INTRODUCTION

Studying patterns of biological diversity has been the foundation of numerous ecological pursuits over the past two centuries (Andrewartha & Birch, 1954; Stauffer, 1957). Today, environmental degradation coupled with the widespread introduction of non-native species has made identifying the mechanisms that preserve or erode biodiversity a primary focus of biogeography research (Whittaker et al., 2005). Despite recent advances in this topic, there are still substantial gaps in our understanding of how plant and animal diversity varies between ecosystems (i.e. beta diversity) and along environmental gradients over time (i.e. species turnover) (Anderson et al., 2011). Additionally, our ability to maintain ecosystem functioning is hindered by our inability to predict how changes in species distributions may alter the patterns in

ABSTRACT

Aim The highly endemic fishes of the arid Southwest USA have been heavily impacted by human activities resulting in one of the most threatened fish faunas in the world. The aim of this study was to examine the patterns and drivers of taxonomic and functional beta diversity of freshwater fish in the Lower Colorado River Basin across the 20th century.

Location Lower Colorado River Basin (LCRB).

Methods The taxonomic and functional similarities of watersheds were quantified to identify patterns of biotic homogenization or differentiation over the period 1900–1999. Path analysis was used to identify the relative influence of dam density, urban land use, precipitation regimes and non-native species richness on observed changes in fish faunal composition.

Results The fish fauna of the LCRB has become increasingly homogenized, both taxonomically (1.1% based on $\beta_{\text{sim}}$ index) and functionally (6.2% based on Bray–Curtis index), over the 20th century. The rate of homogenization varied substantially; range declines of native species initially caused taxonomic differentiation (~7.9% in the 1960s), followed by marginal homogenization (observed in the 1990s) in response to an influx of non-native species introductions. By contrast, functional homogenization of the basin was evident considerably earlier (in the 1950s) because of the widespread introduction of non-native species sharing similar suites of biological traits. Path analysis revealed that both taxonomic and functional homogenization were positively related to the direct and indirect (facilitation by dams and urbanization) effects of non-native species richness.

Main conclusions Our study simultaneously examines rates of change in multiple dimensions of the homogenization process. For the endemic fish fauna of the LCRB, we found that the processes of taxonomic and functional homogenization are highly dynamic over time, varying both in terms of the magnitude and rate of change over the 20th century.

Keywords Beta diversity, biotic homogenization, functional diversity, native fishes, watershed conservation.
functional diversity (Condit et al., 2002; Harborne et al., 2006; Melo et al., 2009; Baselga, 2010). As non-native species continue to expand outside their historical ranges and the distributions of native species are simultaneously reduced, enhancing our knowledge of the patterns and drivers of beta diversity is paramount.

An area of growing interest in conservation biogeography is the study by which biotas increase their taxonomic, functional, or genetic similarity over time – called biotic homogenization (McKinney & Lockwood, 1999; Olden, 2006). This dynamic process depends on the identities of individual species being lost (e.g. native extirpation) and gained (e.g. non-native introduction) across locations over time, thus making biotic homogenization distinct from the wealth of studies focusing on patterns and drivers of regional species richness. In a landmark study, Rahel (2000) compared the similarity of regional (state) fish faunas in the United States between present-day and pre-European settlement periods and found that, on average, fish faunas have become more similar by 7.2%. Most striking was that 89 pairs of states with zero historical similarity (no species in common) shared, on average, over 25 species; this pattern was particularly pronounced in desert regions of the American Southwest. Recent studies have demonstrated that taxonomic homogenization is not an ecosystem or taxon-specific phenomenon, but occurs across a broad spectrum of plants and animals (e.g. McKinney, 2004; Rooney et al., 2004; Schwartz et al., 2006; La Sorte & McKinney, 2006; Qian & Guo, 2010; reviewed in Olden, 2006).

Previous studies have shed considerable insight into patterns of biotic homogenization, but three important knowledge gaps remain. First, research has primarily been limited to describing the magnitude and geography of change between historical and present-day composition of biotas, but the temporal dynamics of the process remain poorly understood (but see Clavero & García-Berthou, 2006; Spear & Chown, 2008; Taylor, 2010). Limited empirical evidence suggests that the initial consequence of non-native species introduction is to increase the distinctiveness of biotas (Scott & Helfman, 2001); however, a detailed investigation of the spatiotemporal patterns of biotic homogenization or differentiation is lacking. Second, studies to date have focused almost exclusively on changes in the taxonomic composition of biotas (reviewed in Olden et al., 2011), whereas aspects of functional or trait composition have received considerable less attention (but see Smart et al., 2006; Winter et al., 2008). Functional homogenization can occur when introduced species fill similar functional roles (e.g. ecological redundancy of traits into new geographical locations) or when native species with unique functional roles (e.g. trophic specialists) decline in range or abundance (McKinney & Lockwood, 1999; Olden & Rooney, 2006). The non-random selection of ‘winning’ and ‘losing’ trait strategies could result in the functional convergence of communities over time despite diverging taxonomies. Third, recent evidence points to human-induced homogenization of environmental regimes via urbanization, agricultural development, and river regulation by dams (Poff et al., 2007; Winter et al., 2008); yet, formal investigations into the mechanisms underlying this process are scarce (but see Olden et al., 2008).

The aim of our paper is to study the spatiotemporal patterns of taxonomic and functional homogenization of freshwater fish faunas in the Lower Colorado River Basin (LCRB; Fig. 1). The highly endemic fish fauna of this semi-arid basin (approximately three-quarters of the species occur only in the LCRB, Carlson & Muth, 1989) continues to be impacted by human activities that threaten native species persistence and promote the widespread introduction of non-native fishes (Minckley & Deacon, 1968; Olden & Poff, 2005; Rinne & Miller, 2006). Our study has two primary objectives. First, we test for taxonomic and functional homogenization of LCRB fish faunas over the last century and identify those species most responsible for changes in composition. As non-native species expand their range within a region and native species simultaneously experience range declines, we hypothesize a transition from differentiation to homogenization over time. Second, we assess the direct and indirect influence of landscape-scale factors (describing both natural and human created environments) and non-native species introductions on observed patterns of fish faunal homogenization. We expect that non-native species may directly contribute to homogenization, and factors such as increased dam density and urbanization may indirectly influence community similarity by affecting patterns of invasions and extirpations. We hypothesize that increased dam density and urbanization in a watershed will be positively associated with fish fauna homogenization (Olden et al., 2008). Our study is unique by providing the first simultaneous investigation of the spatiotemporal patterns and drivers of both taxonomic and functional homogenization.

METHODS

Study area and fish inventory

Our study examined distributional trends for 23 native species and 39 non-native species (Table S1) according to 1,413,904 fish records collected from 1900 to 1999 as part of the LCRB Aquatic Gap Analysis Project (Whittier et al., 2006). Following the methodology of Sowa et al. (2007), we divided the LCRB into 386 watersheds that ranged from 200 to 1600 km² in size; an effective size range to represent landscape heterogeneity influencing fish assemblages (Pool et al., 2010). A total of 73 watersheds fit our selection criteria by having sufficient sampling effort to capture changes in fish community composition over time (i.e. minimum of three sampling events for each time period and a minimum of 30 total sampling events from 1900 to 1999 for each watershed). Spatial and temporal heterogeneity of fish records existed in our dataset, as is common in studies examining community composition trends from compiled data bases (Brose et al., 2003). To account for the effect of spatial and temporal sampling biases in our study, fish records were summarized according to the following time periods: 1900–1959, 1960–1969, 1970–1979, 1980–1989 and 1990–1999; to derive representative species lists (see Olden & Poff, 2005 for additional rationale).
lists for each time period, we assumed that if a native species was recorded within a watershed in any time period, then it was also present in all earlier time periods. Conversely, if a non-native species was recorded within a watershed, we assumed it remained established in all subsequent time periods (sensu Fagan et al., 2005). A ‘historical’ time period was conservatively defined as all watershed occurrences of native species between 1900 and 1999.

We used a traits-based approach to test for functional homogenization (Olden & Rooney, 2006). We selected two ecological traits and six life-history traits (converted to categorical trait states as needed in parentheses) reflecting the ecological niche for each species within the LCRB. Unlike plants where the traits of a given species may be directly linked to their function (e.g. leaf area and photosynthetic rate), the measurable traits of fish species are often one step removed from the function performed within their environment. For example, animal body size is a universal trait correlated with growth rate, which in turn is associated with mortality rates, longevity, and reproductive output (Peters, 1983). Our ecological traits included the following: (1) water temperature preference defined as cold (10–17 °C), cool (18–26 °C), or warm water (> 26 °C) based on species distributions and perceived physiological optima, and (2) trophic guild defined as omnivore (approximately < 5% plant matter), invertivore, invertivore–piscivore, piscivore, herbivore–detritivore (approximately > 25% plant matter). Our life-history traits included the following: (1) maximum total body length categorized as 0–400 mm, 401–800 mm or > 800 mm; (2) age at maturation categorized as 0–1 years, 1.1–2 years, and > 2 years; (3) fecundity defined as total number of eggs or offspring per breeding season and categorized as 0–1000 or > 1000; (4) egg size defined as mean diameter of mature (fully yolked) ovarian oocytes and categorized as 0–1.49 mm, 1.5–3 mm or > 3 mm; (5) parental care defined as the total energetic contribution of parents to their offspring and categorized as none, low or high care (codes were 1, 2, ≥ 3 respectively following Winemiller’s (1989) 1 to 8 coding); and (6) reproductive guild categorized as bearers (internal), guarders

Figure 1 Map of the Lower Colorado River Basin displaying the major rivers and basin boundaries.
(nest spawners or substratum choosers), or non-guarders (brood hiders or open substratum spawners) following Balon (1975). Trait assignments were constructed utilizing comprehensive texts of state fish faunas, primary literature, state agency reports, university reports, and graduate theses (Olden et al., 2006) attempting to account for trait uncertainties by using categories.

Statistical analysis

Compositional similarity of fish faunas

Species presence/absence data were used to calculate taxonomic compositional similarity (CS) among watersheds across time periods based on the βsim index (Lennon et al., 2001). This index focuses on compositional differences by minimizing the influence of variation in species richness (Koleff et al., 2003). Similarity matrices were produced for each time period (e.g., historical, 1900–1959, 1960–1969, etc.), and the changes in pairwise βsim values were calculated as ΔCS = CShistorical – CS{time period of interest}. When the ΔCS value for a watershed is positive, it indicates biotic homogenization, whereas a negative value indicates basin differentiation (Olden & Rooney, 2006).

Our quantification of functional homogenization followed the same approach as above. We calculated a watershed-by-trait matrix by multiplying the watershed-by-species matrix and the species-by-trait matrix and dividing by watershed richness for each time period. The result is a watershed-by-trait matrix where each cell represents the relative proportion of species in each watershed exhibiting each trait state. The functional similarity for each watershed-by-trait matrix was calculated according to the Bray–Curtis index (CSbc), accommodating our continuous data in this portion of our analysis. Following the same approach we used for the taxonomic analysis, changes in pairwise functional compositions between watersheds for each time period were calculated. We tested for differences in watershed ΔCSbc and ΔCSsim (i.e., difference in community similarity between two time periods) using a Student’s one-sample t-test.

Species contributions associated with compositional changes over time were calculated by sequentially removing each species from the data matrix and repeating the aforesaid analysis. Calculating the change in ΔCS between these analyses identified individual species as having a homogenizing (positive values) or differentiating (negative values) influence on the community composition during each study period. All analyses were performed in R 2.51 (R Development Core Team, 2007).

Predictors of fish faunal change

We modelled taxonomic and functional ΔCS as a function of three variables that have been identified as important determinants of fish species occurrence in the LCRB (Pool et al., 2010). These variables included dam density (no/km²), urban development (% of total area), and mean annual precipitation (mm) from 1971 to 2000; calculated for the upstream contributing watershed. Dam density represents the effects of regulating river flow regimes, fragmentation of waterways, and the homogenization of flow conditions (Poff et al., 2007). Percent urban development represents the threat of short- and long-term ecological impacts of land-use conversion to impervious surfaces (Wheeler et al., 2005). Mean annual precipitation of a watershed is a principal component of local climate within watersheds that influences the magnitude of runoff and degree of habitat connectivity in intermittent and ephemeral rivers that dominate the LCRB (Propst et al., 2008). Data sources for these variables included the National Inventory of Dams (USEPA, 2006), National Land Cover Database (MRLC, 2001), and Climate Source (USDA-NRCS 2007). Non-native species richness within watersheds was also used as a variable in our models to assess the strength of the relationship between invasion and faunal homogenization.

We used path analysis – a special case of structural equation modelling – to examine the direct and indirect relationships between taxonomic and functional ΔCS and the factors described earlier (Mitchell, 1993; Shipley, 2000). Traditional statistical methods are unable to treat individual parameters as both independent and dependent within the same analysis when assessing the influence of multiple parameters in a model. Path analysis allows this type of model structure facilitating specific hypothesis testing, making it unique from multiple regression techniques.

We created three alternative path models for both our taxonomic and functional analysis. Each set of models consisted of a full model comparing the relative influence of our predictor variables (dam number, % urban land-use, and mean annual precipitation) and non-native species richness on the magnitude of the taxonomic and functional ΔCS. In addition, we examined two nested models from each full model to assess the relative importance of the direct and indirect effects of the predictor variables by constraining some model paths to zero and contrasting the model path values (see Light & Marchetti, 2007). No significant collinearity of our model variables were found with all variance inflation factors (VIF) values under 5 (Menard, 1995). Model chi-squares and associated P values were used to determine the goodness-of-fit of our models. This test quantified the fit of the path structure and the probability that the observed and expected correlation matrices differed by more than would be expected by chance (P-values greater than 0.05 indicate a good model). Our analysis was based on correlation matrices with all the path coefficients in the figures being standardized values. All of our model analysis was performed using R 2.51 utilizing the SEM library (R Development Core Team, 2007).

RESULTS

Spatiotemporal patterns in taxonomic and functional homogenization

Fish faunas of the LCRB have become taxonomically homogenized, albeit slightly, over the 20th century increasing from a mean historical similarity among watersheds of 30.8% to the
present-day 31.9%. By contrast, the basin showed considerable functionally homogenization, increasing 6.2% from a mean historical similarity among watersheds of 45.2% to the present-day 51.4%. Although taxonomic and functional homogenization was the general pattern for the entire basin, compositional changes of individual watersheds were much more spatially variable. For example, higher than average homogenization was evident for watersheds in the geographically distant Virgin (n = 7 watersheds) and Gila (n = 8 watersheds) river basins (Fig. 1). Historically, these basins had only 4 native species in common (Catostomus clarkii, desert sucker; Catostomus latipinnis, flannelmouth sucker; Agosia chrysogaster, longfin dace; Rhinichthys osculus, speckled dace), but currently they share twenty species (four native and sixteen non-native species).

The LCRB witnessed a dynamic change in the both the taxonomic and functional composition of its watersheds throughout our study time period. Taxonomic similarity among watersheds with their historic faunal compositions initially decreased by as much as 7.9% in the 1960s (i.e. differentiation), followed by a 1.1% increase in the 1990s (Fig. 2; 1950: \( t_2 = 10.12, P < 0.001 \); 1960 \( t_2 = 41.51, P < 0.001 \); 1970 \( t_2 = 40.11, P < 0.001 \); 1980 \( t_2 = 3.32, P < 0.001 \); 1990 \( t_2 = 0.57, P = 0.57 \)). Native species such as speckled dace and desert sucker were most responsible for changes in watershed similarity historically, but by the end of the 1990s, the non-native Lepomis cyanellus (green sunfish), Pimephales promelas (fathead minnow), and Cyprinus carpio (common carp) were the most influential species driving a transition from taxonomic differentiation to homogenization (Table 1).

Despite the fact that the majority of non-native species were present by the end of the 1960s (36 out of 39 species), taxonomic homogenization within the basin did not occur for another three decades, reflecting the considerable time course over which these species spread throughout the basin. In contrast to patterns in taxonomy, functional homogenization was evident as early as the 1960s and continued to gradually increase to 6.2% by the turn of the century (Fig. 2; 1950: \( t_2 = -6.58, P < 0.001 \); 1960 \( t_2 = -4.17, P < 0.001 \); 1970 \( t_2 = -5.08, P < 0.001 \); 1980 \( t_2 = -4.65, P < 0.001 \); 1990 \( t_2 = -5.06, P < 0.001 \)). The same native and non-native species that played prominent roles in driving taxonomic homogenization also shaped the functional homogenization of fish faunas; native species accounted for initial watershed faunal similarity followed by non-native species driving faunal similarity by the end of the 1990s (Table 1).

Changes in taxonomic and functional similarity were positively correlated across all time periods, with the majority of watersheds becoming increasingly homogenized by the end of the 1990s (Fig. 3). An initially weak relationship between taxonomic and functional homogenization of fish faunas became progressively stronger with each decade. In the 1950s, most watersheds were taxonomically differentiating while functionally homogenizing (67 of 73 watersheds), but by the 1990s, almost half of watersheds exhibited both forms of homogenization (31 of 73 watersheds; Fig. 3).

### Predictors of fish faunal change over time

The best fitting models for both taxonomic (\( \chi^2 = 5.72, \text{d.f.} = 6, P = 0.45 \)) and functional (\( \chi^2 = 4.48, \text{d.f.} = 6, P = 0.61 \)) \( \Delta CS \) revealed a positive direct effect of non-native species richness on fish faunal similarity, whereas dam number and urbanization showed minimal direct effects but strong indirect effects (Fig. 4). The full models incorporating direct paths between all variables were also supported (Taxonomic \( \chi^2 = 4.67, \text{d.f.} = 4, P = 0.32 \); Functional \( \chi^2 = 3.35, \text{d.f.} = 4, P = 0.50 \); Fig. S1). A reduced model excluding a linkage between non-native species richness and \( \Delta CS \) performed poorly (taxonomic \( \chi^2 = 20.34, \text{d.f.} = 5, P < 0.01 \); functional \( \chi^2 = 29.19, \text{d.f.} = 5, P < 0.01 \); Fig. S1). Dam number and mean annual precipitation were significantly correlated with non-native species richness in all models, indicating that their potential role in driving faunal homogenization is likely to be indirect.

### DISCUSSION

In the present study, we quantified both patterns and drivers of changes in the taxonomic and functional composition of an endemic fish fauna. We found that fish assemblages of the LCRB have become homogenized over the 20th century in terms of taxonomy (species composition) and function (trait composition); however, the rate and magnitude of change varied substantially as have the roles of the native and non-native species driving those processes. Notably, changes in species composition resulted in taxonomic differentiation decades preceding the eventual marginal homogenization of the fish fauna. Declining native species distributions in the middle of the century primarily drove the initial changes in faunal similarity, for example speckled dace historically occurred in 83% of our study watersheds but experienced a range decline of 34% by the end of the 1960s. The introduction and proliferation of non-native species mid-century continued into the present day, thus playing an increased role in promoting basin homogenization. For example, non-native

![Figure 2](https://example.com/figure2.png) Changes in mean pairwise similarity among watersheds for each time period. The bars represent the mean change in taxonomic (grey) and functional (white) similarity of watersheds, with negative values representing overall basin differentiation and positive values representing basin homogenization.

Figure 2
fathead minnow was first introduced in the early 1950s (Olden & Poff, 2005) and spread into 65% of our study watersheds by the end of the century. In a study of the Iberian Peninsula fish faunas, Clavero & García-Berthou (2006) found a comparable temporal transition in community similarity with initial differentiation followed by a homogenization in fish species composition. Our results indicate that fish faunal change is highly dynamic and can transition between periods of differentiation and homogenization depending on the time period of investigation and the relative contributions of native species loss and non-native species gain. As we look to the future of the LCRB, if non-native species continue to spread and native species ranges decline, we expect continued taxonomic homogenization of fish faunas unless considerable conservation action is taken to reverse this trend.

Functional homogenization of regional diversity can result in both ecological and evolutionary consequences, including a reduction of ecosystem resistance to environmental change (Olden et al., 2004), simplification of food web structure (Beisner et al., 2003), and an increased potential for further non-native species invasion (Grosholz & Tilman, 2005). In the LCRB, we found that fish faunas were functionally homogenized to a greater extent than the taxonomic composition even in areas where native taxonomic richness had not significantly changed during the 20th century. The functional homogenization of fishes occurred by mid-century when the basin was taxonomically differentiating in part because of the widespread introduction of non-native species such as sunfishes (Family: Centrarchidae). The diverse array of sunfishes that accounted for taxonomic differentiation within the basin (i.e. green sunfish; bluegill; Micropterus salmoides, largemouth bass) also shared suites of traits (Olden et al., 2006) that led to the simultaneous functional homogenization of fish faunas. Many of those non-native species

<table>
<thead>
<tr>
<th>Taxonomic Status</th>
<th>Mean species importance (%)</th>
<th>Functional Status</th>
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Scientific names for species are provided in Table S1.

**Table 1** The mean contribution of the top five species (native and non-native) to the homogenization of the Lower Colorado River Basin by decade.
were introduced to the LCRB to promote recreational fishing and subsequently spread to become widely distributed throughout the basin. Similarly, Smart et al. (2006) found that plant functional composition in Britain increased over a 20-year period, while taxonomic similarity concurrently declined. Some of the non-native species introduced into the LCRB were also functionally redundant with native species occupying the basin (Olden et al., 2006). The non-native Gambusia affinis (western mosquitofish), possessing traits similar to that of the native Poeciliopsis occidentalis (Gila topminnow), established in many areas that historically did not support the native topminnow, further increasing the functional similarity between formerly distinct faunas. Interestingly, by the end of the 1990s, the widespread establishment of a few functionally distinct non-native species (fathead minnow, common carp, and green sunfish) played the dominate roles in driving both the taxonomic and functional homogenization of the basin.

The link between taxonomic and functional fish homogenization has proven to be temporally dynamic, but several clear trends emerged from our analysis. Despite the weak association between taxonomic and functional community similarity in the 1950s and 1960s, by the end of our study we found that the majority of watersheds exhibiting taxonomic homogenization were similarly homogenized in terms of their trait composition. This relationship suggests that correlated patterns of taxonomic and functional homogenization may become increasingly predictable over time. A recent study by Baiser & Lockwood (2011) used simulated data to show that an increasing ratio of trait states to species richness strengthened the correlation between the taxonomic and functional similarity of bird assemblages in the USA. These findings support our results; in that, the weak relationship between fish taxonomic and functional similarity in the early time periods may have been driven by the trait redundancy associated with introduced sport fishes within the basin. The introduction and proliferation of

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**Figure 3** Bivariate relationship between $\Delta C_{SBC}$ and $\Delta C_{Sim}$ compositional similarity of individual watersheds between historical and intermediate time periods. Each quadrant represents a different combination of taxonomic and functional change of each watershed’s fish fauna (a). Each intermediate time period is represented by watersheds mean change in similarity with each watershed’s historical watershed compositions (b–f).
cannot be compared between two non-hierarchical models such as fish faunas. The values near each path are the standardized coefficients indicating that non-native species play a role in changes in fish composition across the USA and found comparable results indicating that non-native species play a dominating role in the homogenization of fish faunas at a large spatial scale. Prior research also suggests that dams in the LCRB promote non-native species by altering downstream river flows (Propst & Gido 2004; Propst et al., 2008) and by supporting enriched non-native communities in impounded reservoirs (Johnson et al., 2008). The work of Olden et al. (2008) similarly identified a suite of human disturbance factors, including dams, as drivers of fish faunal homogenization in Australian drainages. Non-native species may also contribute directly to fish faunal homogenization by spreading throughout the basin predating on and competing with native fishes (Carpenter & Mueller, 2008). While our analysis identified non-native species richness and dam density as important drivers of fish faunal homogenization in the LCRB, further work incorporating additional ecological threats (Paukert et al., 2011) may facilitate a better understanding of the full scope of factors influencing the homogenization process.

Understanding the patterns and drivers of species turnover in a rapidly changing environment is important for conservation and restoration efforts (Whittaker et al., 2005; Hobbs et al., 2006). Our study highlights the dynamic nature of the homogenization process by showing that the rate of fish compositional change may vary over long time-scales. Recognition that the taxonomic and functional homogenization of faunas may be linked but are not synonymous with each other, particularly for areas in the early stages of environmental change and species invasion, emphasizes the need to focus on both taxonomic diversity and ecosystem functioning as conservation priorities (McGill et al., 2006). While a majority of studies to date have identified low levels of taxonomic homogenization within faunas, we have shown that significant changes in community structure can occur at time steps typically not captured in historic to contemporary faunal comparisons. Furthermore, if freshwater environments continue to be altered in ways that favour the spread of non-native species and hinder endemic native species, additional homogenization of regional biotas should be expected. Although the specific conservation implications of biotic homogenization are still emerging (Rooney et al., 2007), we believe that managing for native species that are highly imperilled and functionally distinct should be prioritized in addition to the protection of watersheds that are minimally invaded (Strecker et al., in press). Future studies that identify prioritization areas that may mitigate the homogenizing effect of non-native species are also needed to curtail further simplification of ecosystems.

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Path diagrams displaying the full model (a), the nested passenger model (b) and the nested driver model (c).

**Table S1** Native ($n=21$) and non-native ($n=36$) fish in the Lower Colorado River Basin that were examined in our study.

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