Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin

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Abstract: Freshwater conservation efforts require an understanding of how natural and anthropogenic factors shape the present-day biogeography of native and non-native species. This knowledge need is especially acute for imperiled native fishes in the highly modified Lower Colorado River Basin (LCRB), USA. In the present study we employed both a taxonomic and functional approach to explore how natural and human-related environmental drivers shape landscape-scale patterns of fish community composition in the LCRB. Our results showed that hydrologic alteration, watershed land use, and regional climate explained 30.3% and 44.7% of the total variation in fish community taxonomic and functional composition, respectively. Watersheds with greater dam densities and upstream storage capacity supported higher non-native functional diversity, suggesting that dams have provided additional "niche opportunities" for non-native equilibrium life-history strategists by introducing new reservoir habitat and modifying downstream flow and thermal regimes. By contrast, watersheds characterized by greater upstream land protection, lower dam densities, and higher variation in spring and summer precipitation supported fish communities with a strong complement of native species (opportunistic–periodic strategists). In conclusion, our study highlights the utility of a life-history approach to better understand the patterns and processes by which fish communities vary along environmental gradients.

Résumé : Les efforts de conservation en eau douce nécessitent une compréhension de la manière dont les facteurs naturels et anthropiques affectent la biogéographie actuelle des espèces indigènes et non indigènes. Cette connaissance est particulièrement indispensable pour les poissons indigènes en péril dans le bassin versant inférieur fortement modifié du Colorado (LCRB). Nous utilisons dans notre étude à la fois des méthodologies taxonomiques et fonctionnelles pour explorer comment les facteurs environnementaux naturels et anthropiques transforment les patrons de la communauté de poissons à l'échelle du paysage dans le LCBR. Nos résultats montrent que les modifications hydrologiques, l'utilisation des terres du bassin versant et le climat régional expliquent respectivement 30,3 % et 44,7 % de la variation totale de la composition taxonomique et fonctionnelle de la communauté de poissons. Les bassins versants avec une densité plus élevée de barrages et une capacité plus importante de rétention en amont contiennent une diversité fonctionnelle non indigène plus élevée, ce qui laisse croire que les barrages fournissent des « possibilités de niches » pour des espèces non indigènes stratèges d'équilibre en créant de nouveaux habitats de réservoir et en modifiant les régimes de débit et de température en aval. En revanche, les bassins versants caractérisés par une plus grande protection des terres en amont, une densité plus faible de barrages et une variation plus importante des précipitations de printemps et d'été contiennent des communautés de poissons avec une forte composante d'espèces indigènes (stratèges périodiques et opportunistes). En conclusion, notre étude souligne l'utilité d'une approche basée sur les cycles biologiques pour mieux comprendre les patrons et les processus qui expliquent la variation des communautés de poissons le long des gradients environnementaux.

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Introduction

Early explorations of desert ecosystems fueled the perception that these arid environments exhibit depressed species diversity with only modest scientific or conservation value. Further investigations, however, have shown that desert ecosystems often harbor high species endemism that disproportionately contribute to regional diversity and support critical ecological functions (Whitford 2002). Highly dynamic physical conditions and a rich geologic history promoting regional isolation have facilitated the evolution of unique species and life-history strategies in deserts. Conversely, these same ecosystem attributes have made many desert species highly vulnerable to human-induced environmental change, such as increasing agricultural and domestic water demand, habitat loss and fragmentation, introduced invasive species (Williams 1999), thereby qualifying deserts among the most critically imperiled global habitats (Olson and Dinerstein 1998). With over two billion people currently inhabiting arid regions around the world, a central challenge in ecology is to understand the critical linkages between environmental change and biological diversity in these fragile ecosystems (Millennium Ecosystem Assessment 2005).

Streams play a vital role in shaping the hydrological, biogeochemical, and ecological structure and function of desert ecosystems (Sponseller and Fisher 2006; Levick et al. 2008). Episodic patterns in precipitation result in extreme hydrologic regimes that structure the ecological processes and productivity of aquatic and riparian communities and shape species life histories over evolutionary time scales (Lytle and Poff 2004; Naiman et al. 2008). In recent decades, human use of arid system rivers has elevated conflicts between societal and ecosystem needs for water in desert regions around the world. These pressures are particularly acute in the Colorado River — the lifeline of the American Southwest that provides water for human consumption, agriculture, hydroelectricity, and recreation to over 30 million people in the southwestern United States and northwestern Mexico (Fradkin 1981; Carlson and Muth 1989; Paukert et al. 2010). Concurrently, the highly endemic fish fauna of the Lower Colorado River Basin (LCRB) has been detrimentally impacted by these human activities resulting in extensive native species declines in range or abundance over the past century (Miller 1961; Minckley and Deacon 1968; Rinne and Miller 2006). Approximately 25 of the 31 native fish species within the LCRB are federally listed under the US Endangered Species Act (United States Fish and Wildlife Service 1999), and recent research has suggested that many unlisted species are similarly threatened (Fagan et al. 2005a; Olden et al. 2008). In contrast with declines in native fishes, the distribution and diversity of many non-native fishes throughout the LCRB have increased rapidly during the same time period (Olden and Poff 2005).

Understanding how natural and anthropogenic factors shape the present-day diversity and composition of fish communities is needed to effectively manage and conserve freshwater ecosystems in the future (Olden et al. 2010). Ecologists traditionally have explored linkages between descriptors of the environment and taxonomic composition of fish faunas, including species occurrence and richness (Jackson et al. 2001). However, a functional perspective using biological traits allows the comparison of species compositions that naturally differ because of biogeographic constraints on regional species pools at larger spatial scales (Schlosser 1990; Poff 1997; Mason et al. 2005). Fish species traits and associated life-history strategies are reflections of the physiological constraints or trade-offs made in response to temporal and spatial variation in abiotic environmental conditions, competition for resources, and predation (Winemiller 2005). By incorporating biological traits into community analyses, one can gain greater mechanistic insight into the environmental drivers of freshwater fish species composition and diversity (e.g., Poff and Allan 1995; Lamouroux et al. 2002; Irz et al. 2007). A functional approach is relevant in the LCRB, where there is increasing interest in clarifying the role of both individual and interactive impacts of natural and human-related drivers in shaping native fish persistence and non-native fish invasions in a highly modified basin.

The objective of the present study was to explore landscape-scale patterns and drivers of fish community composition in the LCRB. First, we examined how the functional diversity of native and non-native fish communities related to hydrologic alteration, land use, regional climate, and watershed physiography. Second, we quantified the differential effects of human- and natural-related factors in explaining patterns of taxonomic versus functional fish community composition. By undertaking a multivariate trait-based examination of species–environment relationships, we aim to provide new insight into the drivers of fish faunal change for an iconic river basin recognized as being among the most threatened globally.

Materials and methods

Study area

The LCRB encompasses an area of approximately 362 750 km^2, draining desert and xeric shrublands of the Sonoran Desert and Colorado Plateau and high elevation pinyon–juniper–oak woodlands of the Arizona mountain forests. We defined the boundary of the LCRB as beginning at the base of Glen Canyon Dam and ending at the Gulf of California. The major tributaries of this basin include the Little Colorado, Virgin, Bill Williams, and Gila rivers (Fig. 1). Following the methodology of Sowa et al. (2007) and Hawkins et al. (2000), we divided the LCRB into 386 aquatic ecological system units, hereafter called watersheds, according to abrupt changes in landform, gradient, or stream size. Watershed area ranged from 200 to 1600 km^2, a size considered effective to represent landscape-scale habitat heterogeneity relevant to structuring fish assemblages and provide ecologically meaningful conservation planning units (Sowa et al. 2005; Stagliano 2005).

Fish data

As part of the LCRB Aquatic Gap Analysis Project, we developed a comprehensive database containing >2 500 000 individual fish records for native and non-native fishes covering the period from 1840 to 2006 (Whittier et al. 2006). Records from published, peer-reviewed literature were typically cross-referenced with voucher specimens from museums, and records from agency–institutional reports and other sources of "gray literature" were only used after being

Fig. 1. Map of the Lower Colorado River Basin (LCRB), USA, displaying the major rivers, dams, and basin boundaries.
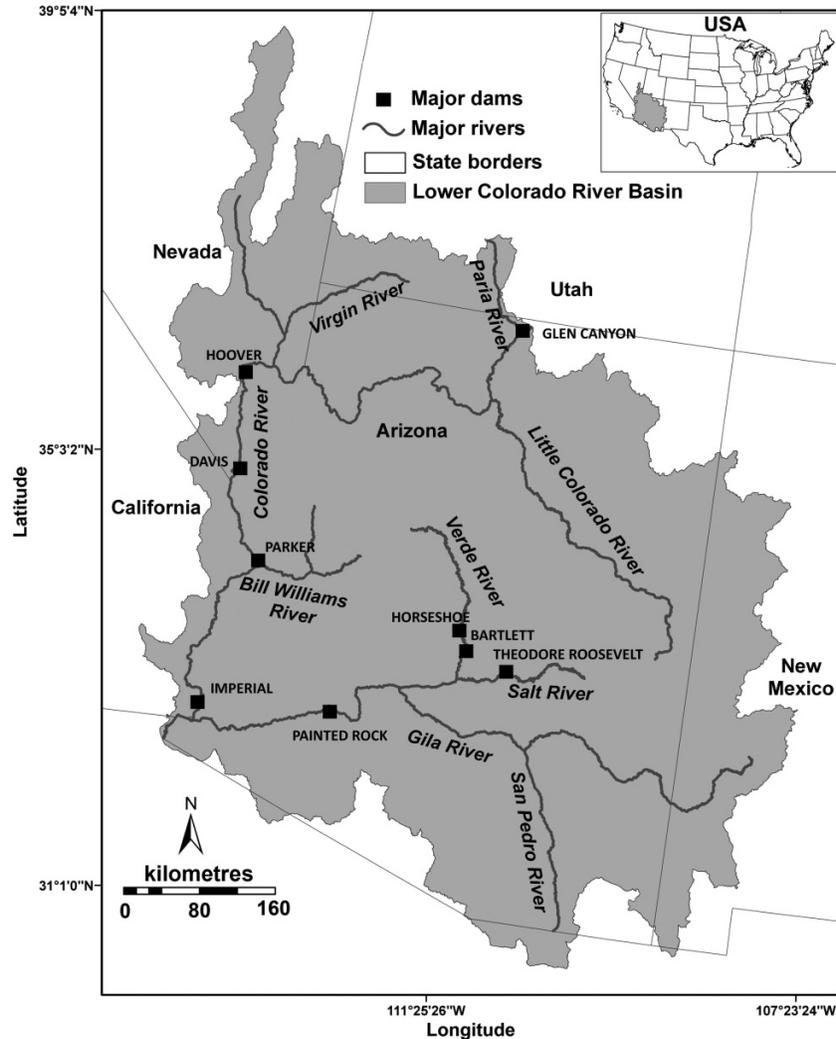
reviewed for accuracy. Records from the electronic data sets were cross-referenced to site localities and voucher specimens if a record's validity was in question. When a voucher specimen was unavailable, we requested record verification. Records include incidence, identity, and collection information for the complete holdings of major museum collections, numerous smaller holdings, and records from state agencies, peer-reviewed, and gray literature sources. While we recognize the potential limitations associated with analyzing compiled data that was not systematically collected, such as museum-based specimen data (Graham et al. 2004), this database was constructed with a high level of quality control. The size, spatial extent, and temporal scope of this database makes it the most extensive source of fish faunal information for the LCRB and unique among data sets for any major drainage basin in the world.

Our study examined present-day fish faunas by utilizing 1 385 874 fish records collected from 1980 to 2006 for 21 native and 36 non-native species (Table 1); excluded were reintroduction records for native fish and records without location collection data or year of observation. Following Fagan et al. (2002), we considered all collections after 1980 to represent present-day fish assemblages — a robust break-

point for comparing distributional trends over time in the LCRB (Fagan et al. 2005b). In addition to Fagan et al. (2005b), Olden and Poff (2005) examined temporal patterns of native and non-native fish distributions in the LCRB by decade and identified 1981 as a breakpoint representing extant species ranges. These modern records in the data set are almost exclusively the result of intensive efforts by federal or state agencies to determine species' complete distributions prior to listing decisions under the US or Mexican Endangered Species Acts (Fagan et al. 2002). In total, our analysis was based on a selection of 159 watersheds after removing watersheds with no fish records or low sampling effort.

Functional attributes were characterized for each fish species by utilizing a database of 14 biological and ecological traits (i.e., morphological, behavioral, trophic, and life history) for the Colorado River Basin assembled by Olden et al. (2006). These traits were chosen to reflect the major ecological strategies exhibited by fishes in this region (Table 2). Trait assignments were constructed using a multitiered data collection protocol, utilizing comprehensive texts of state fish faunas, primary literature, state agency reports, university reports, and graduate theses. Electronic databases and expert knowledge were used to supplement the literature-

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Table 1. Freshwater native ($n = 21$) and non-native ($n = 36$) fish of the Lower Colorado River Basin.

Native species, common name	Code	Non-native species, common name	Code
Catostomidae		**Catostomidae**	
Catostomus clarkii, desert sucker	CACL	*Ictiobus cyprinellus*, bigmouth buffalo	ICCY
Catostomus discobolus, bluehead sucker	CADI	**Centrarchidae**	
Catostomus insignis, Sonora sucker	CAIN	*Ambloplites rupestris*, rock bass	AMRU
Catostomus latipinnis, flannelmouth sucker	CALA	*Lepomis cyanellus*, green sunfish	LECY
Xyrauchen texanus, razorback sucker	XYTE	*Lepomis macrochirus*, bluegill	LEMA
Cyprinidae		*Lepomis microlophus*, redear sunfish	LEMI
Agosia chrysogaster, longfin dace	AGCH	*Micropterus dolomieu*, smallmouth bass	MIDO
Gila cypha, humpback chub	GICY	*Micropterus salmoides*, largemouth bass	MISA
Gila elegans, bonytail	GIEL	*Pomoxis nigromaculatus*, black crappie	PONI
Gila intermedia, Gila chub	GIIN	**Cichlidae**	
Gila nigra, headwater chub	GINI	*Oreochromis aureus*, blue tilapia	ORAU
Gila robusta, roundtail chub	GIRO	*Oreochromis mossambicus*, Mozambique tilapia	ORMO
Lepidomeda mollispinis, Virgin spinedace	LEMO	*Tilapia zillii*, redbelly tilapia	TIZI
Lepidomeda vittata, Little Colorado spinedace	LEVI	**Clupeidae**	
Meda fulgida, spikedace	MEFU	*Dorosoma petenense*, threadfin shad	DOPE
Plagopterus argentissimus, woundfin	PLAR	**Cyprinidae**	
Rhinichthys cobitis, loach minnow	RHCO	*Carassius auratus*, goldfish	CAAU
Rhinichthys osculus, speckled dace	RHOS	*Ctenopharyngodon idella*, grass carp	CTID
Cyprinodontidae		*Cyprinella lutrensis*, red shiner	CYLU
Cyprinodon macularius, desert pupfish	CYMA	*Cyprinus carpio*, common carp	CYCA
Poeciliidae		*Notemigonus crysoleucas*, golden shiner	NOCR
Poeciliopsis occidentalis, Gila topminnow	POOCOC	*Pimephales promelas*, fathead minnow	PIPR
Salmonidae		*Richardsonius balteatus*, redside shiner	RIBA
Oncorhynchus gilae apache, Apache trout	ONGIAP	**Esocidae**	
Oncorhynchus gilae, Gila trout	ONGIGI	*Esox lucius*, northern pike	ESLU
		Fundulidae	
		Fundulus zebrinus, plains killifish	FUZE
		Ictaluridea	
		Ameiurus melas, black bullhead	AMME
		Ameiurus natalis, yellow bullhead	AMNA
		Ictalurus punctatus, channel catfish	ICPU
		Pylodictis olivaris, flathead catfish	PYOL
		Moronidae	
		Morone mississippiensis, yellow bass	MOMI
		Morone saxatilis, striped bass	MOSA
		Percidae	
		Perca flavescens, yellow perch	PEFL
		Sander vitreus, walleye	SAVI
		Poeciliidae	
		Gambusia affinis, western mosquitofish	GAAF
		Poecilia latipinna, sailfin molly	POLA
		Salmonidae	
		Oncorhynchus clarkii, cutthroat trout	ONCL
		Oncorhynchus mykiss, rainbow trout	ONMY
		Salmo trutta, brown trout	SATR
		Salvelinus fontinalis, brook trout	SAFO
		Thymallus arcticus, Arctic grayling	THAR

based trait assignments in a limited number of cases. Trait values were recorded based on research conducted in the LCRB or the closest geographic region when possible to account for interdemic variation in biological traits.

Environmental characteristics

We quantified 17 environmental characteristics associated with natural and human-related landscape features based on their demonstrated importance in shaping patterns of fish species occurrence in arid and semiarid ecosystems. Variables were either calculated for the watershed or included the upstream (US) contributing basin and were grouped into categories describing hydrologic alteration by dams, land use and watershed physiography, and regional climate (numbered sequentially below). Variables describing hydrologic alteration included (1) US dam density (no.·km^{-2}); (2) US dam storage capacity (m^3); (3) US reservoir surface area (km^2); (4) US canal–ditch density (m·km^{-2}); and

Table 2. The functional attributes of each fish species examined in this study.

Category	Trait	Description and (or) units	Abbrev.
Morphology	Maximum total body length*	Maximum total body length (cm)	MS
	Swim factor*	Ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin	SF
Behavior	Water temperature preference	Cold (10–17 °C), cool (18–26 °C), or warm (>26 °C) based on species distributions and physiological optima	TP
	Substrate preference	Rubble–cobble–gravel, sand, silt–mud, or general	SP
	Fluvial dependence	Relying or not relying on flowing waters for completing life cycle, e.g., flow required for feeding or reproduction	FD
	Flow preference	Slow, slow–moderate, moderate, moderate–fast, or fast current velocity	FP
Trophic	Trophic guild	Omnivore (approximately <5% plant matter), invertivore, invertivore–piscivore, piscivore, and herbivore–detritivore (approximately >25% plant matter) based on published adult diet analyses	TG
Life history	Longevity*	Maximum potential life span (years)	LM
	Age at maturation*	Age at maturation (years)	AM
	Length at maturation*	Length at maturation (cm)	LM
	Fecundity*	Total number of eggs or offspring per breeding season	F
	Egg size*	Mean diameter of mature oocytes (mm)	ES
	Parental care	Total energetic contribution of parents to offspring	PC
	Reproductive guild	Bearers (internal), guarders (nest spawners or substratum choosers), or non-guarders (brood hiders or open substratum spawners)	RG

*Continuous trait characteristics that were converted into categorical data for functional community analysis included maximum total body length (1: 0–400 mm; 2: 401–800 mm; 3: >800 mm); swim factor (1: 0–4; 2: >4); longevity (1: 0–5 years; 2: 5–10 years; 3: >10 years); age at maturation (1: 0–1 years; 2: 1–2 years; 3: >2 years); length at maturation (1: 0–100 cm; 2: 101–200 cm; 3: 201–300 cm; 4: >300 cm); fecundity (1: 0–4; 2: >4); and egg size (1: 0–1.5 mm; 2: >1.5–3 mm; 3: >3 mm). Taxonomic and functional analyses using canonical correspondence analysis (CCA) and partial CCA (pCCA) were performed for the full species data set, native species only, and non-native species only.

(5) downstream distance (km) from the tail-water boundary for each watershed to the nearest dam to represent proximity to lentic habitat. Data sources used were the National Inventory of Dams (United States Army Corps of Engineers 2007) and the National Hydrography Dataset (United States Geological Survey 2007). Land use and watershed physiographic variables included (6) US agricultural land use (%); (7) road density (m·km^{-2}); (8) US land in urban development (%); (9) US natural land dominated by barren rock, forest, or scrub brush (%); (10) US land with permanent protection from human development according to a regional management plan (%); (11) canyon habitat (km) calculated as the total length of stream segments dominated by canyon habitat (Whittier et al. 2006); and (12) watershed surface area (km^2). Data sources were the National Land Cover Database (Multi-Resolution Land Characteristics Consortium 2001), Southwest Regional Gap Analysis Project Stewardship Data (United States Geological Survey 2005), and the National Elevation Dataset (United States Geological Survey 2004). Variables describing regional climatic conditions included (13) mean US annual precipitation (mm); (14) variation in winter precipitation calculated as the coefficient of variance (CV) in monthly US precipitation for November to February; (15) variation in spring precipitation (March to April); (16) variation in summer precipitation (May to August); and (17) mean annual temperature (°C) calculated as the midpoint of maximum and minimum air temperatures recorded across each watershed. All precipitation variables were based on records from 1971 to 2000. Data source was Climate Source (United States Department of Agriculture – National Resources Conservation Service 2007).

Additional variables were originally considered but were removed because they were highly correlated with the variables detailed above. We assessed variable collinearity by computing the variance inflation factor (VIF), where VIF values greater than 5 are considered to be indicative of high collinearity (Menard 1995; O'Brien 2007). None of our environmental variables had VIF values greater than this conservative threshold, indicating an acceptable level of collinearity in subsequent analyses. We tested for spatial dependency among our environmental variables in geographic space by regressing the pairwise similarity in environmental characteristics between watersheds (based on Euclidean distance) against the geographical distance separating them (according to Euclidean distance between centroids of each watershed) using a Mantel test. We found very little spatial structure in our environmental variables among watersheds ($r = 0.043$, $P = 0.075$), suggesting that watersheds could be treated as independent observations in subsequent statistical analyses.

Statistical analysis

Indices of taxonomic and functional diversity

Functional diversity can be described by a number of indices (see Petchey and Gaston 2006), including the three primary components of functional richness, functional evenness, and functional divergence (Mason et al. 2005; Villéger et al. 2008). These functional indices are measured on continuous scales and describe independent aspects of trait diversity in community space. Functional richness measures the amount of trait space or volume occupied by the species of a community; functional evenness describes the uniformity of species (or their abundance) that comprise a community in trait space; and functional divergence measures the degree that abundance-weighted functional differences are maximized in niche space among the species within a community.

We quantified species functional richness and evenness

for watersheds using 14 species traits following Villéger et al. (2008); functional divergence was not computed because reasonable estimates of species abundance at the watershed scale could not be estimated with confidence. The functional richness index value for each watershed was assessed using the Quickhull algorithm (Barber et al. 1996), which calculates the minimum convex hull that includes all the species considered in the multivariate trait space. Functional richness values have no upper limit because they quantify the absolute volume represented by the community's suite of traits in each watershed. The functional evenness index value was calculated using a minimum spanning tree method linking all the trait points in multidimensional space with a minimum sum of total tree branch lengths (Villéger et al. 2008). Functional evenness values are constrained between 0 and 1, with low values representing a high proportion of the species trait occurrence concentrated within a narrow range of the functional trait gradient and high values representing evenly spaced species traits throughout the occupied functional space.

To calculate functional richness and evenness, we first summarized similarities in species' trait characteristics by conducting a principal coordinate analysis (PCoA) on the species-by-trait matrix. PCoA is a statistical methodology to explore similarities by optimally representing the variability of a multidimensional data matrix (species-by-trait matrix) in reduced ordination space (Legendre and Legendre 1998). A species dissimilarity matrix based on the 14 traits was calculated using Gower's coefficient, a metric able to accommodate nominal, ordinal, and continuous data (Pavoine et al. 2009). The first two principal coordinate axes each explained a significant proportion of the total variation in trait community composition (30% and 19%) based on the randomized broken-stick method and $\alpha = 0.05$ (Jackson 1993), and both axes were used to calculate the functional richness and evenness values for each watershed. We calculated both native and non-native functional richness and evenness indices individually for our functional diversity analyses, but because of species richness constraints associated with the functional index calculations, only watersheds that had four or more native species (97 watersheds) or non-native species (126 watersheds) could be examined.

Diversity–environment relationships

We used general linear modeling to model native and non-native functional richness and evenness (separately) as a function of environmental factors describing watershed physiography, hydrologic alteration, land use, and climate. Taxonomic species richness was also included in some models, specifically native richness for non-native models, and vice versa. Our analysis was designed to test the relative importance of different subsets of these factors for predicting native and non-native fish diversity (richness and evenness) using an information-theoretic approach to model selection (Anderson and Burnham 2002). We considered 24 candidate models (Appendix A), including a global model with all 17 environmental variables (model 1), models containing single descriptors of environmental variation (hydrologic alteration: model 2; land use: models 3–6; and climate: models 6–9), models depicting the role of riverine fragmentation (model 10), natural physiographic basin features (model 11), and

overall descriptors of human disturbance (models 12–13). Lastly, we examined a series of candidate models derived from the literature reflecting combinations of variables that have been identified as being important in shaping fish community composition in the southwestern USA (models 14–24). These literature-derived models are based on the findings of Moyle and Light (1996), Gido and Brown (1999), Meador et al. (2003), Marchetti et al. (2004), Propst and Gido (2004), Rinne and Miller (2006), Light and Marchetti (2007), and Propst et al. (2008).

Regression diagnostics from the global model indicated a reasonable statistical fit with no significant deviations from the parametric assumptions. Consequently, we ranked our 24 candidate models using Akaike's information criterion (AIC) to evaluate the relative support (given the data) for each model. We also calculated the difference between the best approximating model value and all remaining model values (Anderson and Burnham 2002, ΔAIC_i). Maximum log-likelihood estimates and Akaike weights (w_i), representing the relative likelihood of a model against all candidate models, were calculated for every model. Evidence ratios were computed to quantify the relative support for each model by dividing the w_i of the best approximating model by the w_i for each individual model. For the best approximating model, w_i values and standardized regression coefficients ($\hat{a}_i$) for each environmental factor were calculated to assess variable importance (Anderson and Burnham 2002). We calculated the cumulative Akaike weights (Σw_i) for the top five supported models to estimate overall relative importance of the model. Additionally, we calculated cumulative weights based all models found in 95% confidence intervals of all models. The results did not differ substantially between the two approaches, so we present the results from the latter. All model analysis was performed using R 2.51 utilizing existing scripts in the Ape library (R Development Core Team 2007).

Community–environment relationships

We used canonical correspondence analysis (CCA) (ter Braak 1986) to assess the relationship between fish community composition and environmental characteristics at the watershed scale. In our analysis, CCA allows for the ordination of the fish community data (by reciprocal averaging) to be constrained by a multiple regression on its relationships to the environmental variables. CCA is robust when species' responses to the underlying environmental gradients are unimodal and important predictor variables have been measured and are relatively free from stochastic noise (Gauch 1982; Palmer 1993). We selected CCA because an analysis based on detrended correspondence analysis indicated that, on average, the species (gradient level = 2.7) and the traits (gradient level = 3.7) showed unimodal responses along the environmental gradients (Gauch 1982). Contributions of each environmental variable in the CCA were tested for significance using a Monte Carlo test with 4999 permutations, and only those that were statistically significant at $\alpha = 0.05$ were depicted on the ordination biplots. Distributional properties of the variables were examined and resulted in the $\log(x)$ transformation of watershed area, annual precipitation, and annual temperature; the $\log(x + 1)$ transformation of dam density, dam storage, distance to downstream dam,

reservoir surface area, canal density, and road density; and the arcsine (square-root x) transformation of land use variables expressed as proportions (agriculture, urban, natural, and protected).

Partial CCA (pCCA), a modified canonical ordination technique, is an appropriate method for decomposing species–environment relationships via variance partitioning (ter Braak 1988; Borcard et al. 1992). We used pCCA to partition the total community variance explained by the different sets of environmental variables into their independent (pure) and confounded (intercorrelated) components, thus enabling us to assess the relative importance of hydrologic alteration, land use, and climate in explaining patterns in functional and taxonomic community composition of the native and non-native species pools. Land use was further decomposed into the variation explained by variables of human land use (agriculture, urban, road density) versus natural land use (natural land, protected, canyon habitat, and watershed area). We examined both independent and confounded variation explained by each category of variables.

To assess the relationship between functional community composition and environmental drivers, we calculated a watershed-by-trait matrix by multiplying the watershed-by-species matrix by the species-by-trait matrix and dividing by the watershed-by-richness column vector. To accomplish this, we first were required to categorize the continuous traits (e.g., body length) into discrete trait states (see Table 2), which after combining with the raw categorical traits (e.g., trophic guild, reproductive guild) enabled the creation of a species-by-trait state presence–absence matrix. The end result was a watershed-by-trait matrix containing values that represented the proportion of species in each watershed exhibiting each trait state.

Results

Geographic patterns of taxonomic and functional diversity

Native and non-native fishes showed notable spatial patterns of taxonomic and functional diversity. Native taxonomic diversity was greatest in the main stem and tributaries of the Upper Gila River, Verde River, Salt River, and portions of the Upper Virgin River (Fig. 2a). Patterns of non-native taxonomic diversity mirrored the native fish fauna, but with relatively higher richness in the main stem Colorado River between Lake Powell (Glen Canyon Dam) and Lake Mead (Hoover Dam) and downstream from Imperial Dam (close to the confluence with the Gila River) and relatively lower richness in the Upper Gila River Basin (Fig. 2b). Mean native and non-native species richness throughout the basin was four and seven species per watershed, respectively.

Geographic patterns of functional richness were more concentrated compared with taxonomic richness. High levels of native functional richness were mainly observed in the Verde River, Upper Gila River, and Upper Santa Cruz River (Fig. 2c), whereas non-native functional richness was elevated in the main stem Colorado River between Lake Powell and Lake Mead (Fig. 2d). The mean functional richness of the native community watersheds (2.1) was lower than the mean functional richness of the non-native

community watersheds (3.1) for all watersheds analyzed. By contrast, the mean functional evenness of native communities (0.78) exceeded the functional evenness of non-native communities (0.70).

We found a significant positive relationship between taxonomic richness and functional richness ($r^2 = 0.638$, $P < 0.001$, $n = 159$), but only a weak association between taxonomic richness and functional evenness ($r^2 = 0.041$, $P = 0.101$, $n = 159$). As expected, the positive relationship between taxonomic and functional richness occurred because additional species are likely to introduce additional traits into a community.

Environmental drivers of native and non-native functional diversity

The most supportive model for native functional richness was designed from Propst et al. (2008; model 20) and incorporated watershed area; available canyon habitat; annual precipitation; variation in winter, spring, and summer precipitation; and non-native species taxonomic richness (Table 3). This model was four times more likely given the data than the next most competitive model. According to the top model, all of the aforementioned variables were positively related to native functional richness, with the exception of the negative influence of variation in spring precipitation (Tables 3, 4). Cumulative Akaike weights (Σw_i) based on the top five supported models demonstrate that watershed area, non-native taxonomic richness, canyon density, and all seasonal measures of variation in precipitation were the most predictive of native functional richness (Table 4). The model with the most support in describing the native functional evenness was drawn from Marchetti et al. (2004; model 18) and included canal density, urban development in the watershed, annual precipitation, and non-native taxonomic richness (Table 3). Functional evenness of the native communities was negatively related to all these variables, with the exception of canal density. This model had no close competitors, and the cumulative Akaike weights across the top five models supported the overwhelming importance of the four variables listed above.

The most supportive model for non-native functional richness was based on Gido and Brown (1999; model 15) and showed that increased non-native functional richness was related to increased dam density and dam storage capacity, watershed area, and native species taxonomic richness (Tables 3, 4). A variant of this model including canyon habitat (positive effect), annual precipitation (positive effect), and seasonal (CV) precipitation (negative effect) was also highly competitive (Rinne and Miller 2006; model 23), as well as the same model but including canal density (negative effect) (Marchetti et al. 2004; model 19). Model 15 was 1.5 times more likely given the data than the next most competitive model, but was clearly more parsimonious than the latter, having five less parameters. Watershed area, native taxonomic richness, dam storage capacity, and dam density exhibited the highest cumulative Akaike weights across the top five supported models (Table 4). The most competitive model for predicting non-native functional evenness was model 22 (based on Propst and Gido 2004), which included watershed area, annual precipitation, variation in spring and summer precipitation, and native taxonomic richness

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Fig. 2. (*a*) Native and (*b*) non-native taxonomic richness and (*c*) native and (*d*) non-native functional richness for watersheds in the Lower Colorado River Basin (LCRB). Taxonomic richness ranged from 1 to 22 species, and functional diversity ranged from 0 to 9 functional volume units. Refer to Fig. 1 for location of dams and major rivers.
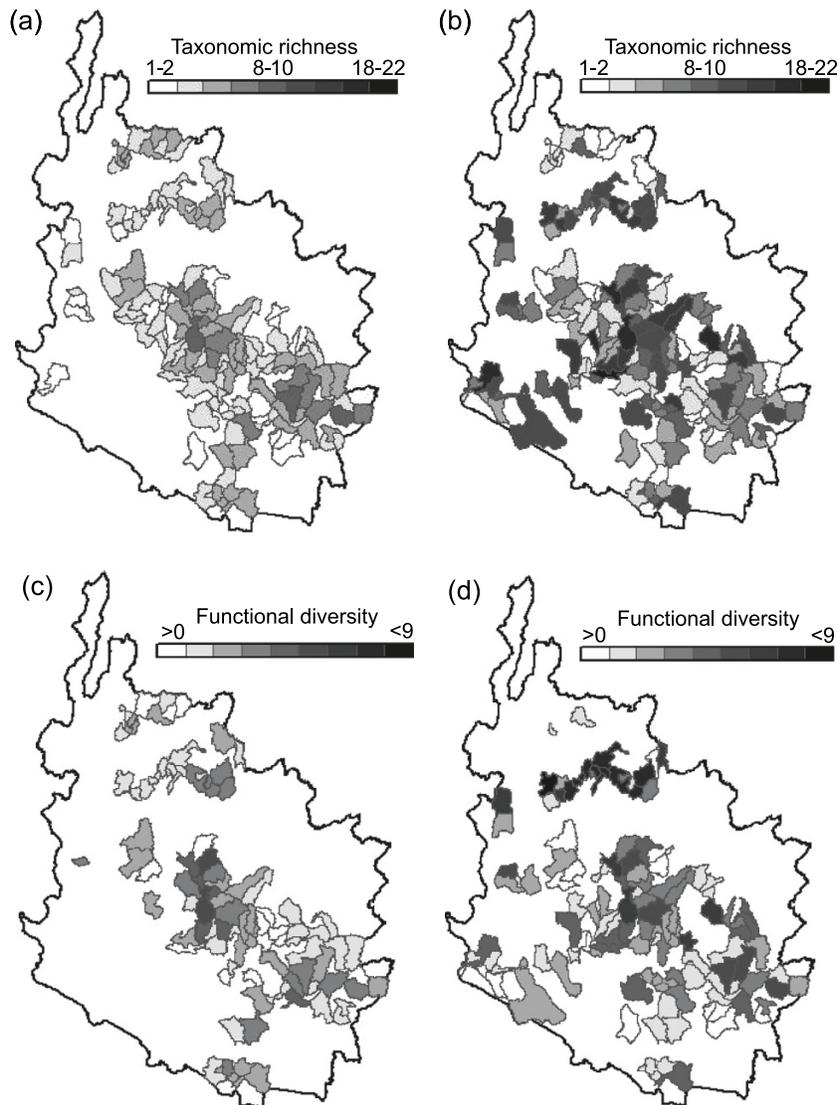
(Table 3). This model was 3.4 times more likely given the data than the next most competitive model, and all of the variables were positively related to evenness except for watershed area (Table 4). Cumulative Akaike weights for the top five supported models illustrated the importance of watershed area, variation in spring and summer precipitation, and annual precipitation. Among the top model competitors were three models incorporating land use disturbance (models 6, 7, and 8).

Environmental drivers of native and non-native functional composition

Environmental factors describing hydrologic alteration, watershed physiography – land use, and climate explained 30.3% of the total variation in fish taxonomic composition (native and non-native together), with the first two canonical axes explaining 14.4% of the variation (both $P < 0.05$ based on Monte Carlo simulation). In general, native species occupy the extreme positions in the lower right and upper left

quadrants of the taxonomic ordination, suggesting that watersheds associated with greater upstream land protection and higher variation in spring and summer precipitation (representing before and after spawning period for native fishes, respectively) are characterized by a complement of native species (Figs. 3*a*, 3*b*, 3*c*). Native species associated with watersheds with higher proportion of protected lands include Virgin River spinedace, woundfin, bluehead sucker, flannelmouth sucker, and humpback chub, and species associated with more variable precipitation regimes include Gila topminnow, longfin dace, headwater chub, Gila chub and Sonora sucker (scientific names provided in Table 1). The upper right quadrant of the taxonomic ordination contained watersheds characterized by a mixture of predominantly native trout (Apache trout, Gila trout) associated with greater availability of canyon habitat and non-native trout (rainbow trout, brook trout, cutthroat trout) associated with higher dam density (Figs. 3*a*, 3*b*). The lower left quadrant of the taxonomic ordination is populated with non-native species-

Table 3. Summary of the model selection statistics for predicting fish community functional diversity indices for native and non-native species.

Model	K	AIC	Δ_i	w_i	Evidence ratio	Model	K	AIC	Δ_i	w_i	Evidence ratio
Native richness						**Non-native richness**					
20	9	278.6	0.0	0.699	1.0	15	7	496.3	0.0	0.405	1.0
24	8	281.3	2.7	0.175	4.0	23	12	497.2	0.8	0.265	1.5
23	12	282.7	4.1	0.088	8.0	19	8	498.3	2.0	0.149	2.7
8	6	286.8	8.2	0.011	61.1	21	9	498.9	2.5	0.113	3.6
7	7	287.3	8.7	0.009	79.2	16	7	501.6	5.3	0.029	14.0
Native evenness						**Non-native evenness**					
18	6	−221.4	0.0	0.538	1.0	22	7	−227.0	0.0	0.495	1.0
19	8	−218.8	2.6	0.148	3.6	8	6	−224.5	2.5	0.144	3.4
14	11	−218.7	2.7	0.141	3.8	20	9	−223.8	3.1	0.103	4.8
15	7	−217.6	3.8	0.080	6.7	6	8	−223.7	3.3	0.095	5.2
21	9	−217.2	4.2	0.067	8.0	7	7	−223.3	3.7	0.078	6.3

Note: All models displayed were the top five models for each functional index analyses. The evidence ratio is calculated as the Akaike weight of the top model divided by the Akaike weight of each model for each functional analysis. Δ_i (AIC difference) is the difference between the top performing model AIC value and each individual model AIC value within each function analysis. w_i is the Akaike weight calculated as the ratio of each model's likelihood to the sum of all the other model likelihoods for each functional analysis.

Table 4. Summary of the cumulative Akaike weights (Σw_i) for the five top ranked models each functional group and standardized regression coefficients ($\hat{a}_i$) for each best fitting model.

	Functional richness				Functional evenness			
	Native		Non-native		Native		Non-native	
Model variables	Σw_i	$\hat{a}_i$	Σw_i	$\hat{a}_i$	Σw_i	$\hat{a}_i$	Σw_i	$\hat{a}_i$
Hydrologic alteration								
Dam density	0.033		0.932	−0.304	0.436			
Dam storage	0.033		0.961	0.454	0.436			
Distance to down dam								
Reservoir surface area			0.029					
Canal density			0.262		0.893	0.432		
Land use and physiography								
Agriculture	0.065				0.141			
Road density								
Urbanization	0.065		0.113		0.745	−0.154		
Natural								
Protected								
Canyon	0.921	0.197	0.265				0.103	
Watershed area	0.990	0.153	0.961	0.056	0.436		0.916	−0.145
Climate								
Annual precipitation	0.358	0.049	0.294		0.678	−0.359	0.669	0.178
Winter precipitation (CV)	0.921	0.483	0.265				0.420	
Spring precipitation (CV)	0.925	−0.133	0.265				0.916	0.172
Summer precipitation (CV)	0.925	0.285	0.265				0.916	0.276
Watershed annual temperature	0.065						0.095	
Taxonomic richness*	0.986	0.336	0.961	0.456	0.974	−0.136	0.599	0.203

Note: Σw_i is the cumulative Akaike weight for each column calculated by summing the Akaike weights for each of the top five models by group. $\hat{a}_i$ is the standardized regression coefficient for each variable in the best fitting model in each functional analysis.

*Native taxonomic richness was used in the non-native analysis and vice versa.

dominated watersheds characterized by high canal and road densities, high urban land use and agriculture, and warmer and wetter climates (Figs. 3a, 3b).

Results from the variance partitioning suggest that the major drivers of taxonomic composition differ between native and non-native species. Of the 34% total variation in native species composition described by the suite of environmental variables, regional climate explained the greatest relative amount (54%) of variation compared with hydrologic alteration and watershed physiography – land use (Fig. 4a). The same trend was evident for non-native species composition (28.6% of the total variation explained); how-

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Fig. 3. Ordination plots resulting from a taxonomic and functional canonical correspondence analysis: (*a*) fish species biplot where letter codes refer to species (Table 1); (*b*) eigenvector plot of environmental characteristics from forward stepwise selection of variables in the taxonomic analysis; (*c*) fish species biplot where solid circles represent native species and open circles represent non-native species; (*d*) trait biplot where letter codes represent the percentage a trait was represented in sites (see Table 2 for letter and number codes); (*e*) eigenvector plot of environmental characteristics from forward stepwise selection of variables in the functional analysis.
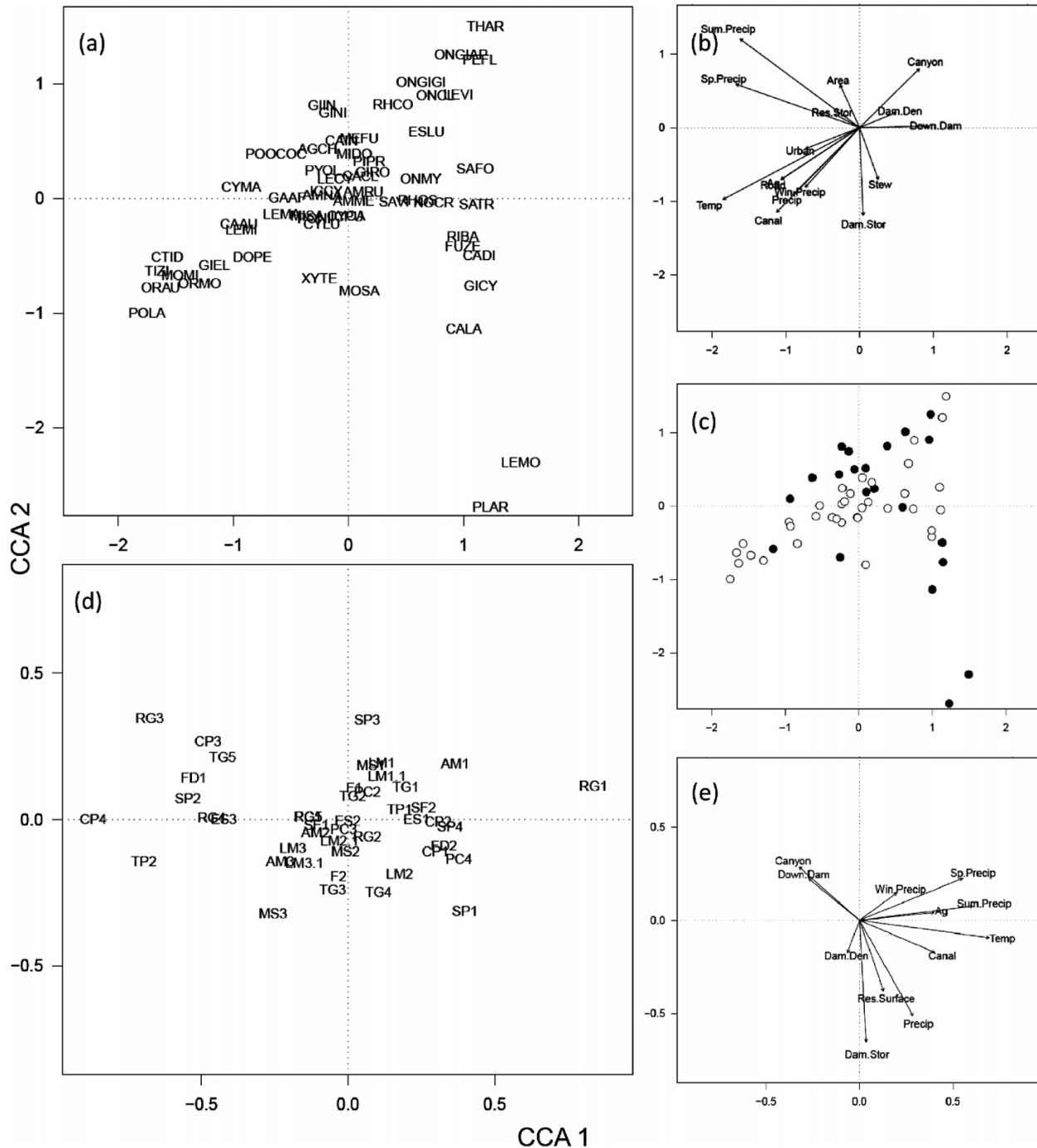
ever, climate accounted for a relatively smaller amount (41%) of the variation explained. Variables describing human-related activities (agricultural, urban, road density) explained a greater percentage of variation in non-native communities compared with native communities, whereas the opposite trend was true for variables depicting more natural physical characteristics (natural land use, canyon, watershed area) (Fig. 4*a*).

Factors describing the environmental categories of hydrologic alteration, watershed physiography – land use, and climate explained 44.7% of the total variation in fish functional composition (native and non-native together), with the first two canonical axes explaining 36.0% of the variation (both $P < 0.05$ based on Monte Carlo simulation), which was about 14% more than the taxonomic variation explained by the same set of variables. The left side of the or-

dination represents fish faunas characterized by biological traits describing large body size (MaxS3), older age at maturation (AM3), reproductive guilds representing low parental care (RG3-5), herbivore–detritivore feeding behavior (TG5), preference for fast currents (CP3-4), and fluvial dependence (FD1) (Fig. 3d). This suite of traits is indicative of a periodic life-history strategy and is more likely to occur in watersheds with available canyon habitat and increased upstream distance from reservoirs (Fig. 3e). The upper right side of the ordination (positive CCA1 and CCA2 scores) is populated by watersheds characterized by species exhibiting small body size (MaxS1), early age at maturation (AM1), low parental care, (PC1), and short life span (Long1) (Fig. 3d): a suite of traits that generally define an opportunistic life-history strategy. These watersheds were characterized by increased variation in winter, spring, and summer precipitation (Fig. 3e). The lower right ordination space (positive CCA1 and negative CCA2 scores) represents fish faunas represented by biological traits describing moderate life span (Long2), high parental care (PC4), ecological traits describing preference for slow currents (CP1), and a lack of fluvial dependence for life-cycle completion (FD2) (Fig. 3d). These trait states are indicative of an equilibrium life-history strategy and were more likely to occur in watersheds with increased canal density, dam reservoir surface area and volume, greater annual air temperatures, and precipitation (Fig. 3e).

The amount of variation in functional composition explained by the environmental variables varied considerably less compared with patterns in taxonomic composition. Environmental factors described 38% and 37% of the variation in native and non-native community functional composition, respectively, where regional climate explained the greatest amount of variation followed by hydrologic alteration and watershed physiography – land use (Fig. 4b). Categorical differences in the variation explained in native and non-native composition was substantially smaller for functional attributes compared with taxonomy (Fig. 4a).

Discussion

Our study explored the patterns and environmental drivers of fish community composition and diversity in the highly modified Lower Colorado River Basin using a combined taxonomic and functional approach. Our results suggest that natural and human-related environmental factors have differentially shaped native and non-native fish communities at the watershed scale. Functional richness of native communities was greater in watersheds characterized by more variable winter and summer precipitation regimes and more stable spring precipitation conditions. The spawning chronology of native species throughout the arid Southwest, in large part, explains this pattern. Larval production for many native species typically peaks during spring runoff, where juvenile fish are believed to have optimal rearing conditions in less variable flow (Gido and Propst 1999; Brown and Ford 2002), and fluctuating summer flows provide juveniles access to critical backwater habitats (Minckley et al. 2003). In our study, seasonal precipitation variation was clearly linked to native communities' functional richness, indicating that natural flow regime variability (a direct result of over-

Fig. 4. Relative independent taxonomic and functional variation explained by hydrologic, land use, and climate variable groups, including subgroups of land use variables associated with human disturbance (land use human) and land use variables associated with natural and (or) protection status (land use protection). Solid bars represent native fishes; open bars represent non-native fishes. Results are presented as a percentage of the total variation explained.
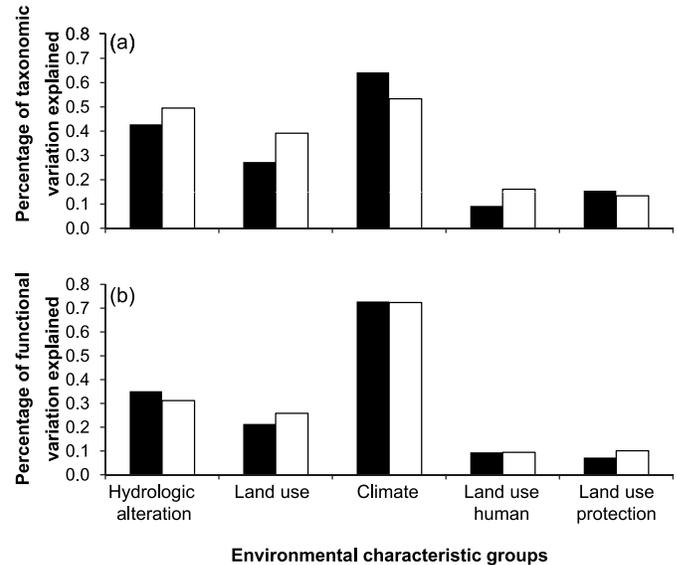
land flow caused by precipitation events) is an important part of the habitat template for native species and can be considered vital for sustaining native species trait diversity at the community scale. Interestingly, variables describing hydrologic alteration and fragmentation by dams were not strong predictors of native functional diversity despite the substantial evidence that dams decouple rivers from their typical seasonal flow patterns (Graf 1999) and negatively impact fluvial-dependent native fishes (Haxton and Findlay 2008). Our results may be related to the spatial grain (i.e., watershed) and numeric resolution (i.e., species presence–absence) of our analysis.

Life-history theory offers a promising path to understanding the patterns and processes by which fish community properties vary along environmental gradients (Winemiller 2005). By comparing trends in native and non-native species distributions among fish life-history strategies in the LCRB, Olden et al. (2006) postulated that century-long modifications in flow variability have likely promoted the spread of non-native equilibrium strategies (favored in constant environments) while leading to greater distributional declines of native species located along the periodic–opportunistic continuum (strategies favored in more unpredictable and variable environments). We explored this reasoning in our study by examining associations between the life-history composition of watersheds and both natural and anthropogenic descriptors of the riverine environments. Watersheds dominated by native opportunistic strategists were characterized by low dam density and seasonally variable precipitation, indicating that unregulated watersheds are indeed more likely to support more native-rich fish communities. These watersheds, particularly tributaries off the main stem Colorado River, which experience extreme seasonal droughts as

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well as intense overland flows in response to monsoonal rain events, have become rare in the highly dammed LCRB (Fradkin 1981). With a majority of native species possessing traits defining opportunistic–periodic life histories, maintaining natural flow variability as well as mitigating the impact of dams via water release based on natural flow patterns (environmental flows) may be paramount to maintaining the overall functional diversity of native communities. At a taxonomic level, Propst and Gido (2004) displayed that flow regimes mimicking natural conditions enhanced native fish recruitment in the semiarid San Juan River. Further work is needed to further elucidate how environmental flows released below dams may be able to assist with maintaining the functional diversity of native fish communities in desert rivers of the American Southwest (Haney et al. 2008; Shafroth et al. 2010).

The functional diversity of non-native communities was prominently explained by regional climate and surrogate measures of hydrologic variation associated with large dams. Our results suggest that watersheds with greater cumulative dam storage capacity and dam density support more functionally diverse communities of non-native fishes, a finding likely reflecting the creation of new niche opportunities for successful establishment (sensu Shea and Chesson 2002). These additional niche opportunities may be associated with both the formation of reservoirs above dams and the modification of downstream flow and thermal regimes. Lentic habitat was historically limited to wetlands and riverine backwaters in the LCRB (Minckley 1973; Carlson and Muth 1989), but today, over 400 large dams and countless small diversions support permanent standing bodies of water (Mueller and Marsh 2002). These novel water bodies provide habitat for many non-native species and are hypothesized to provide superior niche opportunities for the establishment and spread of invasive species (Havel et al. 2005; Johnson et al. 2008). In the LCRB, watersheds with relatively low numbers of dams contain non-native fishes with a narrower range of trait types, more closely resembling the functional breadth of native communities. By contrast, watersheds with higher dam densities support more functionally diverse non-native fish communities, accruing species with equilibrium-type traits that are favored in more stable long-term flow regimes that exist both above and below dams (Olden et al. 2006). Not surprisingly, equilibrium strategists were previously rare in this region given the historically variable hydrologic regime (Olden and Poff 2005). In summary, our results indicate that hydrologic alteration is not only creating niche opportunities expanding the total functional diversity of non-native fish communities, but that those niches are being primarily filled by non-native equilibrium strategist species that are continuing to expand their ranges within the LCRB.

Non-native species also tended to associate with human-altered watersheds characterized by high canal density, roads, agriculture, and urban development. Canal habitat is utilized by a number of non-native fishes for seasonal refuge during low flow periods and can promote the secondary spread of species by increasing landscape connectivity (May and Brown 2002; Cowley et al. 2007). Road construction and urban development have also been identified as having both short- and long-term effects on the physical and chem-

ical conditions in aquatic ecosystems (Angermeier et al. 2004; Wheeler et al. 2005). The ability of many non-native fish species to persist in these altered environments to a greater extent than native species may account for the association of non-native species in those areas. However, many of the land use variables did not significantly influence the functional diversity in our study, suggesting that hydrologic alteration may play a more critical role in shaping the fish communities.

A striking result of our study was that natural and human-related factors explained substantially more variation in functional trait composition compared with taxonomic composition of fish communities. This disparity is expected when species distributions are geographically more limited than the spatial scale of investigation. When multiple species have similar traits but have been historically separated resulting in unique distribution patterns, environmental variation may explain a greater percentage of functional composition variation than taxonomic composition. Our results complement the findings of Hoeinghaus et al. (2007), who found environmental factors explained greater variation in fish functional groups compared with taxonomic composition for major river basins of Texas, USA. Furthermore, although at the watershed level we found taxonomic and functional richness to be positively associated, we expect that functional metrics will more directly capture the mechanistic influence of environmental factors shaping fish community composition. Using species traits as a currency in future community ecology analysis will provide predictability and generality to results and should contribute to general ecological rules associated with competition, predation, and invasion (McGill et al. 2006; Olden et al. 2010).

In conclusion, the landscape factors governing the occurrence of native and non-native species within aquatic environments are inherently complex. A mosaic of anthropogenic landscape drivers interacting with the existing habitat variability appears to dictate the functional composition of fish communities, ultimately defining the species within rivers. With limited resources to invest in the conservation of native fauna and multiple threats simultaneously impacting LCRB biotas (Cowley 2006), effective management of imperiled species depends on determining the primary influences on fishes at a landscape scale. Growing anthropogenic pressures associated with human population growth in the arid Southwest of the United States (Paukert et al. 2010) support the development of multivariate models that provide mechanistic insight into the major drivers of fish community structure. Our results identified multiple landscape-scale environmental influences on fish community composition and diversity; however, hydrologic alteration factors (presence of dams and canals) and seasonally variable precipitation regimes were the most important drivers of fish communities' taxonomic and functional composition. Given that full flow restoration and (or) dam removal in the LCRB is highly unlikely, managing for both native and non-native fish communities may be the most realistic conservation strategy. The implementation of environmental flows to mimic the components of the natural hydrograph is one possible tool to achieve this goal (Valdez et al. 2001; Brown and Ford 2002; Propst et al. 2008). Without acknowledging the critical influence that hydrologic alteration has on fish

community composition, management activities such as mechanical removal of non-native species may have limited long-term success.

Acknowledgements

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Appendix A

Appendix A appears on the following pages.

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Table A1. Variables included in each candidate model describing functional diversity of LCRB watersheds.

		Hydrologic alteration					Land use and physiographic features		
Model	Candidate model	Dam density	Dam storage	Reservoir surface area	Canal habitat	Distance to down dam	Agriculture	Road density	Urban development
1	Global	1	1	1	1	1	1	1	1
2	Hydrologic disturbance	0	1	1	1	1	0	0	0
3	Land use #1	1	0	0	0	0	1	1	1
4	Land use #2	1	0	0	0	0	1	1	1
5	Land use #3	1	0	0	0	0	0	0	0
6	Climate	0	0	0	0	0	0	0	0
7	Climate precip.	0	0	0	0	0	0	0	0
8	Climate precip. CV	1	0	0	0	0	0	0	0
9	Climate temp.	0	0	0	0	0	0	0	0
10	Fragmentation	0	0	0	1	0	0	1	0
11	Natural	0	0	0	0	0	0	0	0
12	Human disturbance #1	0	1	1	1	1	1	1	1
13	Human disturbance #2	1	1	1	1	1	1	1	1
14	Moyle and Light 1996	1	1	0	1	0	1	0	1
15	Gido and Brown 1999 #1	0	1	0	0	0	0	0	0
16	Gido and Brown 1999 #2	0	1	1	0	0	0	0	0
17	Marchetti et al. 2004 #1	0	0	0	1	0	0	0	1
18	Marchetti et al. 2004 #2	1	0	0	1	0	0	0	1
19	Marchetti et al. 2004 #3	0	1	0	1	0	0	0	0
20	Propst et al. 2008	0	0	0	0	0	0	0	0
21	Light and Marchetti 2007	1	1	0	1	0	0	0	1
22	Propst and Gido 2004	0	0	0	0	0	0	0	0
23	Rinne and Miller 2006	1	1	0	0	0	0	0	0
24	Meador et al. 2003	0	0	0	0	0	1	0	1

Note: The number 1 indicates the environmental variable included in the model; 0 indicates the variable was not used in the model. Descriptions of *Native taxonomic richness was used in the non-native analysis and vice versa.

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Natural land	Protected land	Canyon habitat	Watershed area	Climate					Diversity
				Annual precipitation	Winter precipitation (CV)	Spring precipitation (CV)	Summer precipitation (CV)	Annual temperature	Taxonomic richness*
1	1	1	1	1	1	1	1	1	1
0	0	0	1	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0
1	1	0	1	0	0	0	0	0	0
0	0	0	1	1	1	1	1	1	0
0	0	0	1	1	1	1	1	0	0
0	0	0	1	0	1	1	1	0	0
0	0	0	1	0	0	0	0	1	0
0	0	0	1	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	0
0	0	0	1	0	0	0	0	0	0
0	1	0	1	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0	1
0	0	0	1	0	0	0	0	0	1
0	0	0	1	1	0	0	0	0	1
0	0	0	1	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	1
0	0	0	1	0	0	0	0	0	1
0	0	1	1	1	1	1	1	0	1
0	0	0	1	0	0	0	0	0	1
0	0	0	1	1	0	1	1	0	1
0	0	1	1	1	1	1	1	0	1
0	0	0	1	1	0	0	0	1	1

variables are in the Materials and methods section.