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ARTICLE

Effects of Hydrology on Fish Diversity and Assemblage Structure in a Texan Coastal Plains River

Luke M. Bower,* Friedrich W. Keppeler, Eduardo R. Cunha, Yasmin Quintana, David E. Saenz, Edwin O. Lopez-Delgado, and Thethela Bokhutlo
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258, USA

Caroline C. Arantes
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258, USA; and Center for Global Change and Earth Observations, Michigan State University, East Lansing, Michigan 48824, USA

Marcelo C. Andrade
Grupo de Ecologia Aquática, Universidade Federal do Pará, Avenida Perimetral, 2651, Terra Firme, 66077-830 Belém, Pará, Brazil

Clinton R. Robertson and Kevin B. Mayes
Texas Parks and Wildlife Department, Inland Fisheries, River Studies, San Marcos, Texas 78667, USA

Kirk O. Winemiller
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258, USA

Abstract
High-flow pulses affect river ecosystem dynamics in many important ways including by forming connections between the channel and oxbow lakes. This study assessed the influence of discharge on fish assemblage structure and diversity in the channel and oxbows of the Guadalupe River, Texas. Local assemblages of two oxbows and two channel sites were surveyed using standardized methods to test four hypotheses: (1) assemblage structure in oxbow lakes differs from those in the river channel, (2) α diversity decreases during extended periods of low discharge, (3) β diversity decreases during high discharge and increases during extended periods of low discharge, and (4) species turnover and assemblage nestedness decline during periods of high discharge. We found evidence to support the first three hypotheses. Unsurprisingly, lotic-adapted fishes were observed more frequently in the river channel, whereas lentic-adapted species generally were more common in the oxbow lakes. Species richness declined during periods of low discharge possibly due to harsher environmental conditions or stronger species interactions (e.g., predation). Discharge was inversely associated with both β diversity and species turnover, suggesting a stronger mass effect during high-flow pulses, and stronger species sorting during low-flow conditions. Contrary to our fourth hypothesis, assemblage nestedness increased during periods of high discharge. Finally, we also found evidence to support the hypothesis that species turnover decreased as discharge declined. The results of this study demonstrate the importance of flow pulses for maintaining fish diversity and assemblage structure in floodplain river systems. With additional research involving more sites and longer time series, it should be feasible to define and identify thresholds for flow regime changes that alter assemblage structure and species diversity.

*Corresponding author: lbower88@tamu.edu
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Human demand for water and hydropower increases each year, greatly affecting river hydrology, ecosystem processes, and fish assemblages (Jackson et al. 2001; Malmqvist and Rundle 2002). Sixty percent of the world's rivers have altered flow regimes (Revenga et al. 2000). In North America, for example, natural flow regimes of at least 25 large river systems are strongly affected by human alteration, which has resulted in river fragmentation and loss of lateral connectivity (Dynesius and Nilsson 1994; Lehner et al. 2011). Lateral connectivity in rivers can enhance fish recruitment (Zeug and Winemiller 2008a, 2008b), growth (Wahl and Nielsen 1985), and diversity at local and regional scales (Galat et al. 1998; Miranda 2005; Zeug et al. 2005; Shoup and Wahl 2009). Understanding how fish respond to alterations in hydrology is crucial for efforts designed to balance natural resource conservation with human needs for water, particularly in river–floodplain systems; yet little work has been done in North American river–floodplain systems compared with the extensive research carried out in tropical floodplains (Welcomme 1979; Shoup and Wahl 2009). Here we report findings from a study that assessed the influence of hydrology on fish assemblage structure and diversity of the Guadalupe River in the Gulf Coast Prairies and Marshes ecoregion of Texas.

River–floodplain systems are dynamic. Periodic floods can change fluvial geomorphology and create a habitat mosaic that includes meandering channels, backwaters, oxbow lakes, point bars, cut banks, and stands of riparian vegetation at various stages of succession. High-flow pulses create hydrologic connections between the river channel and floodplain habitats, such as oxbow lakes, that strongly influence ecological dynamics of both components (Welcomme 1979; Junk et al. 1989; Sparks 1995; Agostinho et al. 2004; Zeug et al. 2005; Zeug and Winemiller 2008a, 2008b; Joniak and Kuczýnska-Kippen 2016). Periodic connections between the river channel and oxbow lakes promote not only habitat heterogeneity but also lateral exchange of nutrients, particulate organic matter, and aquatic organisms (Junk et al. 1989; Winemiller et al. 2000; Amoros and Bornette 2002; Yang et al. 2008; Kong et al. 2017).

Oxbows lakes are productive aquatic habitats, which function as fish nursery areas and refuges from scouring floods and predators in the river channel (Penczak et al. 2003; Miranda 2005; Zeug and Winemiller 2008a, 2008b; Shoup and Wahl 2009). Consequently, reduced frequencies and durations of connections between river channel and oxbows disrupt exchanges between habitats of both prespawning adults and juveniles, affecting recruitment and growth of many species (Winemiller et al. 2000; Suzuki et al. 2009). In addition, oxbow lakes provide important habitat for several fish species that normally are uncommon within the river channel but attain high densities in oxbow lakes (Zeug et al. 2005; Shoup and Wahl 2009). Hydrologic variation facilitates not only periodic lateral connections but also habitat heterogeneity within riverscapes that promotes β diversity (Winemiller et al. 2000; Miranda 2005; Zeug and Winemiller 2008a, 2008b).

Dispersal of aquatic organisms between channel and oxbow lakes tends to homogenize local fish assemblages (Rodríguez and Lewis 1997; Amoros and Bornette 2002; Zeug et al. 2005), resulting in lower β diversity (i.e., differentiation of species composition among habitats: Bozelli et al. 2015). Conversely, when disconnected, some oxbow lakes develop harsh environmental conditions (e.g., low dissolved oxygen [DO], high temperature, high turbidity) that are detrimental to certain species and create environmental filters that affect local species assemblages and increase β diversity (Winemiller et al. 2000; Thomaz et al. 2007; Benone 2018). Subsets of species capable of survival and growth under increasingly stressful environmental conditions should give rise to nested assemblage structure across spatial hierarchies (Tonkin et al. 2015). Hydrology and connectivity also influence intra- and inter-specific interactions within river–floodplain habitat mosaics (Junk et al. 1989; Arrington et al. 2005; Kong et al. 2017).

As in many areas with stochastic precipitation patterns and growing human populations, Texas has recurring droughts and floods and increasing water demand (TWDB 2017), all of which affect the hydrology and thus stresses fluvial ecosystems (Stahle and Cleaveland 1988; Nielson-Gammon 2012; TWDB 2017). The Texas Conservation Action Plan (TPWD 2012) identifies conservation goals that include maintaining adequate water quantity and quality and increasing the knowledge and understanding of aquatic ecosystems. Other state programs such as the Texas Instream Flow Program (see TWDB 2008), an initiative mandated by the Texas legislature with Senate Bill 2 (Ellis and Houston 2001) to determine conditions necessary to support a sound ecological environment for the state's rivers, recommends developing flow regimes that include subsistence, base, high-flow pulse, and overbanking flow components. Because ecological relationships between high-flow pulses and fish diversity are understudied in temperate regions, understanding these relationships is thus vital for the program.

Here, we addressed how high-flow pulses influences lateral connectivity and fish assemblage structure and diversity in the Guadalupe River, Texas. We first evaluated the hypothesis that, although sharing multiple species, the fish assemblage structure in oxbow lakes differs from that observed concurrently in the river channel. We also predicted that α diversity decreases during extended periods of low flow when oxbows are isolated. We further hypothesized that greater connectivity during high flows would result in lower β diversity due to greater dispersal and reduced habitat heterogeneity. Under low-water conditions, low dispersal and greater habitat heterogeneity should promote species sorting and β diversity (Datry et al. 2016; Benone 2018). Finally, we assessed the contribution of turnover and nestedness to β diversity during periods of high versus low flow. Specifically, we predicted that as discharge increases, greater dispersal would result in weaker patterns of nestedness with lower species turnover among local habitats.

METHODS

Study sites.— The Guadalupe River runs southeast through central Texas for approximately 400 km before emptying into San Antonio Bay on the northern coast of the Gulf of Mexico and has an average annual discharge of 55 m^3/s. The sites investigated in this study were located on the lower Guadalupe River and consisted of two oxbow lakes (oxbow 1 and 2) and two stretches of the main river channel (river 1 and 2) that were each contiguous with their respective point of connection. Oxbow 1 and river 1 were located near Cuero, Texas (29°03′32.24″N, 97°17′11.15″W), while oxbow 2 and river 2 were located downstream near Victoria, Texas (28°40′39.27″N, 96°59′10.69″W) (Figure 1). In lower reaches of the Guadalupe River, most oxbows are isolated from the main river channel but connect periodically at intervals influenced by oxbow and riverbank geomorphology and river discharge (Hudson et al. 2012).

Fish surveys.— Surveys were conducted at each of the four study sites approximately every other month for 1 year (six surveys at each of four study sites) between March 2016 and April 2017. Sampling took place only during daylight hours, roughly between 1000 and 1600 hours. For logistical and safety reasons, surveys were limited to periods when the discharge was below 140 m^3/s; therefore, time intervals between sampling periods were not uniform. At each site, hauls were made using two seines: a 7.6 × 1.8-m seine with a 3.2-mm mesh, and a

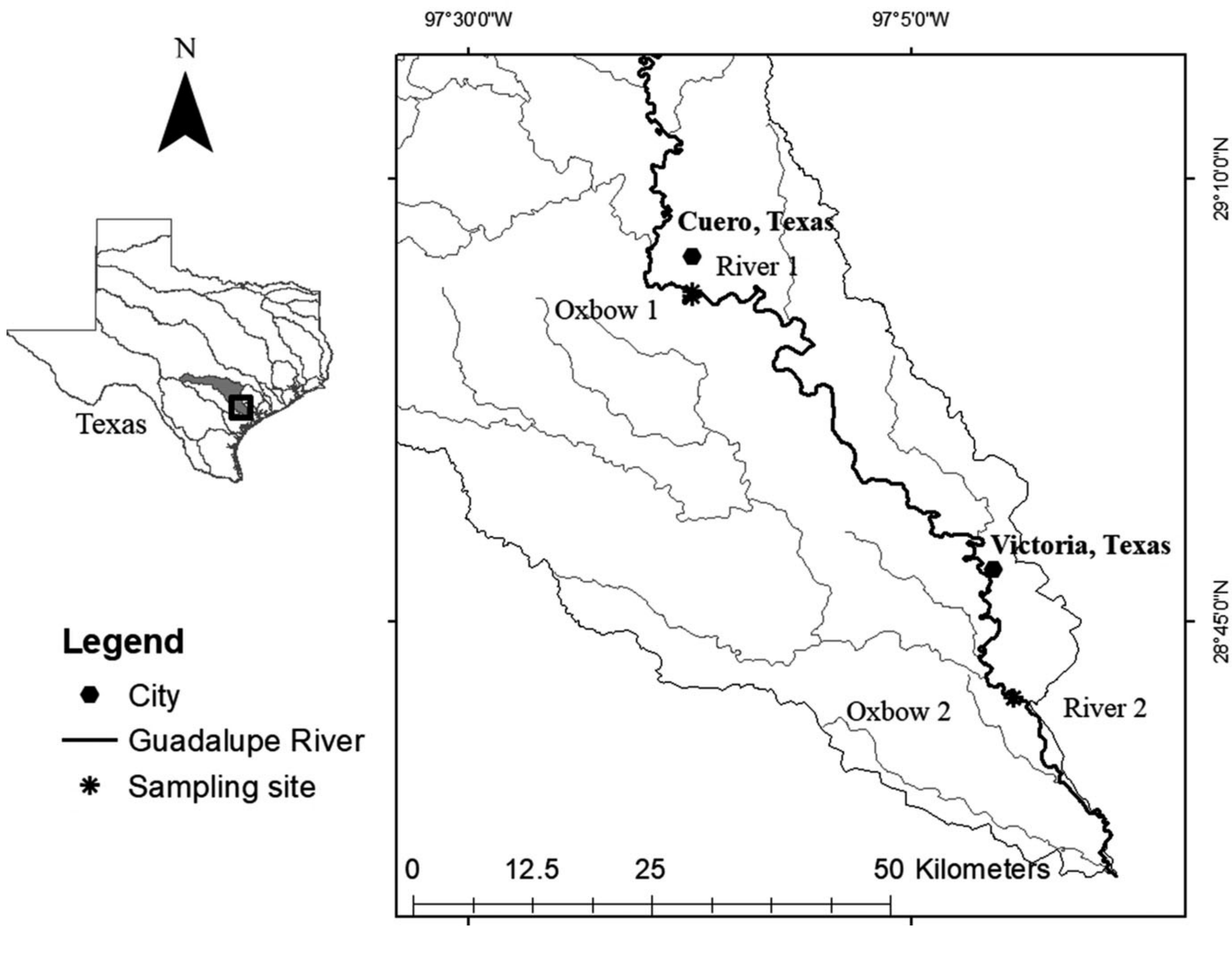

FIGURE 1. Locations of the four study sites (river 1, oxbow 1, river 2, and oxbow 2) in the Guadalupe River basin, Texas.

9.14×3.05-m bag seine, with a 3.05-m bag and 6.4-mm mesh in the wings and 3.2-mm mesh in the bag. Fish were removed from the nets and euthanized according to an approved Texas A&M University animal use protocol (Institutional Animal Care and Use Committee 2015-0290). Specimens were then fixed in a 10% formalin solution and transferred to 70% ethanol for preservation. Fish were identified and deposited in the Biodiversity Research and Teaching Collections at Texas A&M University (Supplementary Table S1 found in the online version of this article).

The average total distance for each seine haul at each site was 39 m (SD = 15). The total distance and the number of times seines were hauled varied among sites and flow conditions, and this was mostly a function of water depth and the steepness of the shoreline gradient available for seining. Additionally, oxbow 2 was smaller than oxbow 1, and during our survey in October, the former contained insufficient water (<20 cm deep) and deep mud, which made seining ineffective; therefore, data for oxbow 2 on that date were excluded from our analyses.

Discharge and environmental variables.— A connection threshold between oxbow lakes and the main river channel was estimated by recording discharge at the nearest U.S. Geological Survey (USGS) streamflow gauge on the dates when each oxbow was connected to the river channel by 2–10 cm of water through the portion of the riverbank with the lowest elevation (i.e., control point). These thresholds were independently confirmed by Bonner et al. (2017) based on an analysis of topographical, surface water elevation, and discharge data. Using USGS gauge 08175800 Guadalupe River at Cuero, we estimated the connection threshold for oxbow 1 at 46.2 m^3/s; and using USGS gauge 08176500 Guadalupe River at Victoria, we estimated the connection threshold for oxbow 2 at 44.7 m^3/s. Based on the connection threshold values and discharge data obtained from the USGS streamflow gauges, the accumulative discharge for a period of 10 d was calculated for each site. Accumulative discharge is the total discharge above the point of connection, giving a combination of frequency and magnitude of connection. This variable was used as a proxy for the magnitude of lateral connection between oxbow lakes and the main river channel, which is expected to affect exchanges of water and fish between channel and oxbows.

To characterize the environmental conditions at each site during each survey period, water physical and chemical features were recorded. Temperature (°C), specific conductivity (μS/cm), dissolved oxygen (mg/L), and salinity (‰) were measured using a YSI Pro2030, and the pH was measured using an Oakton pH meter. Secchi disk depth was recorded to the nearest centimeter. The substrate in both oxbow lakes consisted of mud and silt. The substrate in the main river channel was dominated by silt and mud overlying sand and gravel, with most areas also having patches of exposed sand and gravel.

Data analysis.— To test the hypothesis that assemblage structure in oxbow lakes differs from that observed in the river channel, we analyzed fish survey data using nonmetric multidimensional scaling (NMDS). The NMDS analysis was performed using Bray–Curtis distance and 50 maximum iterations for a stable configuration. To identify how fish assemblages of sampling units varied according to accumulated discharge (i.e., water exchange between habitats during connection; see previous section), a smooth surface function was used to fit this variable of interest on the NMDS ordination.

Because samples varied in terms of survey effort and sampling efficiency, abundance data were standardized before analysis. For α diversity, standardization was performed using individual-based rarefaction (Gotelli and Colwell 2011). For β-diversity indexes, we standardized species abundance before calculating metrics and adjusted the abundance of fish species to obtain a new matrix showing standardized total catch for each site. To do this, we first created a matrix with relative abundance of species for each site. Then, we multiplied the species relative abundances by the smallest site's sum of abundance among all collections (more details are found online in the Supplement). This provides an estimate of the probability of capturing a species given the total catch in the survey and produces a species-by-site matrix with species abundances adjusted to reflect a standardized survey effort among sites, so that rare species would not have a disproportionate influence on patterns of species turnover. These standardized abundance values were rounded to integers. This rarefaction method is similar to those used to adjust species richness values to reflect the same number of individuals within catch curves.

To evaluate our hypothesis that α diversity is related to hydrology, we assessed whether changes in α diversity relates to accumulated discharge and habitat type (oxbow versus river channel) using a multiple linear regression with the categorical variable coded as dummy variables. We tested for the main effects of explanatory variables as well as their interactions to examine whether α diversity varies with accumulated discharge differently between the oxbow lake and the river channel. Before this analysis, we tested for possible temporal dependence among samples by regressing changes in α diversity with time interval between surveys. No autocorrelation was detected, suggesting no violations of independence of samples in linear regressions (Supplementary Figures 1, 2).

To evaluate our hypothesis that β diversity, turnover, and nestedness are related to hydrology, we first obtained measurements of total β diversity, turnover, and nestedness using the Podani family of indices derived from the Ružička coefficient (Legendre 2014). Turnover was expressed as dissimilarities for percentage difference of abundance data, and nestedness as nested abundance of each species (Podani 2013; Legendre 2014); both were calculated using the standardized species abundance matrix (see above). We used the β-diversity metrics for the pairwise comparison between the oxbow lake and the river at each location and used linear regressions to evaluate the relationships between β diversity and accumulated discharge. Significant decrease in β diversity, species turnover, and nestedness with accumulated discharge indicates species homogenization during flow pulses. Significant increase in species nestedness with accumulated discharge indicates that some species are lost within either the oxbow lake or river during flow pulses, suggesting directional dispersal during intervals with lateral connection. Temporal interdependence among samples was examined, and no autocorrelation was detected (Supplementary Figures 1, 2). All analyses were conducted in R (R Development Core Team 2018) using the package vegan (Oksanen et al. 2017).

RESULTS

During our field study, there were nine flow pulses affecting both locations. Between flood pulses, the duration of connectivity at oxbow 1 ranged from 1 to 88 d, and at oxbow 2 the duration ranged from 2 to 92 d. There was no obvious pattern of connectivity during the length of our study, which was during an unusually wet year (Figure 2). Expect for pH (mean = 8.02, SD = 0.57), local physical and chemical variables varied according to sampling periods or habitat type (Table 1). Periods with high discharge were positively related to DO and turbidity, and negatively with conductivity. Temperature varied according to seasonal periods (minimum of 13.9°C in winter and maximum of 33.4°C in summer). A total of 12,265 fish specimens representing 36 species were collected. The most species-rich families were Cyprinidae and Centrarchidae, and the most abundant species were Red Shiner *Cyprinella lutrensis*, Orangespotted Sunfish *Lepomis humilis*, Bluegill (*L. macrochirus*), Bullhead Minnow *Pimephales vigilax*, Western Mosquitofish *Gambusia affinis*, and White Crappie *Pomoxis annularis*.

The first two NMDS axes reflected strong gradients of fish assemblage structure (stress = 0.16; Figure 3). Axis 1 represented variation in assemblage structure associated with habitat type (oxbow versus river). In general, centrarchids (except Largemouth Bass *Micropterus salmoides* and Longear Sunfish *L. megalotis*, which were common in both habitats), clupeids and Alligator Gar *Atractosteus spatula* were more frequent in oxbow lakes, whereas cyprinids (except Weed Shiner *Notropis texanus*) were more

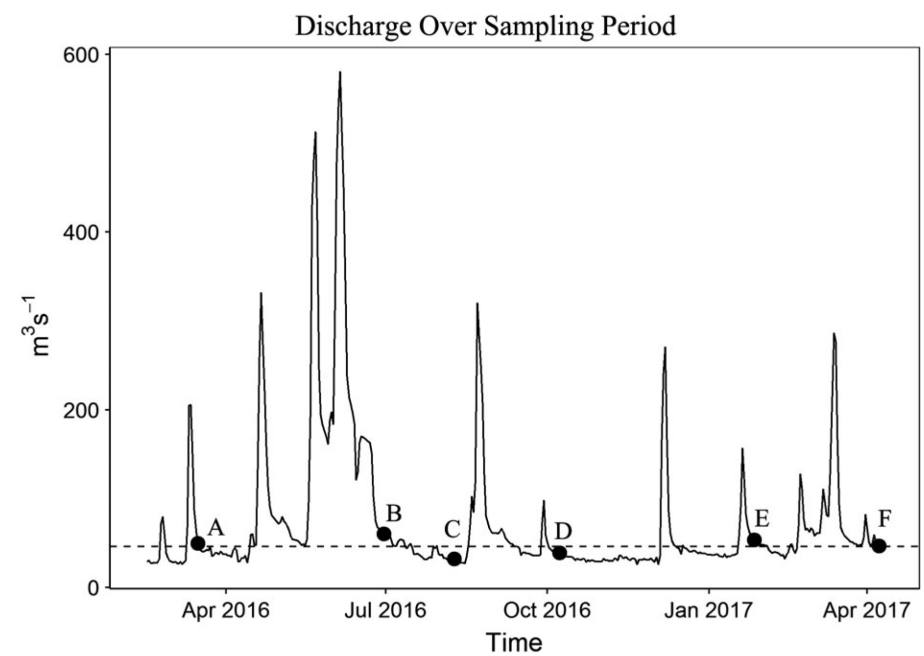

FIGURE 2. Discharge at USGS gauge 08175800 Guadalupe River near Cuero, Texas, from March 1, 2016, to April 30, 2017, and discharge at USGS gauge 08175800 Guadalupe River near Victoria, Texas, from March 1, 2016, to April 30, 2017. Black dots indicate the six survey dates; dotted line indicates the approximate minimum discharge when oxbows connect to the river channel (46.2 m^3/s for oxbow 1 and 44.7 m^3/s for oxbow 2). The letters indicate the estimated number of days the oxbows were connected during the previous 30-d intervals: (A) Cuero, 10 d; Victoria, 11 d; (B) Cuero, 30 d; Victoria, 30 d; (C) Cuero, 5 d; Victoria, 9 d; (D) Cuero, 10 d; Victoria, 10 d; (E) Cuero, 10 d; Victoria, 11 d; (F) Cuero, 30 d; Victoria, 30 d.

TABLE 1. Measurements of water temperature (°C), pH, Secchi disk depth (cm), DO (mg/L), and specific conductivity (μS/cm) for each collection habitat (oxbow or river), season, and date. NA indicates no data was collected.

Season	Date	Temperature	pH	Secchi	DO	Conductivity
			Oxbow 1			
Winter	Jan 27, 2017	15.0	8.4	20	7.0	628
Spring	Mar 16, 2016	22.8	8.2	17	6.9	358
Spring	Apr 8, 2017	24.6	6.8	8	6.5	610
Summer	Jul 1, 2016	30.2	7.8	50	9.5	640
Summer	Aug 9, 2016	33.4	8.3	20	8.2	873
Fall	Oct 8, 2016	26.8	8.5	11	9.5	627
			Oxbow 2			
Winter	Jan 28, 2017	13.9	8.2	15	4.8	610
Spring	Mar 17, 2016	22.6	8.2	13	5.6	293
Spring	Apr 9, 2017	22.7	7.0	10	7.5	491
Summer	Jun 30, 2016	31.0	8.3	40	15.3	428
Summer	Aug 10, 2016	32.2	8.1	10	4.3	599
Fall	Oct 9, 2016	NA	NA	NA	NA	NA
			River 1			
Winter	Jan 27, 2017	15.8	8.5	25	7.6	504
Spring	Mar 16, 2016	22.5	8.3	16	8.4	405
Spring	Apr 8, 2017	22.9	7.3	20	6.8	512
Summer	Jul 1, 2016	29.8	8.3	25	9.1	500
Summer	Aug 9, 2016	32.0	8.4	30	7.6	587
Fall	Oct 8, 2016	26.2	8.4	20	8.8	545
			River 2			
Winter	Jan 28, 2017	15.6	8.5	19	7.5	573
Spring	Mar 17, 2016	22.7	8.3	20	8.5	380
Spring	Apr 9, 2017	23.0	7.0	25	6.6	575
Summer	Jun 30, 2016	30.8	8.2	25	8.6	546
Summer	Aug 10, 2016	31.7	8.5	30	7.4	608
Fall	Oct 9, 2016	26.4	7.0	17	7.9	573

common in the river channel. The difference between fish assemblages of river 1 and oxbow 1 appeared to be greater than the difference between those of river 2 and oxbow 2. River channel and oxbow sites tended to be more similar during periods of high discharge, and these samples were clustered near the center of the NMDS plot (Figure 3).

During low-water periods, Mexican Tetras *Astyanax mexicanus*, Red Shiners, Western Mosquitofish, and Bullhead Minnows were only captured from the river channel. As the water level increased, these species were captured from both habitat types, indicating dispersal from the channel into oxbows (Figure 4). The opposite pattern was seen for Orangespotted Sunfish and Threadfin shad *Dorosoma petenense*, whereas Bluegills were common in both habitat types regardless of water level (Figure 4). White Crappies were abundant in oxbow lakes during low-water periods, and its abundance in oxbows declined markedly during and after flow pulses (Figure 4).

Alpha (α) diversity was significantly affected by the accumulated discharge (t = 2.66, P = 0.015; Figure 5), but not by habitat types (t = 0.146, P = 0.88) nor by the interaction between habitat type and accumulated discharge (t = −1.382, P = 0.18). An outlier was identified in this analysis, but its removal did not significantly change the regression slope (0.00011 versus 0.00013). The outlier was caused by many Red Shiners being collected at a site during one sampling trip (river 1 on March 16, 2016).

Beta (β) diversity between habitats was inversely related to accumulated discharge (R_{adj}^2 = 0.41, F = 7.86, P = 0.02; Figure 6A), indicating that assemblages were more similar during periods with high flows. Similarly, species turnover between habitats decreased with accumulated discharge (R_{adj}^2 = 0.39, F = 7.47, P = 0.03; Figure 6B), indicating that oxbow lakes and channel sites shared more species during periods with high flows and lateral connections. Species nestedness increased with accumulated discharge (R_{adj}^2 = 0.40, F = 7.57, P = 0.02; Figure 6C),

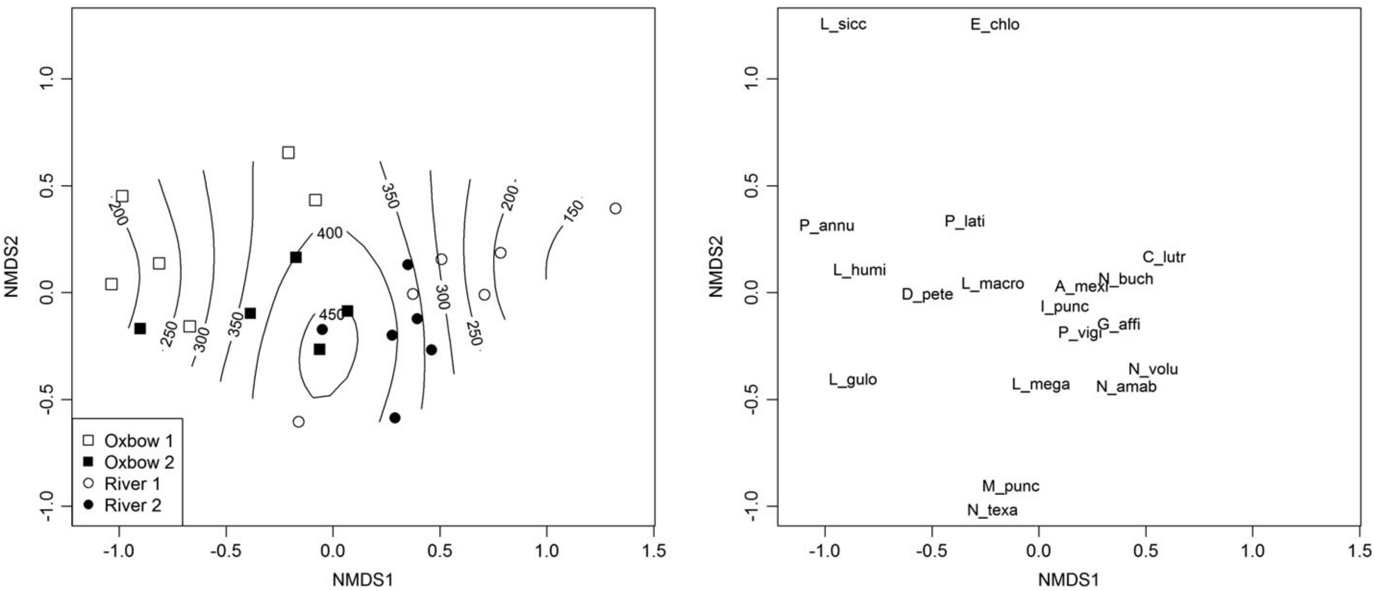

FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination (Bray–Curtis dissimilarity) with fish abundances during 1 year at four sites (two oxbow lakes, two river channels) of the Guadalupe River, Texas. The left panel shows the similarity between sampling units and the right panel highlights similarities between species. Lines in the left panel indicate a gradient of accumulated discharge for 10 d. Species abbreviations: Mexican Tetra *Astyanax mexicanus* (A_mexi), Red Shiner *Cyprinella lutrensis* (C_lutr), Threadfin Shad *Dorosoma petenense* (D_pete), Bluntnose Darter *Etheostoma chlorosoma* (E_chlo), Western Mosquitofish *Gambusia affinis* (G_affi), Channel Catfish *Ictalurus punctatus* (I_punc), Brook Silverside *Labidesthes sicculus* (L_sicc), Warmouth *Lepomis gulosus* (L_gulo), Orangespotted Sunfish *L. humilis* (L_humi), Bluegill *L. macrochirus* (L_humi), Longear Sunfish *L. megalotis* (L_mega), Spotted Bass *Micropterus punctulatus* (L_mega), Texas Shiner *Notropis amabilis* (N_amab), Ghost Shiner *N. buchanani* (N_buch), Weed Shiner *N. texanus* (N_texa), Mimic Shiner *N. volucellus* (N_volu), Bullhead Minnow *Pimephales vigilax* (P_vigi), Sailfin Molly *Poecilia latipinna* (P_lati), and White Crappie *Pomoxis annularis* (P_annu).

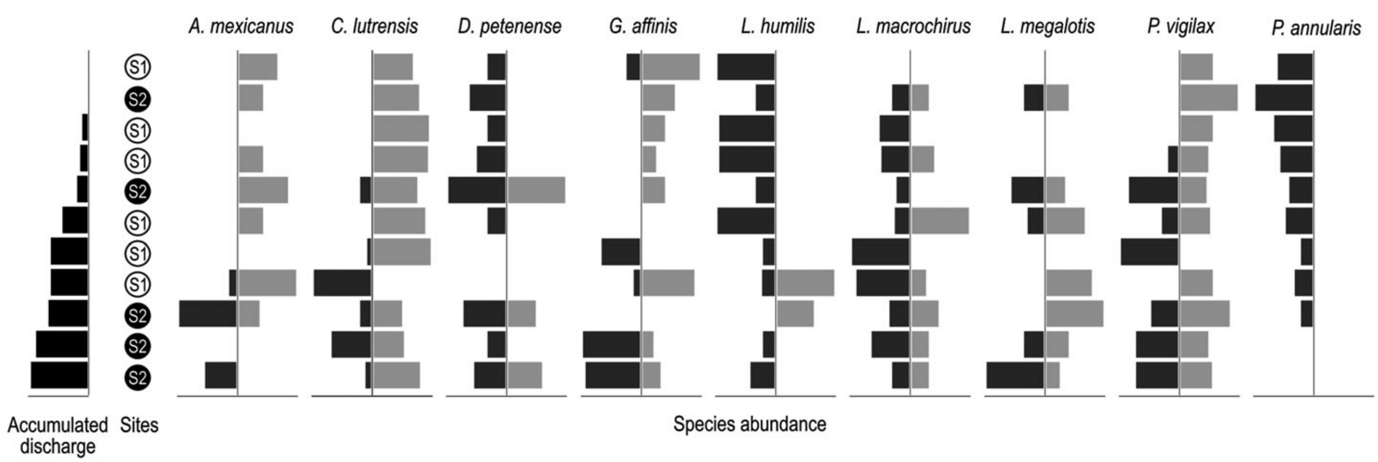

FIGURE 4. Variation in species abundances for site 1 (S1, open circles) and site 2 (S2, filled circles) between the oxbow lakes and the river channel for the most abundant species. Bars indicate species abundance (log scale) in samples from the oxbow lakes (dark gray) and river channel (light gray). See Figure 3 for species common names.

indicating that certain species were absent in one of the habitat types.

DISCUSSION

Our study revealed the importance of hydrologic variation to fish diversity and assemblage structure in the lower Guadalupe River, a finding consistent with those from similar studies conducted on the Brazos River in east-central Texas (Winemiller et al. 2000; Zeug et al. 2005) and other regions (Miranda 2005; Shoup and Wahl 2009). Hydrology of the lower Guadalupe River is highly variable and flood pulses occur at irregular intervals in any given year (Hudson et al. 2012). Alternating periods of connection between oxbow lakes and the river channel regulate the exchange of nutrients, sediments, and organisms between these habitats. As we hypothesized, fish assemblage structure differed between the river channel and oxbow lakes, especially during periods of extended low flows. This differentiation of fish assemblage structure was likely driven, at least in part, by species-specific preferences for lentic or lotic habitat. For example, lentic-adapted fishes, such as sunfishes, crappies, and Largemouth Bass (Centrarchidae), were much more common in oxbow lakes than channel sites, whereas rheophilic species, such as minnows and shiners (Cyprinidae), were abundant in the river channel and only occasionally captured from oxbows. These findings are consistent with those from studies of fish assemblages in channel and oxbow habitats in other North American rivers (Winemiller et al. 2000; Miranda et al. 2008; Shoup and Wahl 2009). This between-habitat differentiation of fish assemblage structure was less pronounced when oxbow 2 was compared with river 2. The connection distance between the oxbow lake and river channel was much shorter for site 2, and this oxbow dried completely during one sampling period. Therefore, the greater accessibility and recent recolonization of this oxbow by river fish may have increased faunal similarity of these sites as seen in other river systems in Texas with similar river–oxbow connection frequency

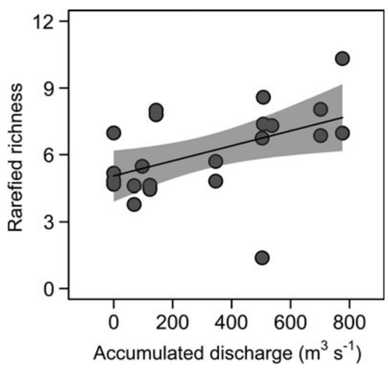

FIGURE 5. Relationship between rarefied richness (α diversity) and accumulated discharge for fish samplings conducted in the Guadalupe River, Texas. Solid line (light gray band denotes the 95% CI) represents the linear relationship using the whole data set.

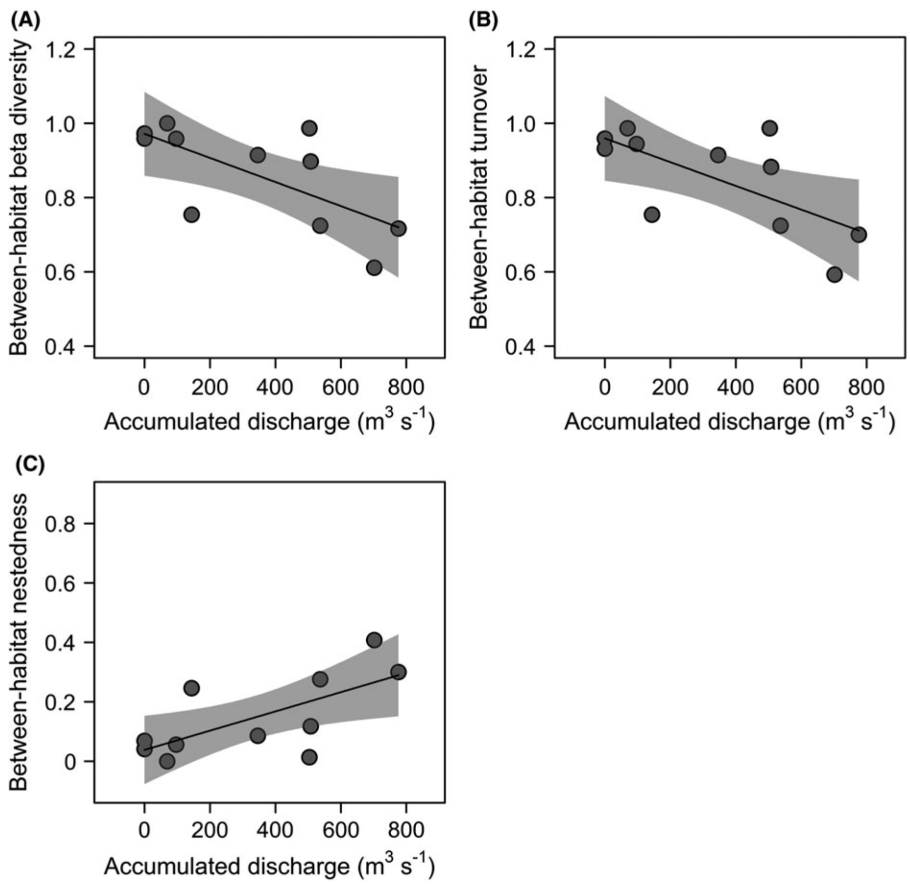

FIGURE 6. Linear regression used to assess the relationship of between-ecosystem β diversity with accumulated discharge. Different figures indicate the between-habitat **(A)** total β diversity, **(B)** species turnover, and **(C)** species nestedness.

patterns (Winemiller et al. 2000). A positive relationship between diversity and distance from oxbow lake to the river channel has been reported by previous studies (Lubinski et al. 2008; Shoup and Wahl 2009), so with shorter distances the frequency and magnitude of lateral connections are increased (Miyazono et al. 2010). More flooding events would likely lead to increased lateral dispersal in oxbow 2 than in oxbow 1.

Accumulated discharge had a pronounced influence on local assemblage structure and diversity. Lower accumulated discharge was associated with lower α diversity, supporting our second hypothesis that low flows reduce α diversity. Accumulated discharge also influenced β diversity, particularly in terms of species turnover, which supported our third hypothesis that fish assemblages homogenize during periods with high flows and frequent lateral connections of relatively long duration. Lateral connectivity of lowland rivers and floodplains facilitates fish dispersal and increases assemblage similarity among habitats (Amoros and Bornette 2002; Zeug et al. 2005; Thomaz et al. 2007). Studies of similar systems have suggested that high flows are associated with the rapid colonization of oxbows by fishes from the river channel (Zeug et al. 2005), where species turnover between habitats would be relatively low. Moreover, greater dispersal between habitats should increase α diversity and reduce β diversity. Flow pulses also can result in an influx of river water that can improve water quality in shallow oxbows during warm summer months when degraded conditions may exclude sensitive species from the oxbows (Shoup and Wahl 2009). As water levels drop within disconnected oxbows, water quality degradation (e.g., reduced dissolved oxygen or increased hydrogen sulfide) may exclude rheophilic fishes, reducing α diversity and increasing β diversity. During low-water periods, Red Shiners, Mexican Tetras, and Bullhead Minnows were not collected in oxbow lakes but were common in the river channel. These species often were captured in both habitat types during or following periods with high flows. Thus, occurrence of these species in oxbows seems to reflect environmental filtering (involving dispersal and subsequent differential survival in response to abiotic and/or biotic conditions), species sorting (habitat selection), or both. Field experiments could be employed to test alternative mechanisms causing temporal patterns of α and β diversity in oxbows.

We found greater species nestedness with increasing accumulated discharge, which contradicts our expectation that higher accumulated discharge would decrease species nestedness due to species homogenization. Explanations for this pattern may be related to the lateral dispersal of species. Bullhead Minnows, for example, were more prevalent in oxbows during periods of high accumulated discharge. Other studies, especially those conducted in tropical rivers, have reported seasonal migrations of fish from floodplains to the river channel during the annual period of floodwater recession (e.g., Fernandes 1997; Castello 2008; Górski et al. 2010; Layman et al. 2010). Alternatively, environmental conditions are more spatially heterogeneous during extended periods of low flow (Tockner et al. 1999; Thomaz et al. 2007), conditions that should be conducive to high species turnover of local assemblages. Under these conditions, the landscape mosaic of divergent habitat conditions should function as an environmental filter that promotes β diversity with nested assemblage composition in relation to influential environmental gradients (Poff 1997; Karaus et al. 2005; Tockner et al. 2006; Baselga and Jiménez-Valverde 2007; Freitas et al. 2013). Finally, fish surveys in the two habitat types could have been differentially affected by conditions during high discharge. Whereas higher discharge increased water depth in both habitats, only in the river channel did water currents affect deployment of the seine. In this case, false negatives (species not collected when present) would contribute to between-habitat differences in species richness and assemblage nestedness. This source of bias should have been minimized by our use of a standardized survey methodology and data rarefaction and other means of standardization controlling for effort.

Flow pulses and channel–floodplain connectivity contribute to fish diversity in river–floodplain systems (Bayley 1995; Winemiller et al. 2000; Miranda 2005; Zeug and Winemiller 2008a, 2008b; Shoup and Wahl 2009); consequently, reduction of the frequency and magnitude of pulses would reduce α diversity and regional (γ) diversity to some extent. Dams, water withdrawal, and climate change have altered river hydrology with impacts to fish stocks worldwide (Freeman and Marcinek 2006; Palmer et al. 2008; Miyazono et al. 2010; Arthington et al. 2016; Lynch et al. 2016; Closs et al. 2017). Water managers and policy makers should consider the levels of discharge required to maintain sufficient lateral connectivity between the river and its floodplain wetlands, such as oxbow lakes. The Texas Commission on Environmental Quality (TCEQ) adopted a two-per-season small-flow pulse (magnitude, duration) and only a one-per-season large-flow pulse standard for both discharge gauges on the lower Guadalupe River near our study sites (www.tceq.texas.gov). Although this project did not evaluate ecological functions of overbanking flows, they are probably the most beneficial to aquatic organisms with respect to lateral connectivity and are not protected under existing environmental flow standards in Texas. Current standards for the Guadalupe River may be insufficient, especially regarding lateral connectivity facilitating recruitment, movement of juvenile fishes to the river, and spatial food web subsidies from floodplain to river channel (Roach and Winemiller 2015). Reduction of the frequency and magnitude of high-flow pulses would alter dynamics of river and floodplain geomorphology, including oxbow formation and succession (Sun et al. 1996). Loss of oxbows and/or lateral connectivity clearly would affect fish stocks and diversity by eliminating critical habitat for several species. For example, Orangespotted Sunfish, White Crappie, and other centrarchids were common in oxbow lakes throughout the year but uncommon in samples from the river channel. This finding corroborates those from a similar study conducted in the lower Brazos River, Texas (Zeug and Winemiller 2008a, 2008b). Changes in natural flow pulse dynamics could impact fish populations and reduce biotic resistance against invasive species (Shea and Chesson 2002; Fitzgerald et al. 2016). During our surveys, Common Carp *Cyprinus carpio* and Amazon Molly *Poecilia formosa* were the only nonnative fish species encountered and only were captured in low abundance. Future flow regulation and other environmental changes might facilitate establishment and spread of these or additional invasive aquatic species.

River–floodplain systems have high habitat heterogeneity that, combined with hydrological variation, create a dynamic system that maintains fish diversity and productivity. Periods of low flow apparently promote differentiation of local species assemblages, whereas high-flow pulses and overbanking flows result in greater lateral connectivity and dispersal, higher local species diversity, and lower β diversity. Our findings support the view that conservation of native fish diversity requires flow pulses of sufficient magnitudes and frequencies to maintain river–floodplain geomorphology and lateral connectivity during appropriate periods to accommodate fish dispersal at various life-cycle phases.

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ORCID

Luke M. Bower http://orcid.org/0000-0002-0739-858X
Friedrich W. Keppeler http://orcid.org/0000-0002-5165-1298
Eduardo R. Cunha http://orcid.org/0000-0001-7858-2133
Yasmin Quintana http://orcid.org/0000-0002-1051-0202
David E. Saenz http://orcid.org/0000-0003-0238-0919
Edwin O. Lopez-Delgado http://orcid.org/0000-0002-4010-1880
Caroline C. Arantes http://orcid.org/0000-0002-9752-1499
Marcelo C. Andrade http://orcid.org/0000-0002-3573-5774
Kevin B. Mayes http://orcid.org/0000-0002-2743-1252
Kirk O. Winemiller http://orcid.org/0000-0003-0236-5129

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.