discharge at the Four Corners USGS gage [m^3/s]
$Q_{G,3}$	Discharge at the Mexican Hat USGS gage [m^3/s]

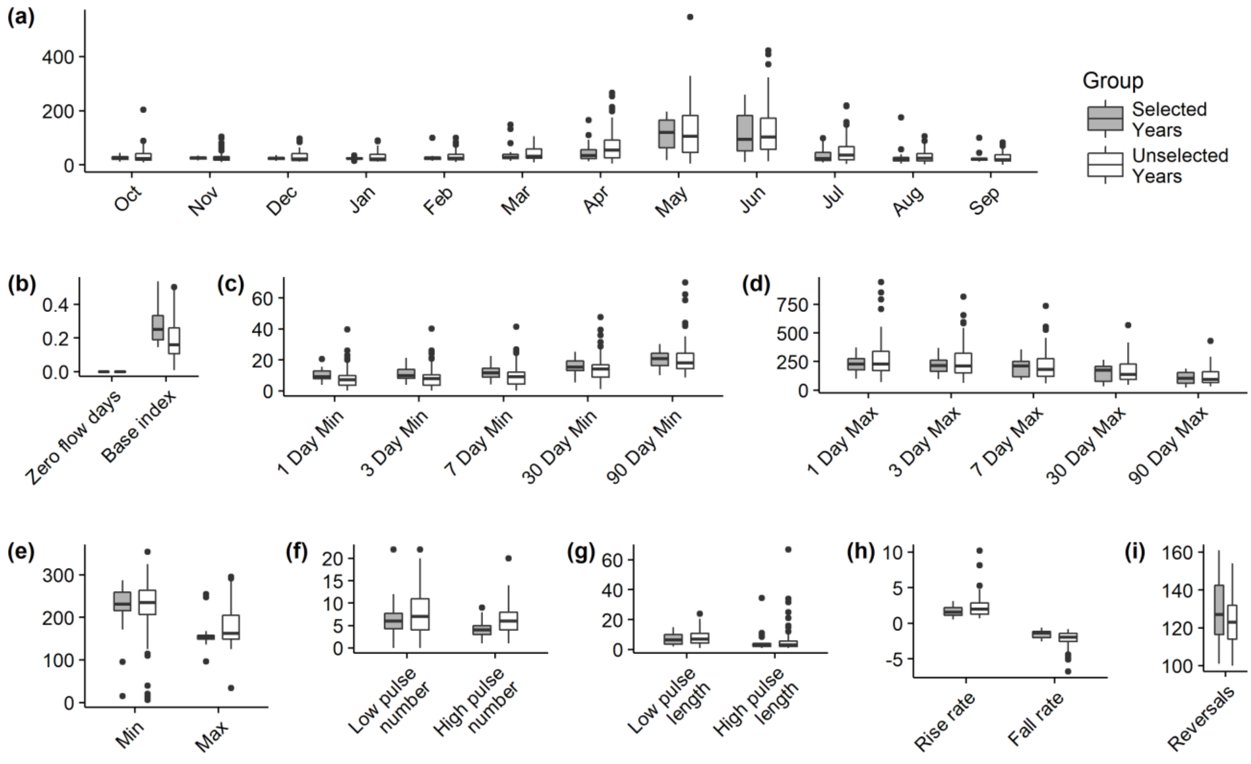


Supplementary Figure 1.1. Daily response of native and nonnative fish assemblages per unit increase in daily log-transformed discharge aggregated from flow-ecology models. Aggregated natives' (blue, dashed line) and nonnatives' (red, solid line) relative fall abundance response per unit increase in log-transformed discharge on each day of an antecedent year. Results derived from flow-ecology functional regression models.

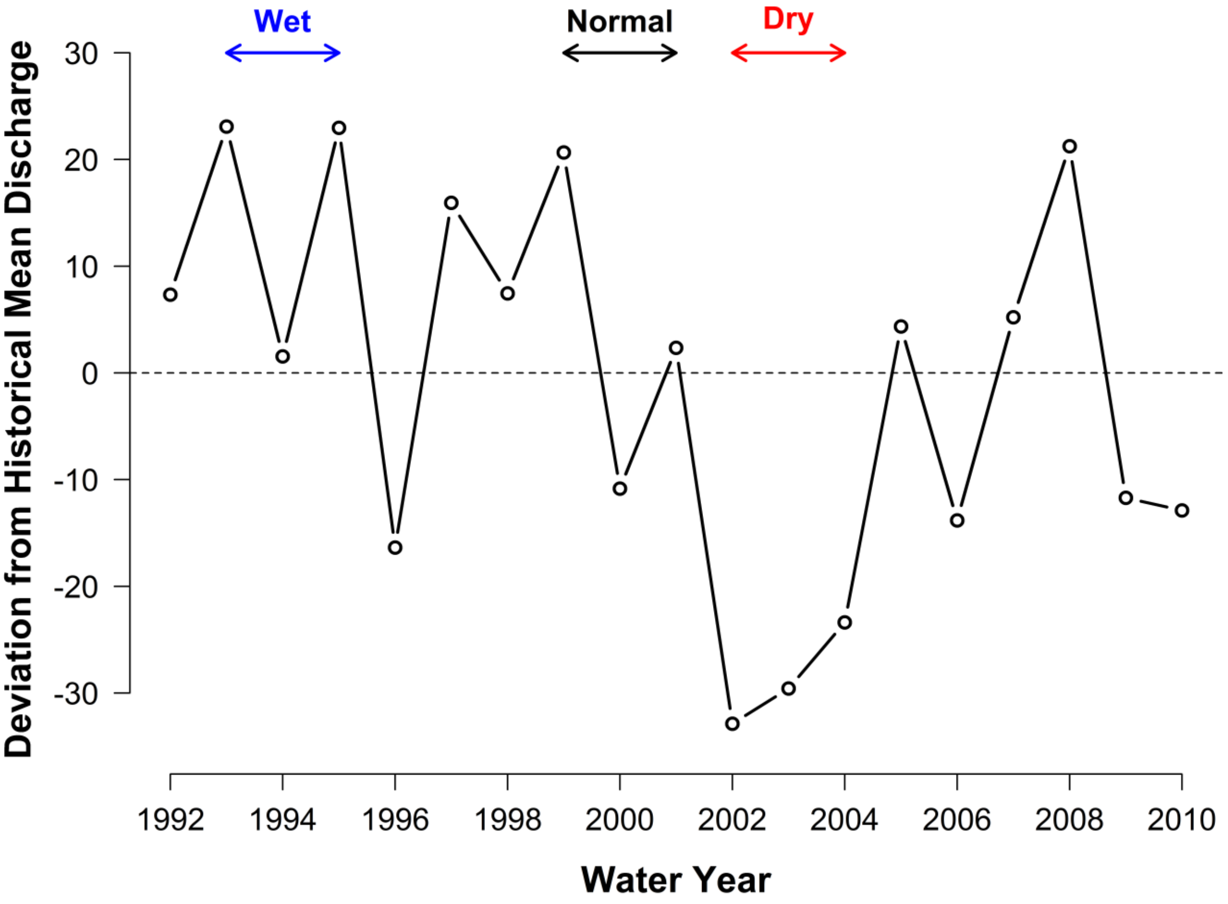


Supplementary Figure 1.2. San Juan River hydrologic regimes before (1935-1956) and after (1963-2015) the construction of Navajo Dam.

Comparison of San Juan River hydrologic regimes at the USGS flow gage station 09368000 near Shiprock, NM before (pre-dam) and after (post-dam) the construction of the Navajo Dam, using Indicators of Hydrologic Alteration[1]. (a) Mean monthly discharges [m^3/s]; (b) Base flow conditions; (c) Minimum flow conditions [m^3/s]; (d) Maximum flow conditions [m^3/s]; (e) Timing of minimum and maximum discharge [calendar day]; (f) Number of flood pulses; (g) Length of flood pulses [days]; (h) Mean of rising and falling discharge rates [m^3/s/day]; (i) Number of reversals between rising and falling daily discharge. Discharge was similar at USGS flow gage stations near Four Corners, CO and Bluff, Utah.

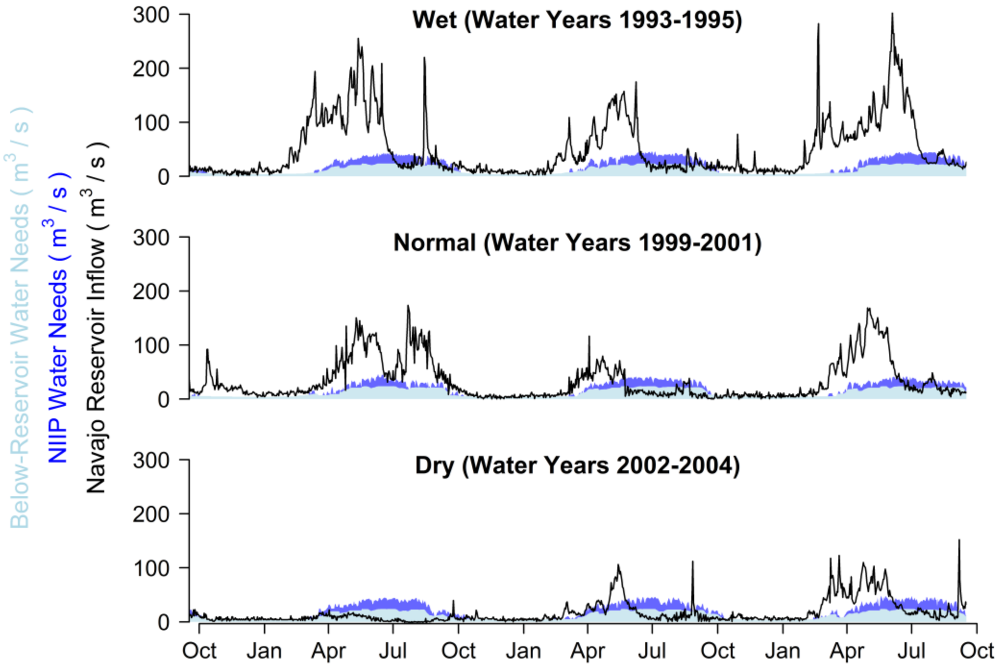


Supplementary Figure 1.3. San Juan River post-dam hydrologic regimes in study period (1993-2010) and outside of the study period (1963-1992, 2011-2015) after dam construction. Comparison of San Juan River hydrologic regimes at the USGS flow gage station 09368000 near Shiprock, NM within and outside our study period (Selected and Unselected Years, respectively), using Indicators of Hydrologic Alteration[1]. (a) Mean monthly discharges [m^3/s]; (b) Base flow conditions; (c) Minimum flow conditions [m^3/s]; (d) Maximum flow conditions [m^3/s]; (e) Timing of minimum and maximum discharge [calendar day]; (f) Number of flood pulses; (g) Length of flood pulses [days]; (h) Mean of rising and falling discharge rates [m^3/s/day]; (i) Number of reversals between rising and falling daily discharge. Discharge was similar at USGS flow gage stations near Four Corners, CO and Bluff, Utah.



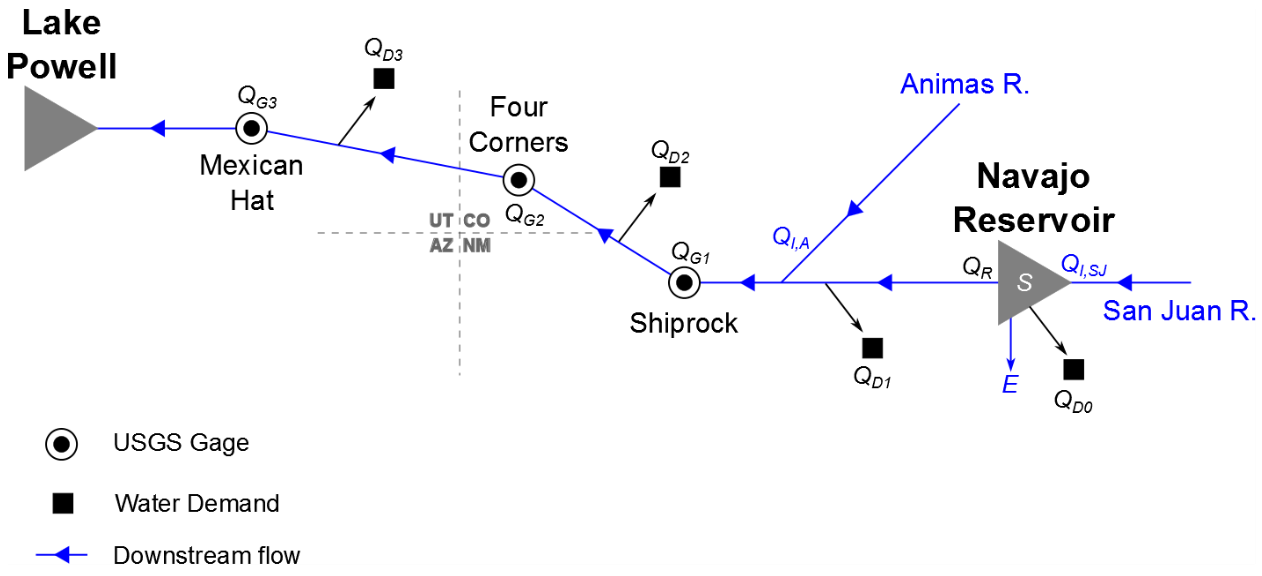
Supplementary Figure 1.4. Annual river discharge anomalies and selected climatic scenarios.

River discharge anomalies from historical seasonal trend for water years 1992 through 2010 (based on USGS flow gage station 09368000 near Shiprock, NM). Climatic scenarios representing wet, normal, and dry flow periods are characterized by positive, minimal, and negative anomalies, respectively.



Supplementary Figure 1.5. Reservoir inflows and water diversion needs for the San Juan River Basin.

Daily inflow into Navajo Reservoir (solid line), water diversion demands from the Navajo Indian Irrigation Project (blue fill), and water diversion demands from downstream of Navajo Reservoir (light blue fill) during each of the three climatic scenarios. The patterns of inflow were scaled to match the total amount of water used in optimized flow designs when simulating a hypothetical natural flow mimicry approach in the San Juan River.



Supplementary Figure 1.6. Schematic of San Juan River operating model.

Schematic of the San Juan River depicting water inflows, depletions and demands (described in Table S1.2) that were included in the optimization framework. Black lettering signifies decision variables to optimize over while blue lettering signifies known values. Map not drawn to scale.

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2 Evaluating transferability of flow-ecology relationships across space, time, and taxonomy

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Contributions

WC and JDO designed research, performed research, analyzed data, and wrote the paper.

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flow-ecology, transferability, freshwater fish, environmental guilds, flow regulation, environmental flows

2.1 Abstract

1. Environmental flow assessments are becoming increasingly central to ecologically-sustainable river management. Rigorous evaluations of flow-ecology relationships serve a vital role in guiding these assessments to meet targeted ecosystem objectives. However, limited resources and widespread environmental change are outpacing the ability to develop understanding of species' flow responses and assess environmental needs for rivers individually. Successfully transferring flow-ecology relationships across space and time would facilitate regional-scale environmental flow assessments, yet the necessary contexts for such success remains a critical knowledge gap.
2. Here, we leverage long-term, multi-species datasets across multiple river basins in southwestern United States as a case study to explore whether relationships between species abundances and hydrologic conditions are transferable across space and time. Additionally, we evaluate the potential for ecological guilds based on fluvial dependence and life-history strategies to facilitate the transfer of flow-ecology knowledge across taxonomic boundaries.
3. Species varied in the spatial transferability of their flow-ecology relationships. Spatial transferability was similar when comparing a species' flow-ecology relationships within a river basin versus across different river basins, although transferability was considerably greater across free-flowing rivers compared to regulated rivers. Species' flow-ecology relationships transferred through time just as well as across space. Ecological guilds defined according to fluvial dependence and life-history strategies offered just as much potential for transferring flow-ecology knowledge among species as transferring within species identity.

4. Our study provides insights into transferring flow-ecology knowledge to support effective, regional-scale environmental flows. Further research into developing transferable flow-ecology relationships for a wide range of environmental predictors and biological responses across different spatial scales and flow regimes will enable us to keep pace with the increasing demand for sustainable river management.

2.2 Introduction

Recent decades have witnessed a growing appreciation of and reliance on environmental flow assessments to inform ecologically-sustainable river management (Arthington, 2012). Core to these efforts is the fact that the flow regime defines the physical template of riverine ecosystems, acting as both an evolutionary selective force and an ecological filter to shape the distribution, abundance and diversity of plant and animal life (Poff et al., 1997; Bunn & Arthington, 2002; Naiman, Latterell, Pettit, & Olden, 2008). Consequently, it comes as no surprise that across the hundreds of environmental flow methodologies, the overwhelming majority share the need to quantify how species or ecological processes respond to specific facets of the flow regime (Tharme, 2003; Arthington, Bunn, Poff, & Naiman, 2006; Poff & Zimmerman, 2010; Acreman, Overton et al., 2014).

The fundamental role of flow-ecology relationships dates back to the origins of environmental flows, where prescriptions of minimum wetted areas or flows as part of water withdrawal management were based on the ecological requirements of fish (Tennant, 1976; Gippel & Stewardson, 1998). Flow management recommendations based on mimicking natural flow regimes quickly became commonplace in the literature, based largely on measured or modeled associations between flow conditions and species of interest (e.g., Tharme, 2003; Richter, 2010; Poff et al., 2010; Rosenfeld, 2017). More recently, designer flows have emerged as a branch of environmental flows intended to go beyond natural flow mimicry by relying even more heavily on explicit, informative flow-ecology relationships to tailor flow regimes for targeted ecosystem objectives (Acreman, Arthington et al., 2014; Poff et al., 2016; Yarnell et al., 2015).

The Brisbane Declaration (2007) proclaimed the need to understand the environmental flow needs for the vast majority of unstudied global rivers, yet the simple reality is that limited resources and widespread environmental change are rapidly outpacing the ability to prescribe environmental flows on a river-by-river basis (Poff et al., 2010; Rulli, Saviori, & D'Odorico, 2013). Indeed, a recurring barrier to environmental flow implementation at regional scales is the dearth of explicit and robust flow-ecology relationships (Poff & Zimmerman, 2010), which are greatly understudied in comparison to environmental flows (Davies et al., 2014). Despite this, the Brisbane Declaration also celebrated the "recent advances [that] enable rapid, region-wide scientifically credible environmental flow assessments". Although there is no denying that regional approaches to environmental flow assessments are gaining traction, the robustness of flow-ecology relationships across space and time is still unresolved. That is, how consistently do the same flow regime features influence species and how consistent are the magnitudes of response? The consistency of flow-ecology relationships is also likely to vary across hydrologic conditions and ecological indicators (Kennard, Olden, Arthington, Pusey, & Poff, 2007). We must reconcile this gap in knowledge to truly realize the potential of environmental flow prescriptions at broader scales.

Establishing distinct flow-ecology relationships for every river is simply infeasible, even with infinite resources. Thus, advancing the science of environmental flows relies on understanding generalities based on empirical and functional relationships that integrate across species and span multiple spatial and temporal scales. We might expect flow-ecology relationships to be highly consistent given the strong evolutionary forces (Lytle & Poff, 2004) that drive the coordinated responses of species to hydrologic regimes (e.g., Mims & Olden, 2012). However, there are numerous factors that might disrupt the transferability of such associations. Changing land use practices and dam operations that alter streamflow in a heterogeneous manner (Allan, 2004; Poff et al., 2010) may ultimately compromise the ability to transfer flow-ecology models between different rivers or at different points in time. Species' flow-ecology relationships across space and time may also diverge in response to local adaptations to changes in peak flow, minimum flow, flow stability, and flow variation.

Species traits represent a powerful currency to evaluate the responses of freshwater organisms to past and current hydrologic regimes (Olden, 2016). For example, reach-scale hydrological characteristics are highly predictive of the functional trait composition (i.e., life history strategy, functional feeding group, and mobility) of macroinvertebrate communities (Richards, Haro, Johnson, & Host, 1997; Brooks & Haeusler, 2016). In addition, Statzner and Bêche (2010) demonstrated the utility of traits such as body size, feeding group, dispersal mode, and reproductive strategy for disentangling the responses of macroinvertebrates to multiple environmental stressors. In riparian ecosystems, Stromberg and Merritt (2016) showed that plant traits such as canopy height, leaf length, and seed dispersal were strongly correlated with water availability and fluvial disturbance. For freshwater fishes, species that depend on flowing-water habitats (fluvial specialists) tend to be more adversely affected by flow regulation and water withdrawals than habitat generalists (Freeman & Marcinek, 2006), and life-history strategies are highly predictive of fish assemblage responses to natural and altered patterns in hydrologic seasonality, variability, and predictability (Mims & Olden, 2012, 2013; McManamay & Frimpong, 2015). The strength of species traits as predictors for environmental responses can inform the formulation of ecological guilds (*sensu* Simberloff & Dayan, 1991) that consist of species with similar biological traits and environmental responses (e.g., Olden, Poff, & Bestgen, 2006; Welcomme, Winemiller, & Cowx, 2006; Merritt, Scott, Poff, Auble, & Lytle, 2010).

Given their promise in studying the response of multiple species broadly, trait and environmental guilds offer the opportunity to reliably transfer flow-ecology relationships and meet the challenges of setting environmental flows across the world's rivers. Indeed, there are already several examples illustrating the strong coupling between various guilds and flow responses. Lytle, Merritt, Tonkin, Olden, and Reynolds (2017) categorized riparian vegetation into five flow-response guilds to study the network connectivity of plant communities in natural and altered flow regimes and illustrate the destabilization of these communities with increasing levels of drought. Guilds such as habitat preference and trophic position also strongly characterized the flow response of freshwater fishes across 25 natural and regulated rivers in Canada (Macnaughton et al., 2016). Dunbar et al. (2010) found river discharge and physical habitat greatly influenced aquatic invertebrates in line with species' preferences for rapidly-flowing water.

Despite the potential benefits of transferring flow-ecology relationships across river basins, there has yet to be a rigorous evaluation of the feasibility of this transferability in different contexts. Here, we examine 40 freshwater fish species throughout five river basins in the southwestern United States to evaluate the transferability of flow-ecology relationships for individual species across space, time, and taxonomy (Fig. 2.1). Although there are multiple ways to measure ecological function (e.g., biomass, nutrient recycling, recruitment), as well as multiple facets of flow regimes, our study focuses on species abundance in response to temporal patterns in flow magnitude. To evaluate the merit of using environmental guilds to transfer knowledge of flow responses across taxonomy, we compared flow-ecology relationships of species within the same flow guild (fluvial specialists that are more dependent on rapidly flowing water versus habitat generalist that can persist in more lentic flow conditions) and of species exhibiting similar life-history strategies (equilibrium, opportunistic, or periodic as defined by Olden et al., 2006). We expected species-specific spatial transferability to be higher across river reaches within the same basin when compared to river reaches across different river basins, due to decreased environmental similarity occurring across a larger spatial extent (Fig. 2.2a). These environmental differences may be dampened (flow homogenization) or amplified (free-flowing vs. altered) by land-use activities and infrastructure that regulates flow regulation (Poff, Olden, Merritt, & Pepin, 2007), thus potentially influencing spatial transferability. We expected flow-ecology relationships to be more transferable across time than across space (Fig. 2.2b), due to consistent taxonomic and environmental contexts across time. Given their shared dependency on high flows, we expected fluvial specialists to have more transferable flow-ecology relationships than habitat generalists (Fig. 2.2c). Alternatively, fluvial specialists may be adapted differentially to local flow regimes, resulting in lower flow-ecology transferability. Furthermore, habitat generalists have shown greater plasticity and adaptability to a wide range of flow regimes (Freeman & Marcinek, 2006), which could confer greater flow-ecology transferability across space and time in comparison to fluvial specialists. We expected life-history guilds to provide a relatively high degree of transferability for flow-ecology relationships among guild members, given the strong coupling between hydrology and life-history strategies, though we predicted there would not be significant differences in transferability by life-history guild (Fig. 2.2d). Taken together, we assess the transferability of flow-ecology relationships under various contexts to support opportunities for maximizing research and management effort as our freshwater resources – both human and natural – become increasingly constrained.

2.3 Methods

2.3.1 Study extent and data collation

We utilized streamflow monitoring and multi-decadal fish time series for five river basins of various sizes located in southwestern United States (Table 2.1): Virgin River (Utah), San Juan River (New Mexico), Pecos River (New Mexico), Gila River (New Mexico), and San Pedro River (Arizona). Although all river basins are perennial and characterized by spring high flows and summer monsoons (Supplementary Fig. 2.1), the construction of dams and weirs for water diversions and hydropower has altered the flow regimes of the Virgin, San Juan, and Pecos rivers, whereas the Gila and San Pedro rivers remain free from large dams and extensive land-use change. This provides the opportunity to coarsely compare the impact of flow alteration on the transferability of flow-ecology relationships.

Extensive monitoring in these regions includes time series of annual surveys of fish species abundances and daily observations of streamflow at various sites within each river basin. Fish samples were collected once a year in autumn or spring under low-velocity, wadeable flow conditions, using either standardized backpack electrofishing or seines. For additional details see Gido, Propst, Olden, and Bestgen (2013) regarding the San Juan, Gila and San Pedro River, Golden and Holden (2004) regarding the Virgin River, and Duran (2016) regarding the Pecos River. Sites were grouped into river reaches in accordance to nearby USGS flow gages. We restricted our analyses to combinations of river reach and species that included at least 20 samples (Yen, Thomson, Paganin, Keith, & Mac Nally, 2015), of which the species occurred in at least ten percent of those samples. After this process, 18 river reaches (Table 2.1) and 40 species (Table 2.2) remained for the analysis.

2.3.2 Quantifying flow-ecology relationships

For each river reach and species, we estimated the influence of streamflow on species abundance by regressing species' annual density estimates against daily discharge time series for the antecedent year as a covariate. Species abundance estimates were standardized within each time series to be between zero and one so that resultant flow-ecology relationships would be of comparable scale despite inevitable differences in sampling procedures across river basins. Flow data were log-transformed to reduce the influence of extreme values. Antecedent flow on the time-scale of a year has been shown to influence fish abundances greatly (Balcombe & Arthington, 2002), and though we acknowledge the influence of flow on longer time scales (Kennard et al., 2007), we elected to balance the risk of overfitting our statistical models by restricting our predictor to only the year prior to fish sampling. Rather than use a suite of hydrologic metrics as covariates for species density, we used functional regression models to incorporate antecedent flow as continuous functions spanning the days of the year (Ramsay & Silverman, 2005; Yen et al., 2015),

$$Density_i = \beta_0 + \sum_{t=1}^{365} \beta_1(t) \cdot Flow_i(t) + \epsilon_i \,, \qquad [2.1]$$

where $Density_i$ is the sampled species' density in year i, $Flow_i(t)$ is the measured daily discharge on calendar day t (ranging from day 1 to 365) in year i, β_0 is the estimated average density for that species, $\beta_1(t)$ is the estimated unit increase in species density per unit increase in discharge on calendar day t, and ε_i is the model residual associated with year i. Such functional approaches are more appropriate than traditional linear regression methods for characterizing flow regimes in a holistic manner (Stewart-Koster, Olden, & Gido, 2014). Here, rather than a suite of single-valued regression coefficients, flow-ecology relationships are represented by the function-valued regression coefficients $\beta_1(t)$. Furthermore, we used a method – termed functional regression that is interpretable (FLiRTI) – that preserves the desired, continuous function estimation of the basic functional regression approach, but improves the interpretability of the estimate by constraining nonzero effects of predictor variables to only the most relevant parts of the function's domain (James, Wang, & Zhu, 2009). We tuned each model and assessed model fit using 10 iterations of *10*-fold cross-validation, and selected models that minimized the median cross-validated error across the 10 iterations.

2.3.3 Comparing flow-ecology relationships

We examined the pair-wise distances among flow-ecology relationships ($\beta_1(t)$ regression coefficients from flow-ecology models above) to quantify the similarity and potential transferability of these relationships across environmental contexts of flow regulation and across species within the same flow guild or exhibiting similar life-history strategies. We used dynamic time warping (DTW) to align flow-ecology relationships for slight temporal shifts before measuring the distance between them (Giorgino, 2009). Dynamic time warping can be used to compare two temporal sequences of observations that exhibit the same pattern, but be misaligned in time – for example: the sequences (0, 1, 2, 3, 0, 0) and (0, 0, 1, 2, 3, 0). Simply taking the absolute, pair-wise difference of the two sequences would mistakenly suggest a large distance between the two sequences (6) when the two are similar. By shifting the alignment of one of the sequences one observation over, the distance shrinks to zero. Dynamic time warping integrates the point-wise distances between two sequences after aligning the sequences to minimize differences. Similarly, we may be concerned that two flow-ecology relationships are marked as different when the patterns are misaligned by only a day, virtually no difference at all to the biology of a fish whose lifespan is on the order of years. We limited excessive warping of flow-ecology relationships by using a 7-day Sakoe-Chiba window, which constrains shifts in alignment to within 7 days of the original regression coefficients (Giorgino, 2009). After this alignment, the distance between two flow-ecology relationships is the sum of the pair-wise differences between the two corresponding regression coefficients. Overall, smaller distances indicate greater transferability. We used an empirical cumulative distribution function (CDF) to standardize these distances to between 0 and 1 (hereafter referred to as transferability scores) for comparing across the study. For clarity, we standardized all distances d to give relative transferability scores T,

$$T = 1 - \frac{n_d}{N_{total}}, \qquad [2.2]$$

where n_d is the rank of distance d relative to all other distances sorted in ascending order and N_{total} is the total number of distances calculated in the study. Thus, lower relative transferability is represented by a lower value of T. This standardization procedure replaces the raw distances with its percentile in the distribution of all distance values, thus mitigating the influence of extreme outlier distances.

2.3.4 Quantifying spatial and temporal transferability

We quantified the spatial transferability of flow-ecology relationships by comparing relative transferability scores across two spatial extents while separating by species identity: between river reaches within the same river basin versus among two different river basins. We also investigated the impact of flow regulation on the species-specific, spatial transferability of flow-ecology relationships by further dividing the among-basin comparisons into those that involved two basins of similar flow regulation status (either free-flowing or regulated) and those with different regulation statuses. We used linear regression models to assess whether there were significant differences in spatial transferability for river reaches (1) within versus across river basins and (2) when transferring between different contexts of flow regulation. A random intercept term was added to control for differences in spatial transferability among species.

To measure temporal transferability of species' flow-ecology relationships, we used a subset of our data where fish sampling time series could be split in half to give two samples, each containing at least 20 observations with at least a 10% occurrence rate (Table 2.1). This subset included 22 unique species spanning both flow guilds and all three life-history strategies and covered river reaches across three out of the five river basins. Start years for the earlier half of time series ranged from 1975 to 1994 while the start years for the latter half ranged from 1988 to 2003. For each pair of samples, we constructed a flow-ecology model as before and computed relative transferability scores for the inferred flow-ecology relationships before and after the temporal split.

Finally, we evaluated the potential of environmental guilds for informing flow responses across taxonomy (Welcomme et al., 2006). We considered two types of guilds. First, we examined species' dependence on flowing water as informed by habitat use and distribution, designated as fluvial specialists that require flowing water for at least some part of their life history versus habitat generalists that can persist in more lentic flow conditions (Freeman & Marcinek, 2006). Second, we considered guilds delineated by life-history strategy (equilibrium, opportunistic, and periodic) following Winemiller and Rose (1992). Opportunistic strategists are small-bodied species with early maturation and low juvenile survivorship and are associated with habitats with frequent and intense disturbance. Equilibrium strategists are typically small to medium in body size with moderate age at maturation, low fecundity per spawning event, and high juvenile survivorship largely associated with high parental care and small clutch size. They are predicted to be favored in more stable habitats with low environmental variation. Periodic strategists are characterized by larger body size, late maturation, high fecundity, and low juvenile survivorship and are often associated with highly periodic (seasonal) environments. The three life history strategies of the continuum can be interpreted as being adaptive with respect to relative variability and predictability of environmental regimes (Olden et al., 2006).

To assess differences in flow-ecology transferability within different environmental guilds, we calculated transferability scores within and across all river reaches that involved two species from each respective guild. We used linear regression models to determine if there were significant transferability differences among fluvial specialists versus habitat generalists and among the different life-history strategists, adding a random intercept term to control for differences in spatial transferability across river basins and reaches. Additionally, we assessed the ability of guilds to inform individual species' flow-ecology knowledge by using linear regression models to compare relative transferability scores of same-species comparisons versus that of different species from the same guild, using a random intercept term to control for differences among river basins and reaches. We also performed analogous comparisons for native versus nonnative species, given established differences in ecological traits between native and nonnative fish species in the Colorado River Basin (Olden et al., 2006).

2.4 Results

Species exhibited considerable differences in the transferability of their flow-ecology relationships (Fig. 2.3), but for each species there was no significant difference in transferability across river reaches within a single basin versus across different basins (Table 2.3, $p = 0.902$). Of the 40 species in the study, 32 occurred in at least two samples and could have their flow-ecology relationships compared. Sand shiner (*Notropis stramineus*), common carp (*Cyprinus carpio*), and several sunfishes (e.g., *Micropterus punctalatus, M. salmoides, Lepomis cyanellus)* demonstrated strong transferability, whereas flow-ecology relationships for the majority of suckers (Family: *Catostomidae*) transferred relatively poorly across space. Families tended to exhibit similar levels of transferability across its member species, suggesting a phylogenetic component to transferability.

The ability to transfer flow-ecology relationships varied among different river basins. The Gila River exhibited the most transferable flow-ecology relationships, while the flow-ecology relationships from the Virgin River were less spatially transferable (Fig. 2.4). In addition, free-flowing river basins generally contained more spatially transferable flow-ecology relationships than regulated basins (Table 2.3, $p = 0.002$). Spatial transferability did not differ significantly when comparing flow-ecology relationships within a basin, across basins of similar flow regulation status, and across basins of different flow regulation status (Table 2.3, $p > 0.05$).

The magnitudes of flow-ecology transferability across time and space were remarkably similar (Fig. 2.5). Temporal transferability scores averaged 0.446 with a standard deviation of 0.248 while spatial transferability scores for the same species had a similar average of 0.479 and a similar standard deviation of 0.283. There was also no significant difference in average temporal transferability and average spatial transferability when pairing by species (paired *t*-test, $p = 0.468$). Of the 21 species included in the temporal transferability analysis, nine exhibited an average temporal transferability score greater than their average spatial transferability score.

Flow-ecology transferability varied across environmental guilds (Fig. 2.6). Flow-ecology relationships were significantly more transferable within the habitat generalist guild than the fluvial specialist guild (Table 2.3, $p = 0$). The levels of transferability within flow guilds aligned with levels of species-specific transferability across space for its guild members. Numerous species with the greatest spatial transferability of flow-ecology relationships were habitat generalists (e.g., common carp *Cyprinus carpio*, green sunfish *Lepomis cyanellus*, and western mosquitofish *Gambusia affinis*), whereas fluvial specialists were at the lower end of the transferability scale (e.g. sucker species in the Family *Catostomidae*). The three life-history guilds also exhibited significantly different flow-ecology transferability, with periodic strategists having the greatest transferability of the three life-history guilds, significantly greater than equilibrium strategists (Table 2.3, $p = 0$), while equilibrium strategists did not differ significantly from opportunistic strategists ($p = 0.394$). These patterns did not extend to species-level transferability. Each life-history guild included species that exhibited poor within-species spatial transferability, such as the Virgin river chub (*Gila seminuda*, periodic), flannelmouth sucker (*Catostomus latipinnis*, equilibrium), and Virgin spinedace (*Lepidomeda mollispinus*, opportunistic), as well as high within-species spatial transferability, such as the spotted bass (*Micropterus punctalatus*, equilibrium), sand shiner (*Notropis stramineus*, opportunistic), and common carp (*Cyprinus carpio*, periodic). For each species, transferring flow-ecology knowledge from other species of the same guild was just as effective as transferring within species across space (Table 2.3, $p > 0.05$).

The nativity status of this study's fish species aligned strongly with fish flow guilds; the majority of native fishes are fluvial specialists while many of the nonnative species are habitat generalists (Table 2.2). Nonnative species displayed significantly greater spatial transferability with other nonnative species as compared to native species with other natives (Table 2.3, $p = 0$).

2.5 Discussion

Evaluating the transferability of flow-ecology relationships remains a critical aspect of environmental flow efforts that seek to be effective across broad spatial and temporal scales. Despite this, there has been little research that quantifies the transferability of flow-ecology relationships (Poff & Zimmerman, 2010; Pahl-Wostl et al., 2013; Rosenfeld, 2017). Here, we found that flow-ecology relationships for freshwater fish species in the southwestern United States exhibited similar transferability within and across river basins experiencing similar hydrologic conditions (Fig. 2.3). These similarities suggest that flow-ecology relationships may indeed be spatially transferable throughout a region, which is reinforced by the consistency of transferability when comparing flow-ecology relationships from two basins with similar and distinct levels of flow regulation (Fig. 2.4). Although we posited that variation in local environmental contexts would serve to diminish transferability at the regional scale, the findings of our study support the transfer of flow-ecology knowledge between river systems and highlights the utility of grouping environmental flow assessments by river hydrology type (Fig. 2.4; Poff et al., 2010; Mims & Olden, 2012; McManamay, Bevelhimer, & Frimpong, 2015).

Despite the overall robustness of flow-ecology relationships across spatial extents, transferability from regulated river basins was markedly poorer than from free-flowing river basins (Fig. 2.4). Recent decades of research have established the dramatic shifts in fish communities brought on by flow regulation and alteration (reviewed in Olden, 2016). Poff and Zimmerman (2010) conducted an extensive review of the literature and reported that native fish diversity and abundance showed a 20-100% and 16-95% reduction in response to flow regulation, respectively. That flow-ecology transferability is somewhat disrupted for regulated river systems suggests that other confounding factors (e.g., water temperature, habitat conditions) can influence fish species’ relationships with streamflow (Mims & Olden, 2013). Alternatively, these patterns across flow regulation categorizations may be a function of differences in species composition among the five river basins. Fish community similarity was considerably higher between the free-flowing Gila and San Pedro river basins (both tributaries of the Gila River Basin), compared to the regulated San Juan, Rio Grande, and Virgin river basins (Supplementary Table 2.1). Despite this caveat, our results suggest that the transferability of flow-ecology relationships may best be limited to within free-flowing or flow-regulated rivers, not between them.

Mounting concerns over the use of the stationarity assumption in the design and management of water resource systems (Milly et al., 2008) has also raised questions regarding the validity of flow-ecology models applied across time (Wagener et al., 2010; Shenton, Bond, Yen, & Mac Nally, 2012). In the American Southwest, climate models predict reduced rainfall and depressed river discharge (Seager et al., 2007), leading to new ecological challenges for fish species (Jaeger, Olden, & Pelland, 2014). Despite not being the primary focus of our study, we found that flow-ecology relationships were readily transferable across time, at a level comparable those seen for among river basins (Fig. 2.5). Additionally, there was no significant difference between species’ average spatial and temporal transferability scores. These results are promising in the sense that they suggest that flow-ecology models may be applicable across changing hydroclimatic behaviors, however, a rather large caveat is that our analysis examined just a 30-year time period. The timing and extent of hydrologic nonstationarity is unfolding at much longer time scales (Razavi, Elshorbagy, Wheater, & Sauchyn, 2015), thus the question of ecology-flow relationship transferability through time requires continued investigation (Rosenfeld, 2017).

Similarities in flow-ecology relationships across species in shared environmental guilds provide the potential for transferring knowledge for species of concern that have not been or cannot be extensively monitored, as well as for species for which little data exists. It was very encouraging that the transferability of flow-ecology across species within the same guild was comparable to that of individual species (Fig. 2.6). Flow-ecology transferability was especially prominent within the habitat generalist guild and the periodic life-history guild, while the fluvial specialist guild exhibited the least transferability of the guilds examined. Flow-guild transferability aligned with respective species-specific spatial transferability, thus suggesting a link between species-specific transferability and intra-guild transferability. Moreover, the lack of transferability for fluvial specialists suggest that stronger flow dependencies contribute to system-specific flow associations that do not transfer as readily among river basins. By contrast, habitat generalists were more consistent in their lack of relationship with flow at the species and guild levels (Table 2.2), thus resulting in more transferable flow-ecology relationships. In a similar vein, Freeman and Marcinek (2006) found that habitat generalists were not greatly affected by flow alteration while fluvial specialists experienced declines.

Our investigation of flow-ecology transferability among species with shared life-history strategies builds on previous studies that have highlighted the role of flow regimes in favoring particular life histories (Mims & Olden, 2012, 2013). The higher transferability among periodic strategists agrees with expectations from ecological theory (Winemiller & Rose, 1992; Olden & Kennard, 2010; Mims & Olden, 2012). The periodic strategy maximizes fecundity by delaying maturity (to achieve sufficient size and to acquire resources) and producing many smaller eggs as a tactic to increase juvenile survivorship. Therefore, given some degree of predictably in hydrologic disturbance, the periodic production schedule allows a fitness payoff when reproduction coincides with favorable environmental conditions (Keck et al., 2014). For this reason, we might expect that the strong hydrologic fidelity of periodic life-history strategists will promote greater transferability between river systems. Having said this, we did reveal relatively high variability and overlap in transferability scores across the three life-history guilds, suggesting that other factors may be operating (Gido et al., 2013). By contrast, we found that spatial transferability among nonnative species was significantly higher than that of native species. Gido et al. (2013) showed that American southwest fish species responded to flow alteration strongly along nativity designations. Given the strong association between flow guild membership and nativity status, this suggests that flow guild may be a stronger indicator of transferability success over life-history strategy for fish species in the American southwest.

Theoretical and experimental studies point to the strength of guilds over taxonomy in predicting flow responses (Merritt et al., 2010; Macnaughton et al., 2016). We found no significant differences between transferring within species identity versus transferring across guild members for informing a species' flow-ecology relationship, which supports the use of guilds in transferring flow-ecological knowledge across different species. Developing strategies to conserve species which lack flow-ecology knowledge by using similar surrogate species is becoming increasingly important, given limited research resources (Murphy, Weiland, & Cummins, 2011; Webb, Koster, Stuart, Reich, & Stewardson, 2017). The apparent transferability of flow-ecology knowledge via guilds is promising for ensuring that all species are considered in environmental flow assessments.

Nevertheless, the strength of guilding approaches for transferring fish flow-ecology relationships relies on continued research into the drivers of fish populations. Ecological guilds have a strong foundation in predicting the responses of plant communities due to the mechanistic understanding of plant traits (Stromberg & Merritt, 2016). By contrast, the mechanisms linking fish guilds and environmental responses are less well-understood, resulting in greater reliance on correlative models between fish traits and fitness under different hydrological conditions (Freeman & Marcinek, 2006; Mims & Olden, 2012, 2013). As with many correlative approaches, the nuanced relationships between biological responses and flow regime features, such as the strength of underlying mechanisms and the range of variability in data sets, will dictate the potential for transferability (Wenger & Olden, 2012). Here, fish species showed little correspondence in life-history strategy with flow guild nor nativity status, whereas fluvial specialists tended to be native and habitat generalists tended to be nonnative to their rivers. Utilizing data sets with diverse combinations of species traits and guilds, including multiple morphometric traits and environmental responses, and accounting for nonlinearities and interactions among flow-ecology relationships will improve evaluations of transferability (Macnaughhton et al., 2016; Rosenfeld 2017).

It is difficult to overstate the importance of context when evaluating the potential to transfer flow-ecology knowledge. The transferability of flow-ecology relationships depends on the biological indicators and flow regime features of interest. For example, Kennard et al. (2007) found that ecological model predictions for species presence-absence were highly transferable, but ecological relationships were less transferable for predicting abundance or biomass. Here, we considered the influence of flow magnitude throughout the year on freshwater fish abundances. Flow variability and seasonality are also important flow regime features to consider (Naiman et al., 2008; Mims & Olden, 2012; Stewart-Koster et al., 2014) and responses to these features are likely to transfer in manners different from flow magnitude relationships. Additionally, species' responses to thermal regimes for supporting environmental flows need to be better characterized

(Olden & Naiman, 2010; Macnaughton et al., 2016). These factors may explain the relatively low correlations in our flow-ecology models (Table 2.2). Flow-ecology transferability will also depend on the similarity of the flow regimes under consideration (Poff et al., 2010; Stein *et al*., 2017). Our study focused on perennial, flashy rivers in the American Southwest (Supplementary Fig. 2.1). Therefore, it is unclear whether our conclusions extend to other regime types. Finally, taxonomic groups differ in their relationship with flow regimes (e.g. Patrick & Yuan, 2017); thus, transferability will similarly vary.

Several conceptions of transferability exist. Most ecologists view the generality of a model as being proportional to the number of biological systems that a model can capture or to which its conclusions can be applied (Evans et al., 2013). From an applied perspective, generality and transferability should be thought of as a comparative notion. Here, we saw a range of spatial transferability levels across species. Because transferability represents a spectrum from impossible to perfect, there is no threshold of what constituents “sufficient” or “adequate”. Conversely, there is no concrete threshold indicating a lack of transferability. Quite simply, many scientific, economic and social factors determine the level of transferability that is acceptable for regional environmental flow management. Practitioners will have to continue to carefully define their ecological targets and consider the relevant environmental covariates of interest to ensure an effective evaluation of flow-ecology transferability.

The development of transferable flow-ecology relationships and the integration of trait and environmental guilds into such flow response models have been identified as critical needs for advancing the implementation of environmental flow assessments (Arthington, Naiman, McClain, & Nilsson, 2010; Poff & Zimmerman, 2010). Our work brings the science of regional-scale environmental flows closer to the Brisbane Declaration (2007) proclamation of defining environmental flow needs for the greater majority of unstudied global rivers by evaluating the robustness of flow-ecology relationships across space and time. For freshwater fishes in the southwestern United States, we suggest that flow-ecology relationships are equally transferable across local and regional spatial extents and across time. Furthermore, we have shown the potential of guilds for bridging the gap in flow-ecology knowledge across taxonomy. Regional assessments will be the future of environmental flow management as we work to keep up with the pace of climate change and increasing societal water demands, and further research into the transferability of flow-ecology relationships in other taxonomic groups, guilds, and flow regime types will be crucial to support such regionalization.

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2.8 Tables and Figures

Table 2.2. Description of study sites.

River Basin	Watershed Area (km^2)	Reach	Gage #	Number of Sites	Time Period	Number of Species†
Gila	151000	Gila, NM	9430500	1	1988-2012	13
		Glenwood, NM	9444000	1	1988-2011	8
Rio Grande	182000	Lakewood, NM	8399500	1	1993-2013	18
		Artesia, NM	8396500	1	1993-2013	11
		Lake Arthur, NM	8395500	1	1992-2013	15
		Acme, NM	8386000	2	1992-2013	15
		Dunlap, NM	8385630	5	1992-2013	14 (12)
		Fort Sumner, NM	8385522	2	1992-2013	7
San Juan	64000	Bluff, UT	9379500	1	1993-2012	7
		Four Corners, CO	9371010	1	1993-2012	7
		Shiprock, NM	9368000	1	1993-2012	7
San Pedro	12000	Mammoth, AZ	9473000	3	1975-2000	13 (7)
		Charleston, NM	9471000	1	1990-2013	8
		Palominas, NM	9470500	2	1990-2013	6
Virgin	32000	Littlefield, AZ	9415000	3	1976-2003	9 (6)
		Bloomington, UT	9413200	2	1977-2003	8
		Hurricane, UT	9408150	2	1980-2003	8
		Virgin, UT	9406000	2	1983-2003	7

† Numbers in parentheses indicate the number of species (if any) in that reach used to evaluate temporal transferability of flow-ecology relationships

Table 2.3. Fish species profiles, including assignments into flow guild and life-history strategy, and average model performance of flow-ecology models across all comparison. Species are grouped by family.

Scientific Name	**Common Name**	**Flow Guild**	**Life History**	**Average R^2**	**Average MSE**	**Number of models**[§]
Atherinopsidae (silversides)						
Menidia beryllina	inland silverside	Generalist	Opportunistic	-0.057	0.064	1 (1)
Catostomidae (suckers)						
Carpiodes carpio†‡	river carpsucker	Specialist	Periodic	0.094	0.048	4 (0.5)
Catostomus clarkii†‡	desert sucker	Specialist	Equilibrium	0.476	0.038	9 (0.11)
Catostomus discobolus†	bluehead sucker	Specialist	Periodic	0.008	0.054	3 (0.67)
Catostomus insignis†‡	Sonora sucker	Specialist	Equilibrium	0.080	0.046	3 (0.33)
Catostomus latipinnis†‡	flannelmouth sucker	Specialist	Equilibrium	0.171	0.061	7 (0.14)
Centrarchidae (sunfishes)						
Lepomis cyanellus‡	green sunfish	Generalist	Equilibrium	0.108	0.074	7 (0.43)
Lepomis macrochirus	bluegill sunfish	Generalist	Equilibrium	0.377	0.050	1 (0)
Micropterus dolomieu	smallmouth bass	Generalist	Equilibrium	0.151	0.043	1 (0)
Micropterus punctalatus	spotted bass	Generalist	Equilibrium	-0.066	0.088	2 (1)
Micropterus salmoides	largemouth bass	Generalist	Equilibrium	0.027	0.043	3 (0.67)
Characidae (characins)						
Astyanax mexicanus†	Mexican tetra	Generalist	Opportunistic	0.226	0.059	3 (0.33)
Clupeidae (clupeids)						
Dorosoma cepedianum	gizzard shad	Generalist	Periodic	-0.035	0.062	3 (0.67)
Cyprinidae (minnows and carps)						
Agosia chrysogaster†‡	longfin dace	Specialist	Opportunistic	0.258	0.044	5 (0.4)
Campostoma anomalum†	central stoneroller	Specialist	Opportunistic	-0.023	0.083	1 (1)
Cyprinus carpio	common carp	Generalist	Periodic	0.026	0.064	6 (0.67)

Cyprinella lutrensis‡	red shiner	Generalist	Opportunistic	0.349	0.045	13 (0.31)
Gila robusta†	roundtail chub	Specialist	Periodic	0.242	0.037	1 (0)
Gila seminuda†‡	Virgin River chub	Specialist	Periodic	0.150	0.059	4 (0.5)
Hybognathus placitus‡	plains minnow	Generalist	Opportunistic	0.144	0.052	5 (0.2)
Lepidomeda mollispinus†	Virgin spinedace	Specialist	Opportunistic	0.325	0.044	4 (0)
Macrhybopsis aestivalis†‡	speckled chub	Specialist	Opportunistic	0.197	0.049	5 (0.2)
Meda fulgida†‡	spikedace	Specialist	Opportunistic	0.056	0.064	2 (0.5)
Notropis girardi‡	Arkansas River shiner	Generalist	Opportunistic	0.336	0.045	5 (0)
Notropis jemezanus†‡	Rio Grande shiner	Generalist	Opportunistic	0.229	0.042	5 (0.4)
Notropis simus pecosensis†‡	Pecos bluntnose shiner	Generalist	Opportunistic	0.396	0.034	5 (0.2)
Notropis stramineus†‡	sand shiner	Generalist	Opportunistic	-0.069	0.098	4 (1)
Phenacacobius mirabalis	suckermouth minnow	Generalist	Opportunistic	0.229	0.057	1 (0)
Pimphales promelas‡	fathead minnow	Generalist	Equilibrium	0.096	0.064	13 (0.38)
Plagopterus argentissimus†	woundfin	Specialist	Opportunistic	0.284	0.050	4 (0.25)
Rhinicthys osculus†‡	speckled dace	Specialist	Equilibrium	0.185	0.051	9 (0.11)
Tiaroga cobitis†‡	loach minnow	Specialist	Opportunistic	0.084	0.050	3 (0.67)
Fundulidae (topminnows and killifishes)						
Fundulus zebrinus‡	plains killifish	Generalist	Opportunistic	0.384	0.040	5 (0.2)
Lucania parva†	rainwater killifish	Generalist	Opportunistic	0.164	0.067	2 (0)
Ictaluridae (catfishes)						
Ameirus melas	black bullhead	Generalist	Equilibrium	0.122	0.046	2 (0.5)
Ameirus natalis	yellow bullhead	Generalist	Equilibrium	0.050	0.060	2 (0.5)
Ictalarus punctatus‡	channel catfish	Generalist	Equilibrium	0.210	0.054	8 (0.13)
Pylodictus olivaris	flathead catfish	Generalist	Equilibrium	0.234	0.044	1 (0)

Poeciliidae (live-bearers)						
Gambusia affinis‡	western mosquitofish	Generalist	Opportunistic	0.133	0.056	16 (0.5)
Salmonidae (salmon, trout, chars, whitefishes and graylings)						
Oncorhynchus mykiss	rainbow trout	Specialist	Equilibrium	0.374	0.030	1 (0)

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† Native species

‡ Species included in temporal transferability analysis

§ Parenthetical numbers indicate proportion of models estimating no relation to flow magnitude

Table 2.4. Summary of regression results for each transferability comparison conducted. Parameter estimates are given as mean ± standard error.

Comparison	**Predictor**	**Parameter Estimate (Mean ± SE)**	***p*-value**
Species			
Within versus among river basins	Intercept (within basin)	0.503 ± 0.035	0
	Among Basin	-0.003 ± 0.025	0.902
Free-flowing vs. regulated rivers	Intercept (free-flowing)	0.547 ± 0.036	0
	Regulated	-0.060 ± 0.019	**0.002**
Across flow regulation types	Intercept (within basin)	0.505 ± 0.035	0
	Similar Regulation	-0.030 ± 0.024	0.212
	Different Regulation	0.030 ± 0.025	0.236
Flow guild			
Across flow guilds	Intercept (fluvial specialist)	0.418 ± 0.039	0
	Habitat Generalist	0.121 ± 0.008	**0**
Species-specific vs. guild	Intercept (guild)	0.502 ± 0.042	0
	Species	-0.002 ± 0.007	0.763
Life-history guild			
Across life-history guilds	Intercept (equilibrium)	0.474 ± 0.041	0
	Opportunistic	-0.006 ± 0.008	0.394
	Periodic	0.160 ± 0.018	**0**
Species-specific vs. guild	Intercept (guild)	0.502 ± 0.044	0
	Species	-0.013 ± 0.008	0.093
Nativity			
Across nativity group	Intercept (native)	0.439 ± 0.034	0
	Nonnative	0.131 ± 0.007	**0**
Species-specific vs. group	Intercept (guild)	0.507 ± 0.039	0
	Species	-0.001 ± 0.009	0.901

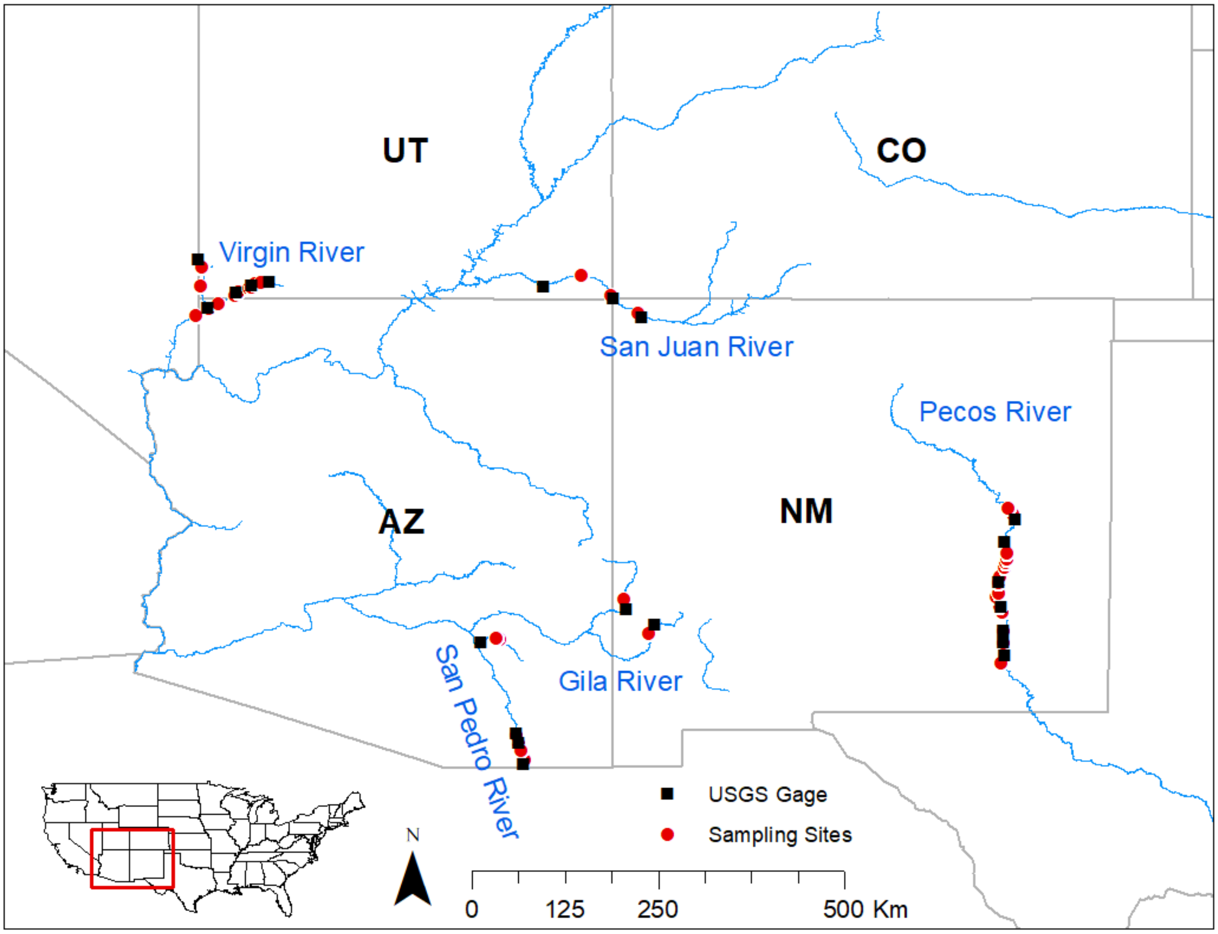


Figure 2.1. Map of study region in southwestern United States. Black boxes indicate USGS gages recording streamflow, and red circles indicate fish sampling sites. Sampling sites were grouped for analysis according to the closest downstream USGS gage.

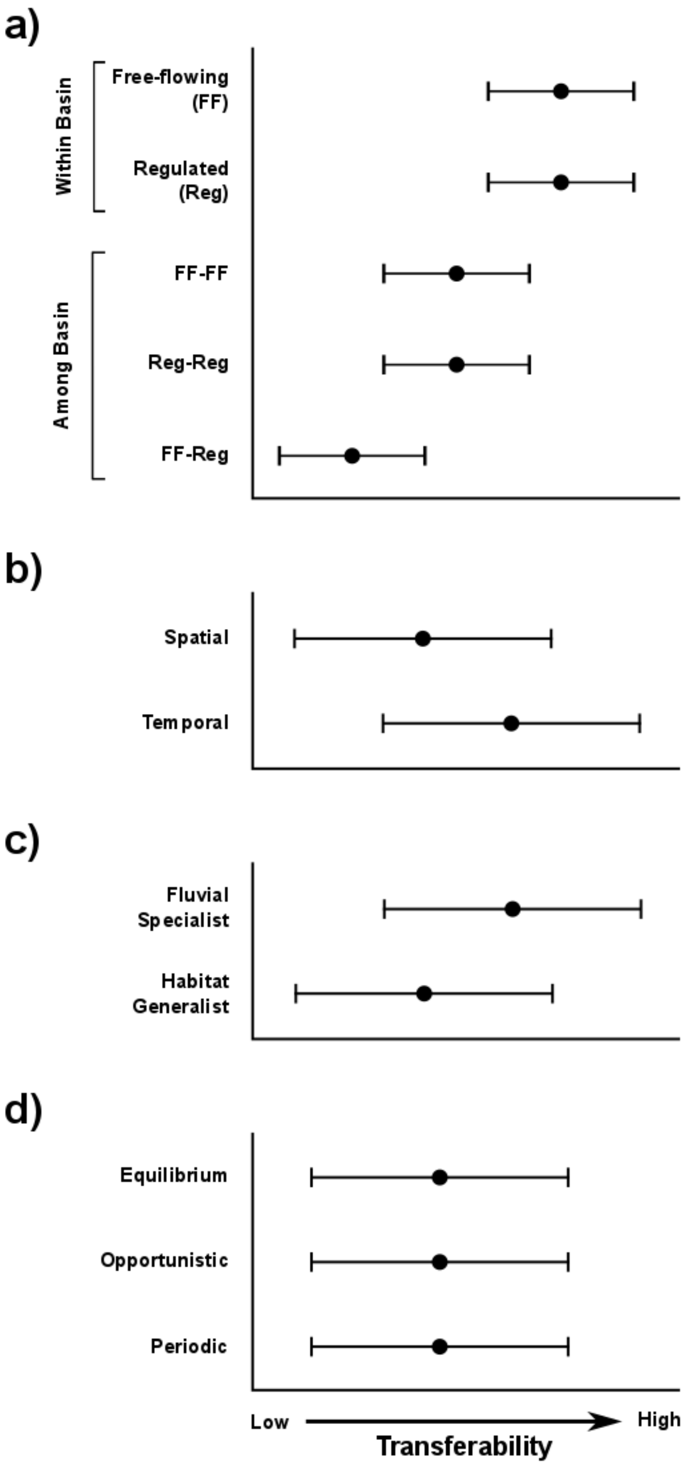


Figure 2.2. Expectations regarding the transferability of flow-ecology relationships: (a) spatial transferability within and among free-flowing versus regulated rivers; (b) temporal versus spatial transferability; (c) spatial transferability across species within flow guilds; (d) spatial transferability across species within life-history strategies.

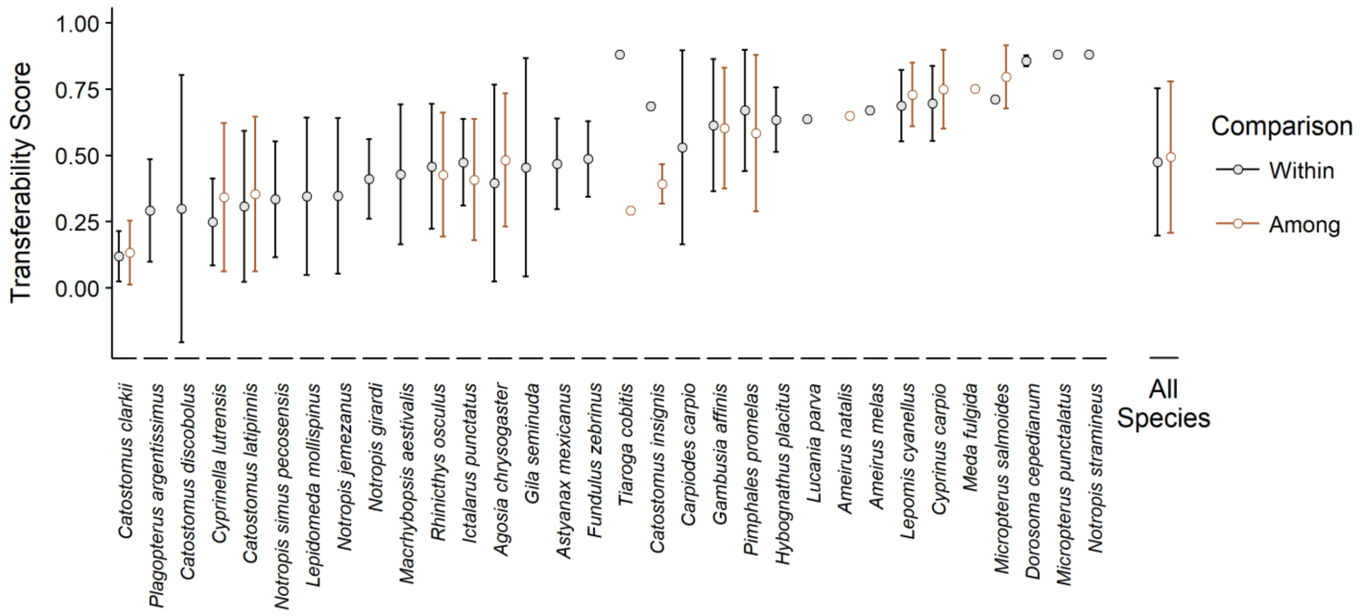


Figure 2.3. Transferability scores of species according to comparisons of flow-ecology relationships across river reaches within the same basin (gray, filled) versus river reaches from different river basins (brown, open). Only species present in more than one river reach are presented. Aggregated, species transferability scores are displayed on the far-right. Transferability scores were standardized using an empirical cumulative distribution function, with lower values indicating lower transferability. Symbols and whiskers represent mean and +/- 1 standard deviation, respectively.

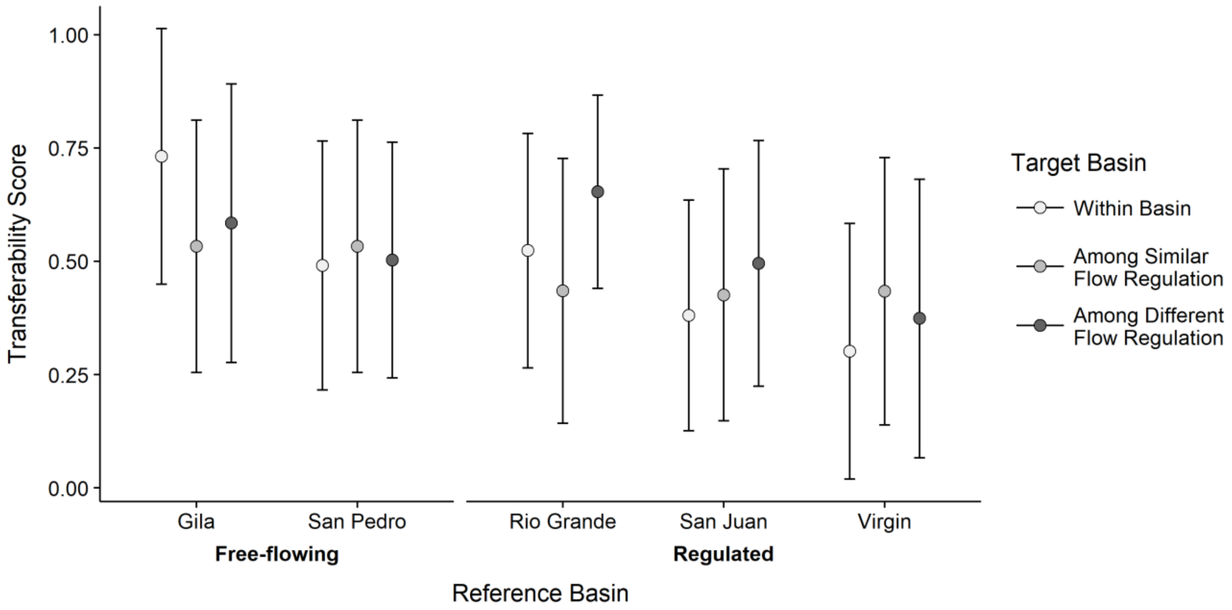


Figure 2.4. Transferability scores of species according to comparisons of flow-ecology relationships from each river basin (x-axis) to river reaches within that basin, to a different river basin with similar flow regulation (free-flowing or regulated), and to a different river basin with different flow regulation (from left to right in each group). Transferability scores were standardized using an empirical cumulative distribution function, with lower values indicating lower transferability. Symbols and whiskers represent mean and +/- 1 standard deviation, respectively.

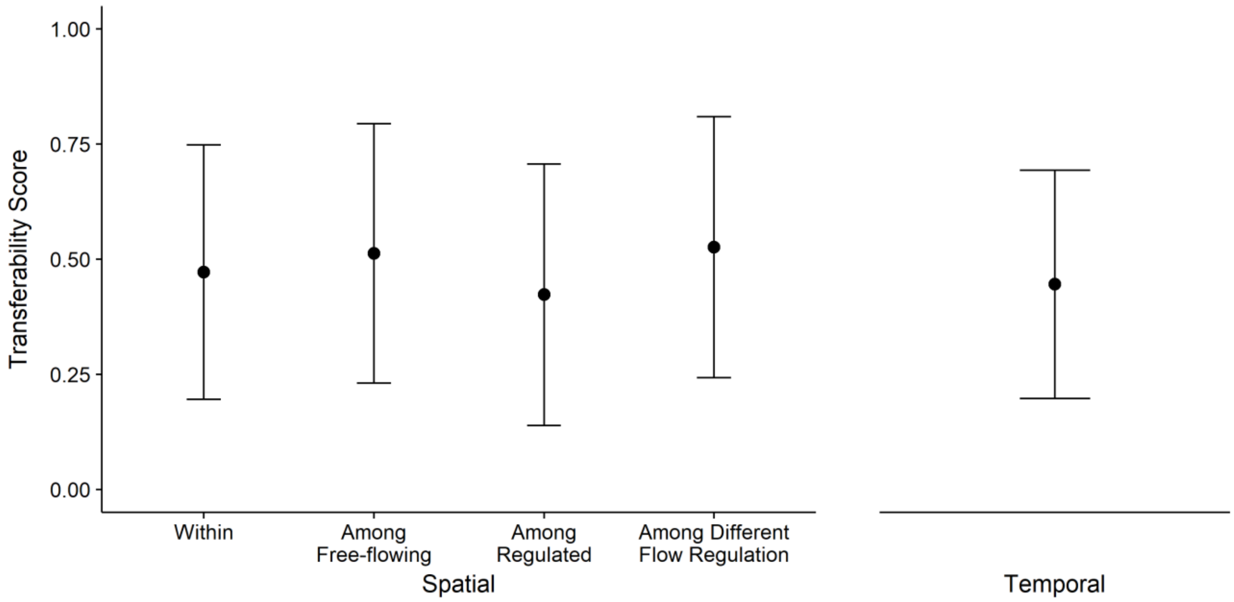


Figure 2.5. Transferablity scores of species according to comparisons of flow-ecology relationships across different river reaches and across time, for species and river reaches where sufficient data was available (Table 2.2). Transferability scores were standardized using an empirical cumulative distribution function, with lower values indicating lower transferability. Symbols and whiskers represent mean and +/- 1 standard deviation, respectively.

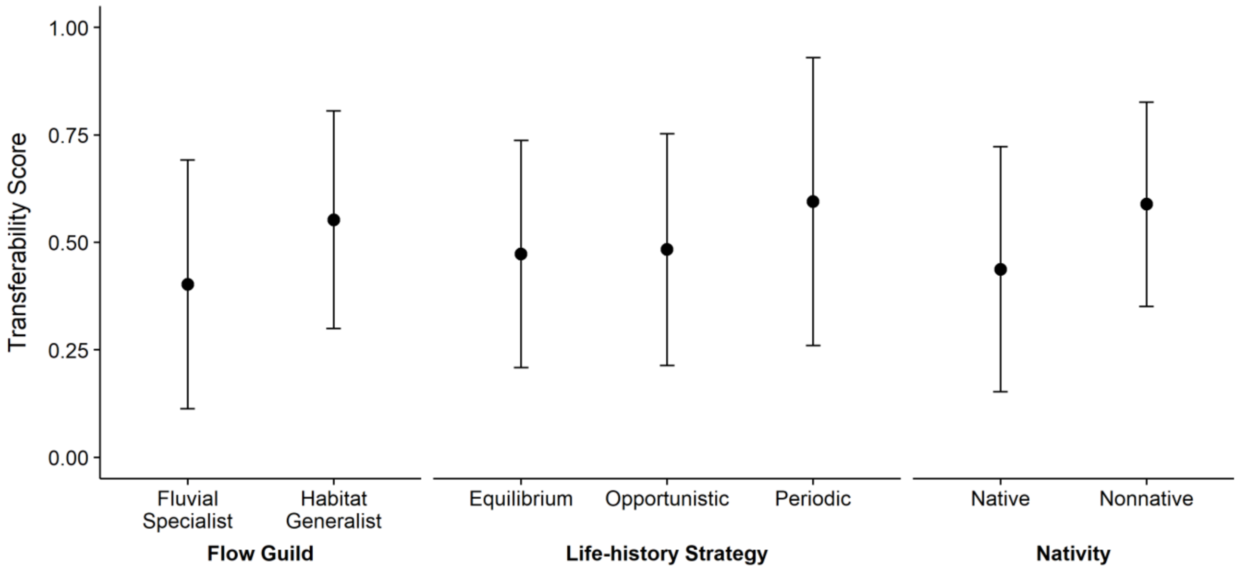
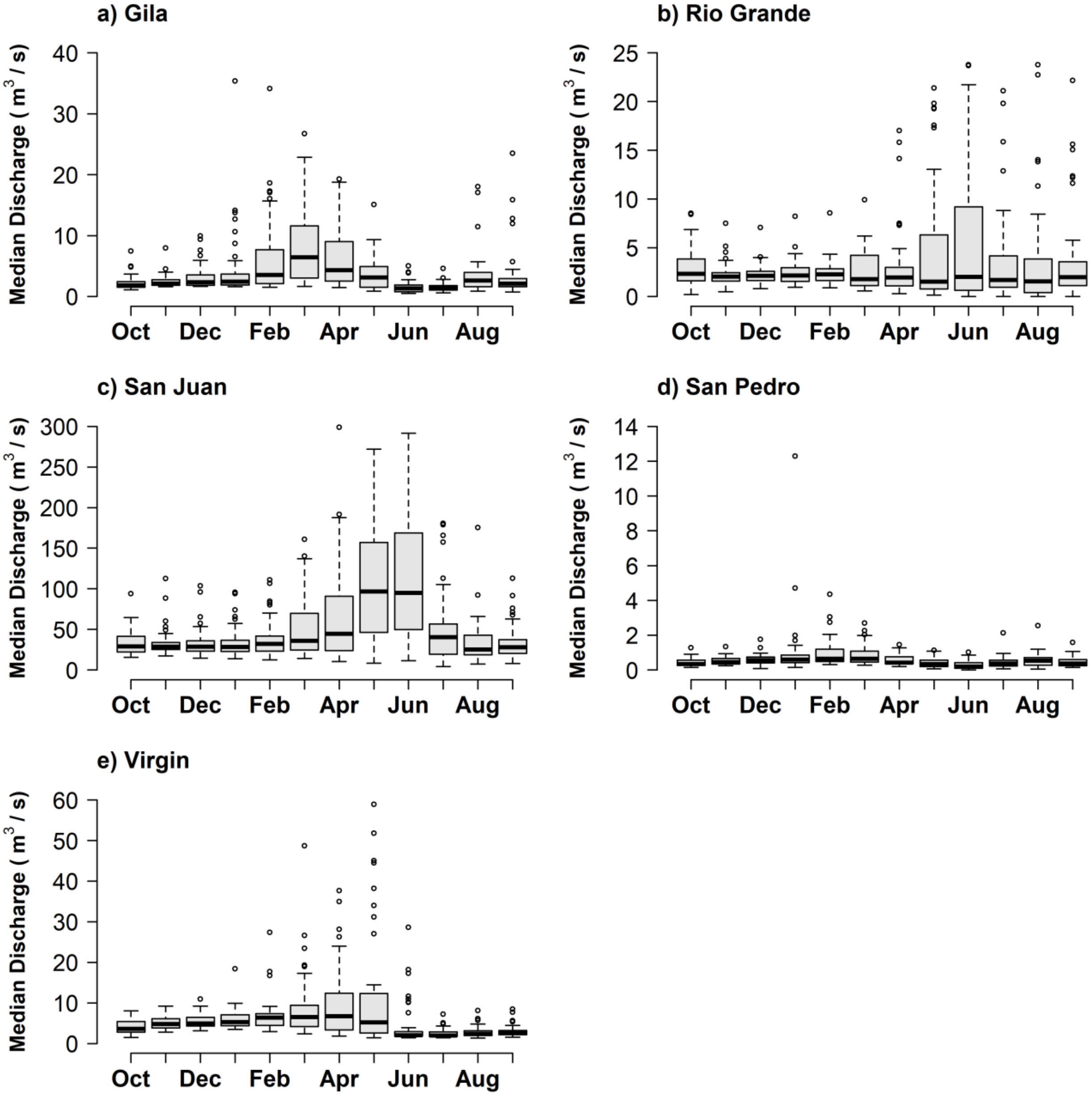


Figure 2.6. Transferability scores of guilds, strategies, and nativity group according to comparisons of flow-ecology relationships among species within each classification. Transferability scores were standardized using an empirical cumulative distribution function, with lower values indicating lower transferability. Symbols and whiskers represent mean and +/- 1 standard deviation, respectively.

2.9 Supplementary Tables and Figures

Supplementary Table 2.1. Jaccard similarity indices of species composition (presence/absence) for each pair of river basins in the study, with 1 indicating perfect similarity and 0 indicating complete disassociation.

	Gila	**San Pedro**	**Rio Grande**	**San Juan**	**Virgin**
Gila	1				
San Pedro	0.67	1			
Rio Grande	0.12	0.16	1		
San Juan	0.22	0.22	0.16	1	
Virgin	0.25	0.32	0.14	0.31	1



Supplementary Figure 2.1. Box plots of median monthly discharge in each of the five study river basins from water years 1975 to 2013: (a) Gila River, (b) Rio Grande River, (c) San Juan River, (d) San Pedro River, and (e) Virgin River. Each box denotes the interquartile range (middle 50%-tile of data), with the median value denoted by a bold line. Whiskers extend to 1.5 times the interquartile range and points beyond the whiskers denote outliers. Note the differing y-axes on each plot.