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Desertification, salinization, and biotic homogenization in a dryland river ecosystem

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HIGHLIGHTS

- Hydrologic/biotic trends and their association were examined in a desert river.
- Decreased tributary flow led to decreased flow and increased salinity downstream.
- This spatially uneven hydrologic change caused region-wide habitat homogenization.
- Habitat homogenization led to biotic homogenization via changes in native fishes.
- Salinization as habitat driver of biotic homogenization is novel finding.

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ABSTRACT

This study determined long-term changes in fish assemblages, river discharge, salinity, and local precipitation, and examined hydrological drivers of biotic homogenization in a dryland river ecosystem, the Trans-Pecos region of the Rio Grande/Rio Bravo del Norte (USA/Mexico). Historical (1977–1989) and current (2010–2011) fish assemblages were analyzed by rarefaction analysis (species richness), nonmetric multidimensional scaling (composition/variability), multiresponse permutation procedures (composition), and paired *t*-test (variability). Trends in hydrological conditions (1970s–2010s) were examined by Kendall tau and quantile regression, and associations between streamflow and specific conductance (salinity) by generalized linear models. Since the 1970s, species richness and variability of fish assemblages decreased in the Rio Grande below the confluence with the Rio Conchos (Mexico), a major tributary, but not above it. There was increased representation of lower-flow/higher-salinity tolerant species, thus making fish communities below the confluence taxonomically and functionally more homogeneous to those above it. Unlike findings elsewhere, this biotic homogenization was due primarily to changes in the relative abundances of native species. While Rio Conchos discharge was > 2-fold higher than Rio Grande discharge above their confluence, Rio Conchos discharge decreased during the study period causing Rio Grande discharge below the confluence to also decrease. Rio Conchos salinity is lower than Rio Grande salinity above their confluence and, as Rio Conchos discharge decreased, it caused Rio Grande salinity below the confluence to increase (reduced dilution). Trends in discharge did not correspond to trends in precipitation except at extreme-high (90th quantile) levels. In conclusion, decreasing discharge from the Rio Conchos has led to decreasing flow and increasing salinity in the Rio Grande below the confluence. This spatially uneven desertification and salinization of the Rio Grande has in turn led to a region-wide homogenization of hydrological conditions and of taxonomic and functional attributes of fish assemblages.

1. Introduction

Changes in hydrological conditions and other habitat alterations caused by anthropogenic activities and the effects of these changes on native aquatic biotas are primary concerns in river ecosystems worldwide (Bailey et al., 2006; Kingsford et al., 2006; Pool and Olden, 2012). The effects could be direct, by impacting the ability of resident species to survive, migrate or reproduce in their native ranges (Kingsford et al., 2006; Cañedo-Argüelles et al., 2013) or indirect, by facilitating the establishment of non-native species (Kingsford et al., 2006; Olden, 2006; Lee et al., 2013) including harmful algae (Paerl and Paul, 2012; Patiño et al., 2014). Environmental drivers of biotic change (e.g., biotic homogenization), however, are not well understood

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(Olden, 2006; Pool and Olden, 2012). In particular, while secondary (anthropogenic) salinization is considered to be among the largest threats to river ecosystems worldwide, its impacts and management remain relatively understudied (Bailey et al., 2006).

Biotic homogenization is the process whereby the introduction of cosmopolitan (generalist) species coupled with extirpation of endemic species increases the genetic, taxonomic, or functional similarities of regional biotas (McKinney and Lockwood, 1999; Olden and Rooney, 2006; Rahel, 2010). Because individual species within a community typically vary in their tolerance limits to environmental variables (Linam and Kleinsasser, 1998), changes in hydrological conditions, such as flow and salinity, can directly affect change in fish assemblages. While flow (Rahel, 2010; Taylor, 2010) and broader watershed drivers of biotic change (Olden, 2006; Olden et al., 2008, 2010; Winter et al., 2008; Rahel, 2010) have been previously addressed, the influence of salinization has been largely – if not completely – ignored in studies of biotic homogenization.

The Trans-Pecos region of the Rio Grande/Rio Bravo del Norte (USA-Mexico international border) offers a unique opportunity to explore and improve our understanding of long-term changes and associations between hydrologic and biotic variables, especially in dryland river ecosystems. This region has historical information available for retrospective analyses of fish assemblages and of relevant hydrological variables such as water quality (salinity), river discharge, and precipitation. In addition, a comprehensive characterization of fish faunas of the region was conducted in the 1970s (Hubbs et al., 1977), which provides a valuable reference point for assessments of later biotic change caused by continuing anthropogenic pressures to the ecosystem. The study of fish faunas found that regional variation in salinity was a prominent factor associated with the distribution of fish assemblages. Namely, in the 1970s, fish assemblages were classified into three groups: a saline Rio Grande fauna above the confluence with the Rio Conchos (major tributary), a Rio Conchos–Rio Grande fauna below the confluence, and a tributary creek fauna, also downstream of the confluence (Hubbs et al., 1977).

Several post-1970s studies provided general information about fish faunas of the Trans-Pecos region (Bestgen and Platania, 1988; Edwards et al., 2002; Calamusso et al., 2005; Garrett and Edwards, 2014), and some also qualitatively described changes (declines) in river discharge below the confluence with the Rio Conchos (Garrett and Edwards, 2014). These studies, however, did not subject their data to quantitative analysis and did not address the role that changes in stream salinity (e.g., due to changes in flow below confluence) may play in affecting fish assemblages. The specific objectives of the present study thus were to quantitatively determine post-1970s change in fish assemblages, river discharge, salinity, and local precipitation, and to examine associations between hydrologic and biotic changes. The working hypothesis was that spatially uneven changes (below/above the Rio Conchos confluence) in hydrological conditions would lead to spatially uneven changes in fish faunas, and to region-wide habitat and biotic homogenizations. To our knowledge, this study is the first to address the interaction of salinity and flow regime, and its influence on the process of homogenization of freshwater habitats and biota.

2. Materials and methods

2.1. Study area

The Trans-Pecos region of the Rio Grande/Rio Bravo del Norte (Rio Grande) is situated in the northern part of the Chihuahuan Desert and defines a >1000-km segment of border between Mexico and the USA (Fig. 1). From El Paso (Texas, USA) to the confluence with the Rio Conchos (Chihuahua, Mexico), its main tributary in the region, anthropogenic degradation of the river and its watersheds over the last century transformed the river into a channelized, shallow, heavily silted stream with relatively slow and saline flow that is often dry during periods of drought (Hubbs et al., 1977; Everitt, 1993; Edwards et al., 2002; Schmidt et al., 2003; Calamusso et al., 2005). Discharge from the Rio Conchos markedly changes the habitat characteristics of the Rio Grande. From the Rio Conchos confluence to Amistad Reservoir ("Big Bend area"), the Rio Grande has relatively deeper runs and larger substrate, is of lower salinity (Bestgen and Platania, 1988), and provides refugia to native fish faunas (Platania, 1990). The Rio Grande in the Big Bend area also receives discharge from a series of intermittent tributaries, which serve as important spawning and nursery grounds for several native fishes (Hubbs and Wauer, 1973; Miyazono and Taylor, 2013a).

According to Hubbs et al. (1977), the saline Rio Grande fish fauna upstream of the confluence with the Rio Conchos is represented by native as well as non-native, salt-tolerant fishes (e.g., *Dorosoma cepedianum*, *Cyprinus carpio*, and *Cyprinella lutrensis*), the Rio Conchos–Rio Grande fauna by south Texas and Mexican species (e.g., *Notropis jemezanus*, *Notropis braytoni*, and *Rhinichthys cataractae*), and the tributary creek fauna by Chihuahuan fish species (e.g., *Notropis chihuahua*). The importance of the Big Bend area to the conservation of native faunas and floras of the Rio Grande Basin is highlighted by the presence of multiple national and state parks and protected areas on both sides of the international border (Raines et al., 2012; Garrett and Edwards, 2014). However, anthropogenic stressors on the hydrology of the area remain important concerns (Schmidt et al., 2003; Calamusso et al., 2005).

2.2. Data sources

Fish information for this study was grouped into current (2010–2011) and historical (1977–1989) data. Current data were obtained from various sources including Miyazono and Taylor (2013a) (sites 7–9 and 11, total 9 samples), Edwards (2013) (sites 10 and 12–20, total 10 samples) (Fig. 1; Table 1), and by new sampling of the mainstem (sites 1–6, total 6 samplings) (Fig. 1; Table 1). New sampling was conducted from 16 March to 2 April in 2011. Samples were collected with a seine (4.2 m × 1.7 m, 5 mm mesh) for 35–45 min per site. All available habitat types (i.e., riffles, pools, and runs) were sampled within a stream reach. Fish > 25-cm total length were identified, counted, and returned to the water. Smaller individuals were fixed in 10% formalin and brought to the laboratory for identification, and preserved in 50% ethanol. All fish collections were deposited into the Texas Natural History Collection. Historical fish assemblage data were gathered from Hubbs et al. (1977) (sites 1–7, 10, and 12–20, total 17 samples), Bestgen and Platania (1988) (sites 1–3 and 5–10, total 9 samples), and Linam et al. (2002) (sites 8 and 11, total 2 samples) (Fig. 1; Table 1).

Water quality monitoring sites, flow gages, and weather stations within the Trans-Pecos region with a similar period of record to the fish assemblage data were selected for analyses (Fig. 1; Table 2). Specific conductance data (1970s–2011) were obtained from 6 monitoring sites in the area (Texas Commission on Environmental Quality; http://www80.tceq.texas.gov/SwqmisPublic/public/default.htm), river discharge data (1977–2011) from 10 selected gage stations (International Boundary and Water Commission, http://www.ibwc.state.gov/), and precipitation data (1977–2011) from 10 selected weather stations (National Climatic Data Center; http://www.ncdc.noaa.gov/).

2.3. Statistical analyses

Multiresponse permutation procedures (MRPPs) with the Sorensen distance measure were used to examine differences between the historical fish assemblage data in 1977 and 1988–1989; MRPP is a nonparametric procedure that examines group differences (McCune and Grace, 2002). This preliminary analysis was done to determine whether the two historical datasets, collected 10 years apart, could be combined for comparisons against current data.

Fish sampling sites were classified into five geographic groups according to the following criteria: all sites (region-wide), mainstem

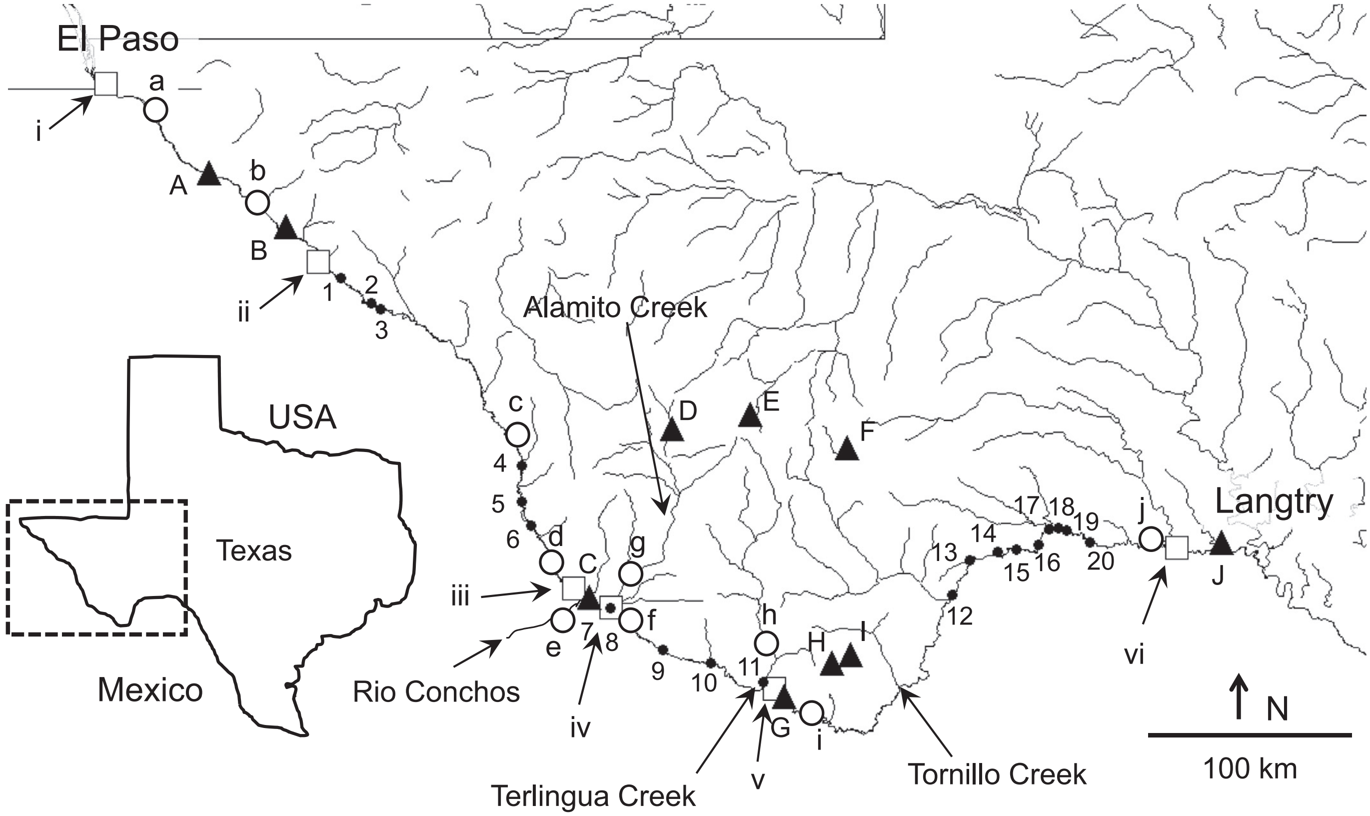

Fig. 1. Location of water quality monitoring station (empty squares with roman numerals), weather stations (solid triangles with large letters), river discharge gages (empty circles with small letters) and fish sampling sites (solid circles with Arabic numerals) in the Trans-Pecos region in Texas, USA.

above the confluence with Rio Conchos, mainstem below the confluence (Big Bend area), Alamito Creek (tributary below the confluence), and Terlingua Creek (tributary below the confluence). Changes in species richness between historical and current fish assemblages were assessed with rarefaction analysis using EcoSim700 (Gotelli and Entsminger, 2001). Rarefaction analysis standardizes species richness to account for differences in species abundances among compared samples (Gotelli and Graves, 1996). Monte Carlo procedures were used to draw 5000 random samples at specified abundance levels permitting 95% confidence intervals to be calculated.

Fish assemblage data were ordinated with nonmetric multidimensional scaling (NMS) to assess the long-term changes. This procedure evaluates the similarities in species and environmental space by using a rank distance measure, and it is not severely affected by zero-truncation problems and nonlinearity (McCune and Grace, 2002). Multiresponse permutation procedures were used to determine

Table 1
Study sites, sampling periods, and references for fish assemblage data in the Trans-Pecos region in Texas, USA. Availability of data for particular sites at particular periods is indicated by an X.

Site	1977	1988–1989	2010–2011	Reference
1	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988); this study
2	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988); this study
3	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988); this study
4	X		X	Hubbs et al. (1977); this study
5	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988); this study
6	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988); this study
7	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988), Miyazono and Taylor (2013a)
8	X	X	X	Hubbs et al. (1977), Bestgen and Platania (1988), Linam et al. (2002), Miyazono and Taylor (2013a)
9		X	X	Bestgen and Platania (1988), Miyazono and Taylor (2013a)
10		X	X	Bestgen and Platania (1988), Edwards (2013)
11		X	X	Linam et al. (2002), Miyazono and Taylor (2013a)
12	X		X	Hubbs et al. (1977), Edwards (2013)
13	X		X	Hubbs et al. (1977), Edwards (2013)
14	X		X	Hubbs et al. (1977), Edwards (2013)
15	X		X	Hubbs et al. (1977), Edwards (2013)
16	X		X	Hubbs et al. (1977), Edwards (2013)
17	X		X	Hubbs et al. (1977), Edwards (2013)
18	X		X	Hubbs et al. (1977), Edwards (2013)
19	X		X	Hubbs et al. (1977), Edwards (2013)
20	X		X	Hubbs et al. (1977), Edwards (2013)

Table 2
Study site information for specific conductance, river discharge, and precipitation in the Trans-Pecos region in Texas, USA.

Site	Variable	No.	Period of record	Location
i	Specific conductance	13272	1972–2013	The Rio Grande at Courchesne Bridge
ii	Specific conductance	13232	1987–2010	The Rio Grande at Neely Canyon
iii	Specific conductance	13230	1977–2013	The Rio Grande above the Rio Conchos
iv	Specific conductance	13229	1972–2013	The Rio Grande below the Rio Conchos
v	Specific conductance	13228	1974–2013	The Rio Grande at Santa Elena Canyon
vi	Specific conductance	13223	1972–2013	The Rio Grande at Foster Ranch
a	River discharge	08-3650.00	1977–2011	The Rio Grande below American Dam at El Paso
b	River discharge	08-3705.00	1977–2011	The Rio Grande at Fort Quitman
c	River discharge	08-3712.00	1977–2011	The Rio Grande near Candelaria
d	River discharge	08-3715.00	1977–2011	The Rio Grande above the Rio Conchos near Presidio
e	River discharge	08-3730.00	1977–2011	The Rio Conchos near Ojinaga
f	River discharge	08-3742.00	1977–2011	The Rio Grande below Rio Conchos near Presidio
g	River discharge	08-3740.00	1977–2011	Alamito Creek near Presidio
h	River discharge	08-3745.00	1977–2011	Terlingua Creek near Terlingua
i	River discharge	08-3750.00	1977–2011	The Rio Grande at Johnson Ranch near Castolon
j	River discharge	08-3772.00	1977–2011	The Rio Grande at Foster Ranch near Langtry
A	Precipitation	419088	1981–2011	Tornillo
B	Precipitation	413266	1977–2011	Fort Hancock
C	Precipitation	417262	1977–2011	Presidio
D	Precipitation	415596	1977–2009	Marfa
E	Precipitation	410174	1977–2011	Alpine
F	Precipitation	415579	1977–2011	Marathon
G	Precipitation	411524	1980–2011	Castolon
H	Precipitation	411715	1977–2011	Chisos Basin
I	Precipitation	416792	1977–2011	Panther Junction
J	Precipitation	415048	1977–2011	Langtry

whether the observed fish assemblage dissimilarities for the two time periods (1977–1989 vs. 2010–2011) were statistically significant. Spatial variability in fish assemblages was assessed by calculating pairwise Bray–Curtis distances for each period and then tested for mean differences with a paired *t*-test. Fish relative abundance data normalized with the arcsine square root transformation were used for NMS, MRPP, and paired *t*-test. PC-ORD version 6 (McCune and Mefford, 1999) was used to perform NMS and MRPP, and statistical program R, Version 3.01 (R Development Core Team 2013) was used to perform a paired *t*-test.

Data for specific conductance (a function of salinity) were relatively sparse and not always uniformly distributed within the calendar year; thus, trend analysis for salinity was based on annual median values using Kendall tau (Helsel and Hirsch, 2002) and Sen slopes (Sen, 1968). Kendall tau evaluates the strength and direction of the monotonic relation between environmental variables and time, and the Sen slope is an estimate of the (annual) rate of change over the period of record. Data density for discharge and precipitation was relatively high, allowing the use of quantile regression for analysis of trends. Quantile regression can be used to estimate trends not only in medians but also in extreme values (Koenker and Bassett, 1978). Daily mean discharge for each selected river gage and monthly cumulative precipitation for each selected weather station were grouped by year and used to estimate long-term trends in median (50th quantile) and extreme quantiles (10th and 90th quantiles). The slope of the regression lines for each quantile is the estimate of its (annual) rate of change over the study period. These analyses were performed in statistical program R, Version 3.01 (R Development Core Team, 2013) using the Kendall 2.2 package (McLeod, 2011), the zyp 0.10-1 package (Bronaugh and Werner, 2013), and the quantreg 5.05 package (Koenker et al., 2013).

Serial correlation is common in hydrological data and may result in underestimation of the variance of correlation coefficients, although estimates of the coefficients remain unbiased (Helsel and Hirsch, 2002). This problem can be addressed by including autoregressive (AR) errors in regression models (Helsel and Hirsch, 2002). Generalized linear models with AR terms (AUTOREG procedure, SAS version 9.3; SAS Institute, Cary, NC, USA) were used to confirm and more closely examine selected associations suggested by results of trend analysis.

3. Results

3.1. Changes in fish assemblages

There were no significant differences in the historical fish assemblage data of 1977 and 1988–1989 (MRPP: $T = 0.76$, $p = 0.45$), and they were combined for comparison against current data.

When data from all sites were combined (region-wide) for analysis, results of rarefaction analyses indicated that the species richness of current fish assemblages was significantly lower than that of historical fish assemblages as indicated by the clear separation of the curves (Fig. 2). When the analysis was conducted on each geographic subgroup separately, however, two patterns emerged. Species richness of current fish assemblages at the Rio Grande below the confluence with the Rio Conchos (Fig. 3B) and at Alamito Creek (Fig. 3C) was still clearly lower than their respective historical fish assemblages. For the Rio Grande above the confluence (Fig. 3A) and Terlingua Creek (Fig. 3D), however, the two rarefaction curves overlapped considerably suggesting that the species richness at these sites did not differ significantly between the

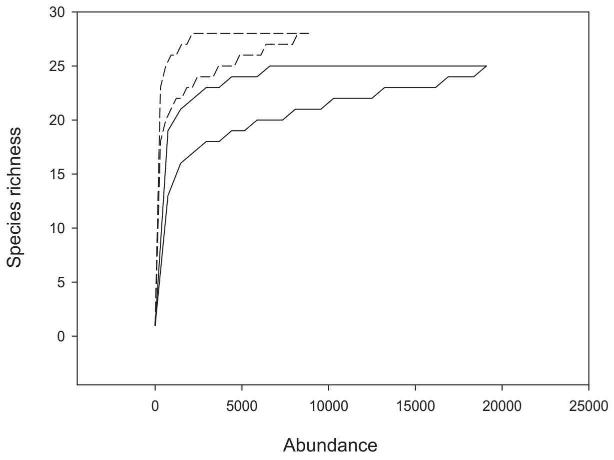

Fig. 2. Rarefaction curves (95% confidence interval) of species richness for fish assemblages at all study sites combined (broken line: historical data; solid line: current data).

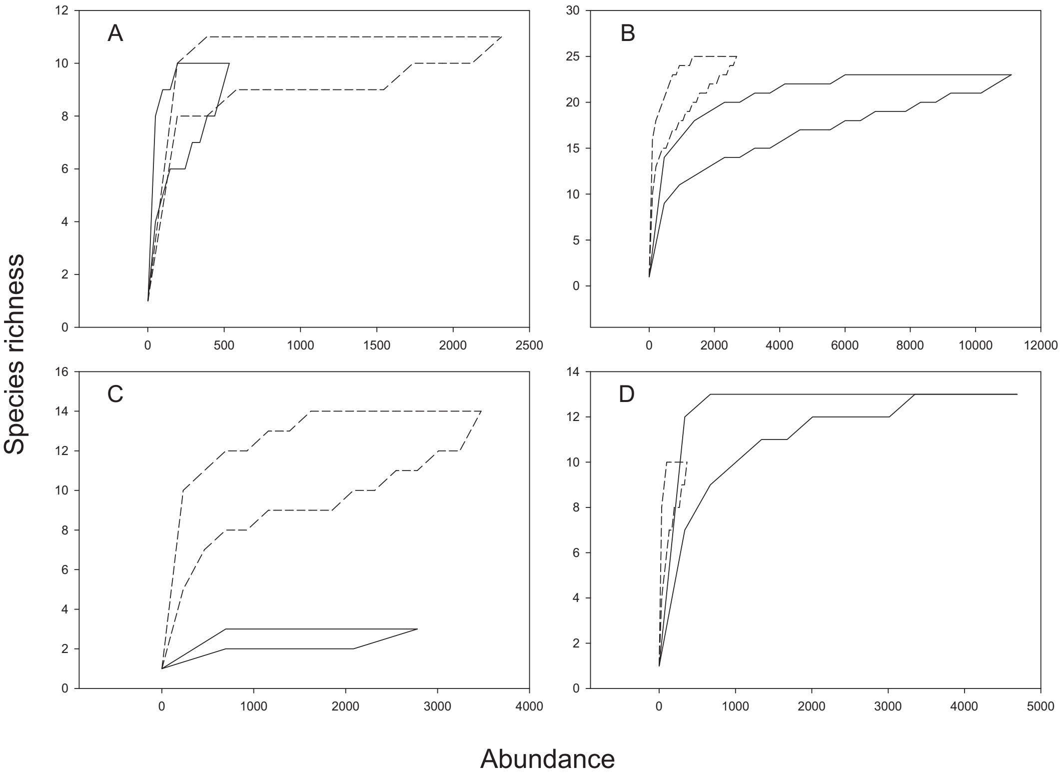

Fig. 3. Rarefaction curves (95% confidence interval) of species richness (broken line: historical data; solid line: current data) for fish assemblages at the Rio Grande above (A) or below (B) the confluence with Rio Conchos, Alamito Creek (C), and Terlingua Creek (D).

two time periods. [Although results for Terlingua Creek were somewhat ambiguous, the shape and direction of the curves appeared to leave little room for separation (Fig. 3D).]

Results of region-wide analysis suggested that fish assemblage compositions were different between the two study periods (MRPP: $T = -8.46$, $p < 0.0001$). In addition, region-wide spatial variability in historical fish assemblages (mean Bray–Curtis distance: 0.68) was significantly higher ($T = 10.13$, $p < 0.0001$) than in current fish assemblages (mean Bray–Curtis distance: 0.53). However, result of NMS indicated that by far the largest change in fish assemblage composition and variability occurred in the Big Bend area (Fig. 4). The NMS produced a three-dimensional solution for the samples (axis 1: 48.3%; axis 2: 22.7%; axis 3: 15.5%, stress: 11.9). Axis 1 was positively correlated with *C. lutrensis* ($r = 0.52$) and *Gambusia affinis* ($r = 0.54$) and negatively correlated with *N. jemezanus* ($r = -0.79$), *Macrhybopsis aestivalis* ($r = -0.79$) and *R. cataractae* ($r = -0.86$). Axis 2 was positively

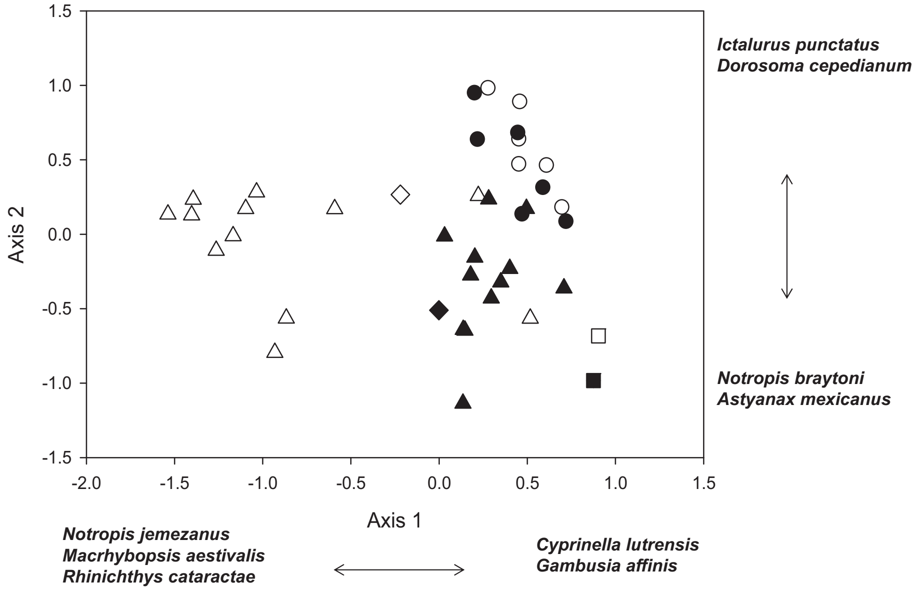

Fig. 4. Nonmetric multidimensional scaling ordination plot of region-wide data for fish relative abundance (open markers, historical data; solid markers, current data). The primary species driving the ordination and their direction are indicated for each axis. Different markers are used to represent the four geographic groups: Rio Grande above Rio Conchos confluence (circles), Rio Grande below Rio Conchos confluence (triangles), Alamito Creek (squares), and Terlingua Creek (diamonds).

correlated with *Ictalurus punctatus* ($r = 0.60$) and *D. cepedianum* ($r = 0.51$), and negatively correlated with *N. braytoni* ($r = -0.67$) and *Astyanax mexicanus* ($r = -0.60$). The primary reason for the change in fish assemblage composition and variability in the Big Bend area was a large decrease in the relative abundance of *N. jemezanus*, *M. aestivalis* and *R. cataractae* and corresponding increase in the abundance of *C. lutrensis* and *G. affinis*.

3.2. Spatial variability in hydrological conditions

Between the mid-1970s and early 2010s (Table 2), median specific conductance was relatively low in El Paso (Courchesne Bridge; ~1200 μS/cm), higher from Fort Quitman (3440 μS/cm) to just above the confluence with Rio Conchos (2880 μS/cm), intermediate from just below the confluence (1900 μS/cm) to Terlingua Creek (2210 μS/cm), and returned to low values at the downstream-most site of the study area near Langtry (1160 μS/cm) (Table 3; Fig. 1). Long-term salinity data for the Rio Conchos and minor tributaries (Alamito Creek and Terlingua Creek) were not available for analysis.

Between 1977 and 2011 (Table 2), overall median (50th quantile) discharge in the mainstem Rio Grande from El Paso to just above the confluence with Rio Conchos was fairly consistent at ~3–4 m^3/s (Table 4), and in Rio Conchos above the confluence, it was ~8 m^3/s (Table 4). Below the confluence, overall median discharge was ~13 m^3/s, which is approximately the sum of both upstream median discharges (Table 4). Median discharge at the mainstem site near Castolon (Table 2; Fig. 1) did not change appreciably (~13.5 m^3/s) relative to just below the confluence, but it nearly doubled at the last study gage near Langtry (~22 m^3/s) (Table 4; Fig. 1). Median discharges at Alamito Creek (0.03 m^3/s) and Terlingua Creek (0.07 m^3/s) were relatively low (Table 4). Between 1977 and 2011 (Table 2), overall median monthly precipitation at each selected weather station ranged between 8.4 and 21.6 mm (Table 5).

3.3. Trends in hydrological conditions

No long-term trends in median salinity were detected at the El Paso and Fort Quitman sites during the study period (Table 3). Salinity monotonically increased in mainstem sites from just upstream of the confluence with Rio Conchos to near Langtry (Table 3). The rate of increase varied from 36 μS/cm per year just above the confluence (1.2% annual increase), to 53 μS/cm per year just below the confluence (2.8% annual increase), to 49 μS/cm per year near Terlingua Creek (2.2% annual increase), to 7.4 μS/cm per year (0.6% annual increase) at the farthest downstream station near Langtry (Table 3; Fig. 1). Thus, the highest rate of change in the Rio Grande was observed just below the confluence with the Rio Conchos, resulting in a 3-fold increase in median salinity at this site during the study period (Fig. 5). Trend analyses for salinity could not be conducted for the minor tributaries because of lack of sufficient data.

Median and extreme (10th/90th quantile) discharges generally decreased monotonically in Rio Conchos and in all mainstem Rio Grande sites below the confluence (Table 4; Appendix A, Figs. S1 and S2). The decrease in median discharge at these sites was 0.55–0.68 m^3/s per year (Table 4), equivalent to 7.3% annual decrease in the Rio Conchos above the confluence, 4.9% in the Rio Grande just below the confluence, 4.7% near Castolon, and 3.1% near Langtry. Conversely, median and extreme-low (10th quantile) discharge generally increased at the mainstem sites above the Rio Conchos (Table 4; Appendix A, Fig. S3). Consistent with findings at the Rio Conchos and the mainstem sites below the confluence, however, extreme-high discharge at the upstream sites also significantly decreased (Table 4). Median and extreme-high discharges all decreased in Alamito Creek but at Terlingua Creek, only extreme discharges (high and low) decreased significantly.

Median and extreme (high and low) monthly precipitation seemed to generally decrease during the study period — all but one estimate were negative regardless of statistical significance (Table 5; Appendix A, Fig. S4). The only exception was an extreme-high precipitation estimate in a weather station near Alpine, Texas (Table 2; Fig. 1), where the sign was positive although not significant. Some of the extreme-low precipitation estimates indicated no trend (estimate = 0) because the 10th quantile value for all or most years already was at the lowest value possible, 0 mm (Table 5).

Associations of Rio Grande salinity below the confluence with time and with upstream discharge variables were further explored using generalized linear models. Akaike's Information Criterion and total R^2 were used to rank the models. Salinity was significantly autocorrelated at this site, but its positive association with time (trend) was confirmed (models 1–3; Table 6). Inclusion of median discharge for Rio Conchos yielded the best model (model 1), and its association with salinity below the confluence was significant and negative. Inclusion of median discharge for Rio Conchos and Rio Grande (above confluence) yielded the next best model (model 2), but the association was significant (and negative) only for Rio Conchos discharge. Inclusion of median discharge only for Rio Grande (above confluence) yielded the lesser model (model 3), and the association between Rio Grande discharge above and salinity below the confluence was non-significant. Linear trend coefficients in models 1 and 2 (~52 μS/cm per year; Table 6) were practically identical to the Sen slope estimate of 53 μS/cm per year (Table 3).

4. Discussion

4.1. Biotic change and homogenization

Results of this study indicated that taxonomic homogenization of fish assemblages occurred in the Trans-Pecos Region of the Rio Grande during the study period. Compared to historical collections (1977–1989), current (2010–2011) species richness decreased in the Big Bend area of the mainstem and in Alamito Creek, especially in the latter. While historical collections for Alamito Creek contained 14 fish species, including state-listed threatened native species such as *Campostoma ornatum* and *N. chihuahua* (Hubbs et al., 2008), current data indicated the presence of only three species at this site (*G. affinis*, *C. lutrensis,* and *Carpiodes carpio*). In addition, the spatial variability of fish assemblages decreased considerably in the Big Bend area of the Rio Grande. This decrease was primarily due to increased relative abundances of *C. lutrensis* and *G. affinis* coupled with decreased relative abundances of *M. aestivalis*, *N. jemezanus*, and *R. cataractae* (all five species are native to the region). Conversely, species richness in the Rio Grande above the confluence with Rio Conchos or in Terlingua Creek did not change between the historical and current collection periods. The net effect of these temporal changes was to make fish assemblages in the mainstem Rio Grande

Table 3

Trend analysis (Kendall tau coefficient) and rate of annual change (Sen slope) for median specific conductance (μS/cm) measured at 6 selected monitoring sites (data are not available for tributaries). Minimum (min), median, and maximum (max) values, and percent annual change [100(Sen slope/median)] recorded at each monitoring site over the study period are also shown. Coefficients highlighted in bold are significant ($p < 0.05$).

	Site i	Site ii	Site iii	Site iv	Site v	Site vi
Tau	0.11	0.15	**0.36**	**0.72**	**0.53**	**0.25**
Sen slope	3.3	25	36	53	49	7.4
Min, median, max	288, 1202, 9560	328, 3440, 6740	300, 2880, 6450	163, 1900, 4421	300, 2210, 5580	500, 1160, 3500
% annual change	+0.3	+0.1	**+1.2**	**+2.8**	**+2.2**	**+0.6**

Table 4
Trend analysis (quantile regression) and rate of annual change for river discharge (m^3/s) measured at 10 selected streamflow gages. The 10th, 50th, and 90th quantile values, and percent annual change [100(rate of change/quantile)] recorded at each gage over the study period are also shown. Significant changes ($p < 0.05$) are in bold type.

Flow gage	10th quantile			50th quantile			90th quantile		
	10th value	Annual change	% annual change	50th value	Annual change	% annual change	90th value	Annual change	% annual change
a	0.04	0.0004	1.0	3.03	**−0.0850**	**−2.8**	7.56	**−0.3744**	**−4.9**
b	0.45	**0.0262**	**5.8**	3.96	**0.0367**	**0.9**	14.50	**−0.5229**	**−3.6**
c	0.11	**0.0150**	**13.6**	3.48	**0.0522**	**1.5**	13.30	**−0.4788**	**−3.6**
d	0.31	**0.0041**	**1.3**	3.34	**0.0394**	**1.2**	12.58	**−0.5159**	**−4.1**
e	0.84	**−0.2377**	**−28.3**	7.57	**−0.5489**	**−7.3**	44.70	**−1.4250**	**−3.2**
f	2.59	**−0.2396**	**−9,2**	12.70	**−0.6283**	**−4.9**	60.60	**−1.9684**	**−3.2**
g	0.01	0.0000	0.0	0.03	**−0.0007**	**−2.3**	0.07	**−0.0017**	**−2.4**
h	0.03	**−0.0005**	**−1.7**	0.07	0.0000	0	1.01	**−0.0191**	**−1.9**
i	2.29	**−0.2415**	**−10.5**	13.50	**−0.6165**	**−4.7**	66.30	**−2.0130**	**−3.0**
j	9.32	**−0.2708**	**−2.9**	21.70	**−0.6833**	**−3.1**	79.00	**−2.3850**	**−3.0**

below and above the confluence with the Rio Conchos taxonomically more similar to each other.

Curiously, the regional taxonomic homogenization of fish assemblages observed in this study was based primarily on changes in relative abundances of native species, either increases or decreases. This finding differs from other studies of biotic homogenization where increased taxonomic similarity of aquatic and terrestrial faunas is typically the result of relative increases and decreases in exotic generalists and native species, respectively (McKinney and Lockwood, 1999; Olden, 2006; Rahel, 2010; Pool and Olden, 2012; Toussaint et al., 2014). The choice of spatial scale can influence the results of studies of biotic homogenization (Rahel, 2010). The present study was geographically limited compared to some earlier studies. However, the analysis based on regional, sub-regional, and individual tributary creek scales (selected according to clear habitat criteria) provided generally unambiguous observations and reasonable confidence in the conclusion that taxonomic homogenization of fish assemblages was based on changes in the relative composition of native species at multiple spatial scales.

4.2. Habitat change and homogenization

Rio Grande discharge above the confluence with Rio Conchos is strongly influenced by water releases from upstream reservoirs in New Mexico (USA) and by water withdrawals, and salinity in this reach of the river increases in a downstream direction (Moyer et al., 2013). Below the confluence, discharge is strongly dependent on Rio Conchos flow (Schmidt et al., 2003), and salinity decreases in a downstream direction (Raines et al., 2012). Rio Conchos discharge is also influenced by upstream reservoir operations and water withdrawals and is the subject of an international treaty (Kelly, 2001). These earlier observations are consistent with the spatial distributions of discharge and salinity recorded during the present study. Also, in agreement with findings of a recent study (Raines et al., 2012), median discharge below the confluence increased in a downstream direction due to local gains in the lower reaches. In the present study, the net gain in median flow was estimated at 71% (nearly double) between the confluence with the Rio Conchos and the last study gage near Langtry.

Post-1970s trends in hydrological conditions were observed primarily in the Rio Conchos and in the Rio Grande below the confluence. In the Rio Conchos, median discharge decreased during the study period at an annual rate of 7.3% and, in the Rio Grande just below the confluence, the rate of decrease was 4.9%. Because streamflow in the Rio Grande below the confluence is mostly derived from Rio Conchos discharge (Schmidt et al., 2003; present study), and because Rio Grande discharge upstream of the confluence showed small positive trends (1.2% per year just above the confluence), the negative trend in flow below the confluence is the direct consequence of the negative trend in discharge from the Rio Conchos. Also, while median discharge declined at all mainstem study sites in the Big Bend area, the magnitude of the decline became progressively smaller in a downstream direction, from 4.9% per year just below the confluence to 3.1% per year at Langtry. This phenomenon was likely due to streamflow gains in the lower reaches (see discussion in preceding paragraph).

Median salinity in the Rio Grande remained monotonically stable during the study period at the upstream sites of El Paso and Fort Quitman, but increased at all other mainstem sites from just upstream the confluence with Rio Conchos (1.2% per year in specific conductance) to the lowermost study site near Langtry. The highest rate of salinity increase (2.8% per year) was observed just below the confluence with the Rio Conchos, and the lowest rate was observed near Langtry (0.6% per year). Water quality data for the Rio Conchos was not available for this study, but other studies have reported that Rio Conchos salinity is about one-half of Rio Grande salinity above the confluence (Gutiérrez and Carreón-Hernández, 2004; Miyamoto et al., 2006; Gutiérrez and Johnson, 2014). Results of generalized linear models showed that mainstem salinity below the confluence is inversely associated with Rio Conchos discharge — the lower the Rio Conchos discharge, the higher the Rio Grande salinity below the confluence. This negative

Table 5
Trend analysis (quantile regression) and rate of annual change for total monthly precipitation (mm) measured at 10 selected weather stations. The 10th, 50th, and 90th quantile values, and percent annual change [100(rate of change/quantile)] recorded at each weather station over the study period are also shown. Significant changes ($p < 0.05$) are in bold type.

Weather station	10th quantile			50th quantile			90th quantile		
	10th value	Annual change	% annual change	50th value	Annual change	% annual change	90th value	Annual change	% annual change
A	0.00	0.000	0.0	11.700	**−0.304**	**−2.6**	47.300	−0.252	−0.5
B	0.00	0.000	0.0	10.400	**−0.193**	**−1.9**	49.900	−0.038	−0.1
C	0.00	0.000	0.0	8.400	−0.220	−2.6	58.990	−1.183	−2.0
D	0.52	−0.044	−8.5	19.800	−0.200	−1.0	87.060	−0.056	−0.1
E	0.50	−0.021	−4.2	18.200	−0.376	−2.2	91.650	0.325	0.4
F	0.00	0.000	0.0	16.300	**−0.425**	**−2.6**	81.540	−0.985	−1.2
G	0.00	0.000	0.0	11.900	−0.290	−2.4	60.190	−0.129	−0.2
H	0.00	−0.025	–	15.800	−0.312	−2.0	73.420	−0.234	−0.3
I	0.30	−0.033	−11	21.600	−0.150	−0.7	104.240	−0.192	−0.2
J	0.50	**−0.030**	**−6.0**	16.300	−0.241	−1.5	73.450	−0.210	−0.3

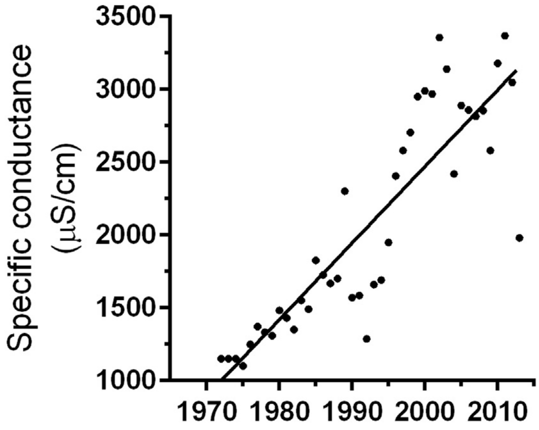

Fig. 5. Scatterplot of median salinity by year in the Rio Grande just below the confluence with Rio Conchos. Kendall tau and generalized linear models indicated a significant, positive trend (Tables 3, 6). A regression line is added to the scatterplot to help visualize the association.

association reflects a progressively diminishing dilution of higher-salinity Rio Grande water as discharge from Rio Conchos decreased over time. Trends in discharge from Rio Grande above the confluence had little if any influence on trends in salinity below the confluence.

Local precipitation in much of the Rio Grande does not normally influence contemporaneous discharge except during heavy precipitation and consequent flooding associated with summer monsoons (Ellis et al., 1993; Moyer et al., 2013). Thus, concurrent trends in precipitation and discharge would be expected to occur only or primarily at their extreme-high levels. This expectation was confirmed in the present study; namely, while region-wide trends in median (50th quantile) and extreme-low (10th quantile) precipitation were not associated with similar trends in discharge, extreme-high (90th quantile) precipitation and discharge both generally declined in magnitude during the study period. Negative trends in extreme-high discharge were statistically significant at all sites. Although most trends in precipitation were not statistically significant at the quantiles examined, the finding that their direction (sign) was negative for the vast majority of trend estimates at all quantiles strongly suggests that precipitation generally decreased in the Trans-Pecos region during the study period [findings of no change (slope of zero) at the 10th quantile were due to overall values of zero for this quantile]. Thus, in terms of stream hydrology, the only association with precipitation suggested by this study was a region-wide decline in the intensity of monsoon-related flooding.

Overall, this study showed that the confluence with the Rio Conchos is an important geographical reference to describe and understand not only the spatial variability in hydrological conditions of the Trans-Pecos region, as previous studies have concluded, but also their long-term trends. Since the 1970s, negative trends in flow and positive trends in salinity below the confluence have greatly modified hydrological conditions below the confluence and made them more similar to those above it. Namely, the aquatic habitat of the Trans-Pecos region is becoming increasingly homogenized. Previous studies of aquatic habitat homogenization have focused almost exclusively on physical attributes such as stream flow and habitat type (e.g., pools, riffles, runs, side channels) (Poff et al., 2007; Rahel, 2010). Results of the present study, however, indicated that water chemistry (e.g., salinity) is also a relevant hydrological variable that should be considered in studies of aquatic habitat homogenization and of its association with biotic homogenization.

4.3. Associations between habitat and biotic homogenization

Examination of contemporaneous change in hydrologic conditions and fish assemblages over a period of ~35 years since the 1970s suggested that region-wide homogenization of salinity conditions was at least partly responsible for biotic change and homogenization (although Rio Grande salinity upstream of the confluence with the Rio Conchos still remains higher than below the confluence, the magnitude of the difference has decreased since the 1970s). The two most prominent species whose relative abundances increased in the Big Bend area, *C. lutrensis* and *G. affinis*, are euryhaline and able to tolerate a wide range of salinities (Echelle et al., 1972; Matthews and Hill, 1977). Thus, their increase in relative abundances at the expense of species with lesser salinity tolerance is associated with and may be driven by the increasing salinity of the area. As fish communities below the confluence become increasingly dominated by salinity-tolerant species, the regional distribution of fish assemblages according to salinity gradients originally described in the 1970s appears to have broken down. Namely, the "saline Rio Grande fish fauna" (Hubbs et al., 1977) is no longer an exclusive attribute of river habitat upstream of the confluence with the Rio Conchos. A similar observation concerning the influence of salinity on fish assemblages was made in a recent study of the Permian Basin portion of the Pecos River (a Rio Grande tributary that confluences below the present study area), where increased salinization over a period of ~25 years resulted in a decline in fish species richness and an increase in salinity-tolerant species (Cheek and Taylor, in press).

C. lutrensis and *G. affinis* have a preference for moderate-to-slow current velocity (a function of discharge), and *M. aestivalis*, *N. jemezanus*,

Table 6

Parameter estimates (and standard errors, SE) from generalized linear regression with autoregression error. Median specific conductance (μS/cm) at the Rio Grande below the confluence with the Rio Conchos was modeled using the following regressor variables: year (linear trend), first-order autoregression error (AR1), median discharge (m^3/s) from the Rio Conchos above the confluence, and median discharge (m^3/s) from the Rio Grande above the confluence. Significant estimates are highlighted in bold font. Models were ranked according to Akaike's Information Criterion (AIC; lower values represent better quality models) and R^2 (higher values represent better model fits). The period of record for this analysis was 1977–2011.

Model rank	AIC	R^2	Parameter	Estimate ± SE	*t*-Value	*p*-Value
1	492	0.88	Intercept	**−100,616 ± 17,552**	−5.73	<0.0001
			Year	**51.6 ± 8.8**	5.87	<0.0001
			Rio Conchos discharge	**−14.2 ± 6.2**	−2.27	0.03
			AR1	**−0.49 ± 0.16**	−3.12	0.0039
2	494	0.88	Intercept	**−100,684 ± 17,889**	−5.63	<0.0001
			Year	**51.7 ± 9.0**	5.77	<0.0001
			Rio Conchos discharge	**−14.1 ± 6.7**	−2.09	0.045
			Rio Grande discharge	−0.5 ± 10.2	−0.05	0.96
			AR1	**−0.49 ± 0.16**	−3.04	0.0049
3	497	0.86	Intercept	**−117,503 ± 18,814**	−6.25	<0.0001
			Year	**60.0 ± 9.4**	6.36	<0.0001
			Rio Grande discharge	−6.8 ± 10.0	−0.68	0.50
			AR1	**−0.56 ± 0.15**	−3.74	0.0007

and *R. cataractae* prefer faster currents (Yu and Peters, 2002; Heard et al., 2012; for *G. affinis*, see Fig. 4 in Heard et al., 2012). Coupled with decreasing discharge in the mainstem of the Big Bend area, relative abundances of *C. lutrensis* and *G. affinis* increased in the area while those of *M. aestivalis*, *N. jemezanus*, and *R. cataractae* decreased. In addition, *C. ornatum* and *N. chihuahua* are known to prefer deep tributary pool habitats in the region, which require adequate levels of flow to be maintained (Miyazono and Taylor, 2013b). While these two species were currently still abundant in Terlingua Creek, which did not experience decreases in median discharge, they were absent in Alamito Creek, which experienced a decrease. These observations suggest that regional shifts in fish assemblage compositions according to flow preferences or tolerances were also caused by the spatially uneven change in discharge during the study period. Similar findings have been reported in other river basins (Rahel, 2010; Taylor, 2010).

Fish assemblages did not significantly change in the Rio Grande above the confluence with the Rio Conchos, but this observation should not be interpreted as an indication that they are in good condition. This reach of the river was severely degraded long before samples for the present study were collected (Hubbs et al., 1977; Everitt, 1993; Schmidt et al., 2003). Also, while the decline in the intensity of monsoon rain-related flooding is likely to have influenced the integrity of the river ecosystem, this phenomenon occurred region-wide and does not seem to have influenced regional habitat or biotic homogenization processes during the study period.

5. Conclusions

Results of this study are relevant to the advancement of current understanding of biotic homogenization. Desertification of aquatic habitats is defined as habitat shrinkage or loss of water (Minckley and Unmack, 2000). Changes in water quantity, however, are often accompanied by changes in water quality and the latter can have major, cumulative effects on the health and sustainability of aquatic ecosystems. This study showed that discharge from the Rio Conchos monotonically decreased since the 1970s causing not only desertification (loss of water) but also considerable salinization of the Big Bend area of the Rio Grande. This regionally uneven change in hydrological conditions made Rio Grande habitat below the Rio Conchos confluence more similar to that above it. Regional hydrological homogenization, in turn, was associated with and likely led to regional functional and taxonomic homogenization of fish faunas. These observations highlight the importance of addressing hydrological variables in studies of biotic homogenization, including water quality which is rarely considered, especially when objectives include the characterization of functional aspects of biotic homogenization. Moreover, unlike results of earlier studies (Rahel, 2010), taxonomic homogenization in the present study was primarily due to changes in relative abundances of native fishes. Changes in exotic species, whose presence in the region generally pre-dates the study period, did not seem to contribute appreciably to biotic homogenization.

The present results are also relevant to the conservation of natural resources of the Big Bend area of the Rio Grande Basin, which has unique ecological value among North American desert ecosystems. If current hydrological trends in the area continue, the integrity of its current fish assemblages may continue to deteriorate and current efforts to reestablish extirpated species (Moring et al., 2014) may not be fully successful or fail. In addition, the increased salinity could bring a new major threat to the area: the highly toxic golden alga (*Prymnesium parvum*). Golden alga was detected in the upper reach of the Trans-Pecos region in 2012 (TPWD, 2014), and it is likely that downstream dispersal is taking place. Because blooms of golden alga are facilitated by salinity levels ≥ 1200–2000 μS/cm (Patiño et al., 2014) and median salinity in much the Big Bend area has already reached these levels, there is growing risk of golden alga establishment in the region. International cooperation to improve and maintain adequate hydrological conditions may be necessary for the long-term sustainability of the Big Bend area ecosystem and the services it provides.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2014.12.079.

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