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Review

A large-scale conservation perspective considering endemic fishes of the North American plains

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ABSTRACT

Regions with unique habitats often harbor endemic taxa associated with temporally stable habitats. We identified such habitats that sustain endemic fishes in the plains of North America. We also summarized threats to their conservation and identified remnant habitats that still harbor endemic fishes (refuges) based on post-1989 surveys. Major springs, smaller, spring-fed streams, larger rivers, and euryhaline habitats were associated with a total of 49 endemics. Endemism was attributable to climatic refugia associated with each habitat type and dispersal limitation among major river drainages and springs. Forty-one endemic fishes (84%) were declining or extinct. Dewatering, habitat fragmentation, and habitat degradation were main causes of declines, often present together. Pollution and non-native species were also threats in many cases. Evidence for 53 existing refuges was found. We considered 34 refuges to be "high-quality" because they harbored three or more endemics. Twenty of these (those with available data) maintained consistent streamflow regimes for at least 50 years up to 2009. Case studies suggest high stream length, more natural flow regimes, and fewer direct human impacts are features of high-quality refuges, but extinction thresholds are unquantified and extinction debts of refuges are unknown. Limited information on past extinctions suggests drought, a natural feature of the plains, combines with other threats to eliminate remnant endemic populations. Long-term conservation planning requires identification, protection, and restoration of high-quality refuges to reduce extinction risk, especially during future drought periods. Planning should be integrated with regional water resource planning, given scarcity of water in the region.

Contents

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1. Introduction

Long-term processes create and maintain biodiversity (Callicott, 2002; Willis and Birks, 2006) and unique landscapes and climates that persist over time promote regionalization of faunas (Morrone, 2009). Endemic taxa arise within discrete habitats where extinction rates are low (Diamond, 1984; Oberdorff et al., 1999). Regions with unique environmental conditions and histories tend to harbor assemblages of associated, endemic taxa if suitable habitats are persistent (e.g. Reyjol et al., 2007; Brown et al., 2009). Patterns of human disturbance tend to be regional in nature as well. Entire regional endemic biotas are threatened when regional-scale disturbances degrade suitable habitats and climatic refugia (e.g. Deacon et al., 2007; Williams et al., 2009a).

The plains region of North America (henceforth, "the plains") provides unique aquatic habitats characterized by periodic or sporadic precipitation, highly erosive (sandy) soils, high evaporation relative to precipitation, and abundant and diverse connections with large aquifers (e.g. Matthews, 1988; Hubbs, 1995; Fausch and Bestgen, 1997). A suite of fishes well adapted for life in these habitats exhibits endemism, with distributional boundaries more or less congruent with the boundaries of the plains (e.g. Brunger Lipsey et al., 2005; Hoagstrom et al., 2007c). Efforts to conserve endemic fishes have ensued within the last 40 years (e.g. Ono et al., 1983; Cross and Moss, 1987) and literature suggests their regional status is poor, yet patterns of endemism and species status have received modest study and existing reviews either do not consider the entire region (e.g. Fausch and Bestgen, 1997; Hubert and Gordon, 2007) or are out of date (e.g. Cross et al., 1986). Here, we survey literature on endemic plains fishes to (1) summarize endemic fish diversity and describe associated habitats in the context of long-term persistence of unique taxa (endemism), (2) summarize the status of endemics, and (3) compile a list of refuges (areas recently inhabited by endemics) to focus future conservation efforts. Our approach provides an example of a preliminary analysis for preservation of regional endemics that have received modest levels of study despite widespread declines.

2. Methods

2.1. The plains

The plains include the Great Plains and Osage Plains regions (Fig. 1), which contain mostly un-glaciated, semi-arid, grasslands that encompass roughly 20° of latitude, including portions of eight major river drainages (Matthews, 1988). Three major drainages are tributary to the Gulf of Mexico via the Mississippi River (Missouri River, Arkansas River, Red River) and five are direct tributaries to the Gulf of Mexico (Brazos River, Colorado River, San Antonio Bay rivers, Nueces River, and Rio Grande). The Rocky Mountain and Basin and Range regions bound the plains on the west. Mountains in these regions contain headwater streams of major rivers of the plains. Headwaters of some smaller rivers originate in highlands of the plains or as springs. The Glaciated Central Lowlands, Ozark–Ouachita Uplands, and Coastal Plain regions bound the plains on the east and south. Rivers of the plains flow into these more humid regions upon exiting the plains.

In the plains, there is a continuum of aquatic habitats from those dominated by groundwater discharge (i.e. springs) to those dominated by surface runoff. Large springs have nearly constant environmental conditions (e.g. temperature, discharge) due to the constancy of groundwater chemistry and discharge (Hubbs, 1995, 2001). Aquifers are also a main source of base flow in perennial streams and rivers (e.g. Sophocleous, 2003; Dodds et al., 2004; Hoagstrom, 2009). Groundwater seepage may comprise the majority of streamflow in smaller streams. Narrow meandering channels, relatively stable substrates, grassy riparian zones, and riffle-pool habitat patches characterize these habitats (Cross and Moss, 1987; Dodds et al., 2004). Larger streams are increasingly influenced by surface runoff as drainage area increases. Much of the plains landscape is covered with sandy soils, so runoff into larger streams delivers abundant sand to the river bed and facilitates channel migrations. This creates wide river channels with high width-to-depth ratios and shifting sand substrata. Open-water habitats are relatively shallow (usually only a few meters, often much less, except in the largest rivers) and perpetual sand transport creates a dynamic habitat mosaic (e.g. Polivka, 1999; Hoagstrom et al., 2008a). Rivers of the plains have wide floodplains, often forested with galleries of trees (e.g. *Populus* spp.), and may include various transient and spring-fed aquatic habitats (Hoagstrom and Brooks, 1999; Dodds et al., 2004). Periodic foods connect floodplains with riverine habitats.

Extreme climatic fluctuations (i.e. alternation between warm, dry and cool, wet periods) have strongly influenced native fish faunas of the plains for several million years (Cross, 1970; Newbrey and Ashworth, 2004; Hoagstrom and Berry, 2006). The grassland environment has extended to the east during warm, dry periods (e.g. King, 1981), at which time conditions in the western plains were more arid (Meltzer, 1999). Fishes endemic to the plains likely extended their range to the east during these times, but simultaneously may have declined from the western plains due to widespread desiccation. However, areas with substantial connections to aquifers likely sustained endemic fishes because groundwater responds relatively slowly to climate change, buffering climatic fluctuations (Smith et al., 1997; Chen et al., 2003). High endemism in major springs of the region is a result of extreme, long-term environmental stability (e.g. Longley, 1981).

Main human disturbances to aquatic habitats of the plains are associated with arid-land agriculture, the dominant land use in the region (Parton et al., 2007). In certain areas, urban and industrial developments also cause disturbance (e.g. Johnson and Hubbs, 1989). Dewatering (Cross and Moss, 1987), damming (Poff et al., 2007), and physical habitat modification (e.g. channelization; Dodds et al., 2004) are widespread. Non-native fishes (Gido et al., 2004) and pollution (Hoagstrom, 2003, 2009) also impact endemic fishes in some areas. These impacts are interrelated and often associated with irrigated agriculture, urbanization, mining, and other land uses.

2.2. Endemic fishes, habitat types, and refuges of the plains

We reviewed literature to compile a list of endemic fishes of the plains with an assessment of their status. Our review was focused on peer-reviewed articles because they are the best and most accessible long-term record of fish assemblage studies, but we supplemented our search with distributional reviews, theses and dissertations, and government agency reports to determine the status of all endemics.

We defined endemic fishes as those with distributions centered in the plains. Some taxa ranged into adjacent regions, but all were characteristic of typical plains habitats and, when present in adjacent regions, were restricted to plains-type habitats. We summarized patterns of endemic diversity among river drainages (beta diversity) by calculating percent of unshared taxa between neighboring river drainages (Hoagstrom et al., 2007c) and noted introductions to drainages outside their native range.

We used our entire library to group endemic taxa into four "status" categories: (1) declining (range or abundance less than historically documented), (2) stable (range unchanged), (3) increasing (existing throughout historical range and expanding via invasions), or (4) unknown. We grouped factors contributing to declines into

Fig. 1. Map of central North America showing the Great Plains and Osage Plains physiographic regions that comprise the plains of North America. State lines (USA) and major river drainages are also shown.

five categories: (1) dewatering, (2) fragmentation, (3) geomorphic and flow regime degradation, including channelization, geomorphic change caused by land use or hydrologic change, changes in flood magnitude or timing, and inundation by reservoirs, (4) non-native species, and (5) pollution, including silt, nutrients, and salts along with agricultural, industrial, and urban pollutants. From this, we determined relative prevalence of each factor in declines of endemic fishes.

We identified habitat types used by endemics based on descriptions of their habitat associations (sensu Cross and Moss, 1987; Fausch and Bestgen, 1997; Propst, 1999) and noted taxonomic and ecological diversity of endemic fishes in each habitat. With the aid of additional references (Page, 1985; Page and Burr, 1991; Johnston and Page, 1992; Baxter and Stone, 1995; Cross and Collins, 1995; Platania and Altenbach, 1998; Holton and Johnson, 2003; Miller and Robison, 2004; Thomas et al., 2007; Durham and Wilde, 2008a,b; Wilde and Durham, 2008), we determined maximum body size and breeding strategies of endemic fishes to provide ecological insight into their long-term survival (Lawton, 1995; Williams et al., 2009b).

Finally, we compiled a list of waters harboring endemic taxa (refuges) and taxon distributions among them. For this, we only used references based on post-1989 surveys. As time goes by, it is decreasingly likely that older surveys accurately reflect modern assemblages because fish assemblages of the plains are highly dynamic (Hoagstrom et al., 2007b, 2009). Our choice of 1989 as a cutoff was arbitrary, but long-enough to include a relatively large number of published surveys. We classified refuges harboring three or more endemics as "high-quality" and plotted mean monthly discharge for a 50-year period (water years 1959 through 2008) for high-quality refuges having available US Geological Survey gaging station data. We used simple linear regression to identify trends in mean monthly discharge over time.

3. Results

3.1. Endemic fishes

At least 49 fish taxa are endemic to the plains (Table 1). Thirty-seven (76%) are native to only one major drainage (Table 2). Taxa with multi-drainage distributions occupy neighboring drainages. Beta diversity among drainages is high, with more than 36% of endemics unshared between all neighboring pairs of drainages (Fig. 2).

Forty-one endemics (84%) have declined or are extinct, including taxa native to a single spring (e.g. *Gambusia amistadensis*) and with broad distributions (e.g. *Hybognathus placitus*). Range declines are linked to dewatering (34 taxa), geomorphic and flow regime degradation (33 taxa), habitat fragmentation (32 taxa), non-natives (16 taxa), and pollution (16 taxa; Fig. 3). It is rare for a taxon to be threatened by a single factor. Twenty-three are affected by the combination of dewatering, fragmentation, and geomorphic change. For two (*Satan eurystomus*, *Trogloglanis pattersoni*), recent status information is unavailable. Six endemics (12%) are stable or increasing and ten (20%) are established outside their native range.

3.2. Habitat types of endemic fishes

Endemic fishes are segregated among four habitat types (Table 2): smaller spring-fed streams (stream endemics, $n = 16$), open-water habitats of larger streams (riverine endemics, $n = 15$), springs and spring runs (spring endemics, $n = 12$), and saline habitats (euryhaline endemics, $n = 6$). Stream endemics are taxonomically diverse (three families) and as a result, use an array of spawning modes (Table 3). Spring and euryhaline endemics use spawning modes similar to stream endemics, but are less diverse (Table 3). Riverine endemics use a single, unique spawning mode associated with unstable (shifting sand) substrata (Table 3). Taxa of all niches are small-bodied (<150 mm) except for the stream endemic *Micropterus treculii* (Table 2). Spring endemics are restricted to the Colorado River, San Antonio Bay, and Rio Grande drainages (Fig. 2) and each is native to a single drainage (Table 2). All riverine and euryhaline endemics, 88% of stream endemics, and half of spring endemics have declined or are extinct (Table 1). Each conservation threat affected endemics of all habitat types. Dewatering, fragmentation, and geomorphic change affected most riverine and euryhaline endemics (Fig. 3).

3.3. Recent refuges for endemic fishes

At least 53 refuges, supporting 1–7 endemic taxa (mean = 3.3 ± 1.57 SD) were reported since 1989 (Table 4). There was distributional overlap among endemics of different habitat types, with 40 refuges (75%) harboring taxa of more than one habitat type (Table 4). Individual taxa occupied from 0 to 27 refuges (Table 2; mean = 3.6 ± 5.23 SD). Seven were widespread (>7 refuges), but ten were undocumented (Table 3). Refuges harboring just one or two endemics typically housed only widespread taxa, whereas those with three or more often harbored at least one rarer taxon. With two exceptions (noted above), undocumented taxa were not extinct (Table 1), but simply absent from assemblages documented in post-1989 literature.

Streamflow data for 1959 through 2008 were available for 20 of 34 high-quality refuges (refuge 2 was included although data for 2008 were unavailable) that harbored three or more endemics. For all of these refuges, time (month and year) explained less than 10% of variation in mean monthly discharge, indicating no appreciable temporal trend (Fig. 4). In fact, percent of variation explained exceeded 3% in only one case (refuge 20), which exhibited a slight decline in mean monthly discharge over time, especially after 2000.

4. Discussion

4.1. Ecological biogeography of endemism in plains fishes

Endemic fishes of the plains diversified via isolation among major river drainages and springs. Four characteristic habitat types maintain endemic taxa. Spring-fed streams, rivers, and saline wetlands are naturally widespread (Matthews, 1988), whereas major springs are concentrated in southern drainages (Stevens and Meretsky, 2008). Major river drainages and major spring systems are thus biologically meaningful management entities for conservation of regional endemism. Within drainages, further dewatering, habitat fragmentation, and geomorphic and flow regime degradation should be avoided and opportunities for habitat restoration should be considered. Major springs should be protected from dewatering. In all cases, pollution and non-native species introductions should be avoided and areas with pollution or established non-native species should be considered for restoration.

With one exception, endemic fishes of the plains are small-bodied. Functional benefits of small size include efficient use of small food items and spawning sites, avoidance of large predators in size-specific refuges, early maturation, and larger population size per area (Miller, 1996; Williams et al., 2009b). Small size is likely advantageous in the plains given predominance of relatively shallow waters and fine substrata (Cross et al., 1985; Matthews, 1988) and intra-regional speciation is more likely for small-bodied taxa if populations are more easily isolated.

River drainages of the plains are geographically extensive and lack physical barriers to fish dispersal (i.e., waterfalls). Endemic fishes appear to have substantial dispersal ability within drainages because, with the exception of spring endemics, only drainage divides and regional boundaries correspond with divergent taxa. Most instances of endemics occupying multiple drainages are attributable to inter-drainage stream exchanges within the plains. Stream connections via headwater stream captures, cross-grading

Table 1
Endemic fish taxa (species and sub species) in the plains of North America with a review of their status in their native range (stable – "–", declining – "↓", increasing – "↑", extinct – "x", unknown – "?", asterisks "*" indicate species introduced outside their native range) and assessment of major causes for declines (dewatering – D, fragmentation – F, geomorphic and flow regime change – G, non-native species – N, pollution – P).

Species	Status	Causes	References
CYPRINIDAE			
Plateau shiner, *Cyprinella lepida*	↓	DFGP	31, 75
Proserpine shiner, *Cyprinella proserpina*	↓	DGNP	3, 51, 53
Nueces shiner, *Cyprinella* sp.	↓	DNP	31, 75
Manantial roundnose minnow, *Dionda argentosa*	–		26, 34, 53, 75
Devils River minnow, *Dionda diaboli*	↓	DFGNP	24, 46, 63
Roundnose minnow, *Dionda episcopa*	↓	DFG	22, 51
Guadalupe roundnose minnow, *Dionda nigrotaeniata*	↓	D	69, 75
Nueces roundnose minnow, *Dionda serena*	–		75
Rio Grande silvery minnow, *Hybognathus amarus*	↓	DFGNP	22, 23, 39, 51, 64, 77
Western silvery minnow, *Hybognathus argyritis*	↓	DFGN	17, 59, 65, 67, 68, 70
Plains minnow, *Hybognathus placitus*	↓*	DFGN	16, 17, 18, 22, 25, 40, 42, 59, 65, 67, 68, 70
Rio Grande speckled chub, *Macrhybopsis aestivalis*	↓	DFGP	22, 51, 55, 60
Prairie chub, *Macrhybopsis australis*	↓	DF	25, 55, 58
Sturgeon chub, *Macrhybopsis gelida*	↓	DFGN	17, 28, 56, 59, 65, 67, 68
Burrhead chub, *Macrhybopsis marconis*	↓	FG	55, 75, 78
Sicklefin chub, *Macrhybopsis meeki*	↓	FG	17, 56
Peppered chub, *Macrhybopsis tetranema*	↓	DF	17, 18, 22, 37, 39
Texas shiner, *Notropis amabilis*	↓	DFG	22, 51
Red river shiner, *Notropis bairdi*	↓*	DF	25, 37, 42
Smalleye shiner, *Notropis buccula*	↓	DF	40, 75
Arkansas River shiner, *Notropis girardi*	↓*	DFGN	17, 18, 22, 38, 39, 48
Rio Grande shiner, *Notropis jemezanus*	↓	DFGP	22, 24, 51, 61, 62
Sharpnose shiner, *Notropis oxyrhynchus*	↓*	DFG	10, 24
Pecos bluntnose shiner, *Notropis simus pecosensis*	↓	DFGP	13, 22, 39, 51, 73, 74
Plains sand shiner, *Notropis stramineus missuriensis*	–*		16, 17, 18, 25, 65, 70, 71
ICTALURIDAE			
Widemouth blindcat, *Satan eurystomus*	?		11, 15
Toothless blindcat, *Trogloglanis pattersoni*	?		11, 15
FUNDULIDAE			
Northern plains killifish, *Fundulus kansae*	↓*	DFG	9, 14, 17, 65, 70
Plains killifish, *Fundulus zebrinus*	↓*	DFGNP	24, 42, 51
POECILIIDAE			
Amistad gambusia, *Gambusia amistadensis*	x	G	3, 4, 12, 20, 52
San Felipe gambusia, *Gambusia clarkhubbsi*	–		50, 66
Largespring gambusia, *Gambusia geiseri*	↑*		1, 24, 43, 51
San Marcos gambusia, *Gambusia georgei*	x	DNP	20, 44, 75
Clear Creek gambusia, *Gambusia heterochir*	–		2, 47, 75
Pecos gambusia, *Gambusia nobilis*	↓	DFN	3, 8, 19, 22, 39, 43, 52
CYPRINODONTIDAE			
Leon springs pupfish, *Cyprinodon bovinus*	↓	DFGNP	3, 33, 49
Comanche springs pupfish, *Cyprinodon elegans*	↓	DFGN	3, 45, 49
Devils River pupfish, *Cyprinodon eximius* sp.	↓	DFG	21, 49, 61
Pecos pupfish, *Cyprinodon pecosensis*	↓	DFGNP	3, 22, 36, 39
Brazos River pupfish, *Cyprinodon rubrofluviatilis* sp.	↓	FG	10, 27, 75
Red River pupfish, *Cyprinodon rubrofluviatilis* sp.	↓*	FGP	27, 30, 57, 75
CENTRARCHIDAE			
Guadalupe bass, *Micropterus treculii*	↓*	DFGN	7, 54, 69, 72
PERCIDAE			
Arkansas darter, *Etheostoma cragini*	↓	DFG	5, 17, 18, 41
Fountain darter, *Etheostoma fonticola*	↓	DGP	6, 75, 78
Rio Grande darter, *Etheostoma grahami*	↓	DGNP	3, 51, 53
Greenthroat darter, *Etheostoma lepidum*	↓	DFGP	3, 7, 22, 39, 51, 69
Plains orangethroat darter, *Etheostoma spectabile pulchellum*	↓	DFG	17, 18, 65, 76, 78
Guadalupe darter, *Percina apristis*	↓	G	54, 75, 78
Texas logperch, *Percina carbonaria*	↓	G	7, 75, 78

1: Hubbs and Springer (1957); 2: Hubbs (1971), 3: Hubbs and Echelle (1972), 4: Peden (1973); 5: Hubbs and Pigg (1976); 6: Schenck and Whiteside (1976); 7: Edwards (1978); 8: Bednarz (1979); 9: Knight et al. (1980); 10: Anderson et al. (1983); 11: Ono et al. (1983); 12: Hubbs and Jensen, 1984; 13: Hatch et al., 1985; 14: Brown (1986); 15: Culver (1986); 16: Propst and Carlson (1986); 17: Cross and Moss (1987); 18: Pigg (1987); 19: Echelle et al. (1989); 20: Miller et al. (1989); 21: Hubbs and Garrett (1990); 22: Sublette et al. (1990); 23: Bestgen and Platania (1991); 24: Hubbs et al. (1991); 25: Winston et al. (1991); 26: Garrett et al. (1992); 27: Ashbaugh et al. (1994); 28: Kelsch (1994); 29: Luttrell et al. (1995); 30: Pigg et al. (1995); 31: Richardson and Gold (1995); 32: Childs et al. (1996); 33: Echelle and Echelle (1997); 34: Valdes Cantu and Winemiller (1997); 35: Gido et al. (1999); 36: Hoagstrom and Brooks (1999); 37: Luttrell et al. (1999); 38: Pigg et al. (1999); 39: Propst (1999); 40: Wilde and Ostrand (1999); 41: Eberle and Stark (2000); 42: Lienesch et al. (2000); 43: Hubbs (2001); 44: Edwards et al. (2002); 45: Garrett et al. (2002a); 46: Garrett et al. (2002b); 47: Hubbs et al. (2002); 48: Wilde (2002); 49: Echelle et al. (2003); 50: Garrett and Edwards (2003); 51: Hoagstrom (2003); 52: Hubbs (2003); 53: Robertson and Winemiller (2003); 54: Edwards et al. (2004); 55: Eisenhour (2004); 56: Everett et al. (2004); 57: McNeely et al. (2004); 58: Miller and Robison (2004); 59: Quist et al. (2004); 60: Bonner et al. (2005); 61: Garrett et al. (2005); 62: Hoagstrom and Brooks (2005); 63: López-Fernández and Winemiller (2005); 64: Moyer et al. (2005); 65: Peters and Schainost (2005); 66: Edwards and Garrett (2006); 67: Hoagstrom et al. (2006a); 68: Hoagstrom et al. (2006b); 69: Bean et al. (2007); 70: Hoagstrom et al. (2007a); 71: Lionberger and Hubert (2007); 72: Thomas et al. (2007); 73: Hoagstrom et al. (2008a); 74: Hoagstrom et al. (2008b); 75: Hubbs et al. (2008); 76: Bossu and Near (2009); 77: Hoagstrom et al. (2010); 78: Perkin and Bonner (2010).

between stream valleys, or downstream drainage interconnections during periods of low sea level were relatively common among Red, Brazos, Colorado, San Antonio Bay, Nueces, and Rio Grande drainages (Conner and Suttkus, 1986; Cross et al., 1986; Smith and Miller, 1986; Mayden et al., 1992), corresponding with multi-drainage distributions of *Dionda nigrotaeniata*, *Dionda serena*,

Table 2
Maximum size, spawning mode (C = crevice spawning adhesive eggs; D = broadcast demersal adhesive or non-adhesive eggs; N = nesting; A = egg attachers; B = egg buriers; P = broadcast pelagic, non-adhesive eggs; L = livebearer), native drainages (1 = Missouri River, 2 = Arkansas River, 3 = Red River, 4 = Brazos River, 5 = Colorado River, 6 = San Antonio Bay, 7 = Nueces River, 8 = Rio Grande), refuges occupied (references in Table 4), and total number of refuges occupied by endemic fishes of the plains of North America within each of four habitat types. Non-native populations are not included.

Species	Size (mm)	Spawning mode	Drainages	Refuges	Total
Stream endemics					
Cyprinella lepida	76	C	7		0
Cyprinella proserpina	76	C	8	49, 50, 51	3
Cyprinella sp.	76	C	7		0
Dionda diaboli	64	D	8	50, 51, 52, 53	4
Dionda episcopa	77	D	8	43, 45, 49	3
Dionda nigrotaeniata	76	D	5, 6	34, 35, 36	3
Dionda serena	76	D	6, 7		0
Notropis amabilis	64	D	4–8	36, 37, 38, 39, 49, 50, 53	7
Notropis stramineus missuriensis	111	D	1–3	1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 30	27
Micropterus treculii	462	N	4–6	36, 37, 38, 39, 41	5
Etheostoma cragini	64	B	2		0
Etheostoma grahami	60	A	8	49, 50, 51, 52	4
Etheostoma lepidum	66	A	5–8	34, 35, 43, 45	4
Etheostoma spectabile pulchellum	72	B	1–6	15, 16, 20, 21, 29, 36, 37, 38, 39, 40, 41	11
Percina apristis	127	B	6	36, 38	2
Percina carbonaria	132	B	4–6	36, 37, 38, 39	4
Riverine endemics					
Hybognathus amarus	89	P	8		0
Hybognathus argyritis	150	P	1	1, 2, 3, 4, 5, 9, 10, 11, 14, 19	10
Hybognathus placitus	150	P	1–5	1, 4, 5, 6, 7, 8, 9, 10, 11, 14, 15, 18, 19, 25, 26, 27, 29, 30, 31, 32	20
Macrhybopsis aestivalis	76	P	8	42, 49	2
Macrhybopsis australis	76	P	3	29	1
Macrhybopsis gelida	111	P	1	1, 2, 9, 11	4
Macrhybopsis marconis	76	P	5, 6	36, 37, 38, 39	4
Macrhybopsis meeki	111	P	1	2, 14	2
Macrhybopsis tetranema	76	P	2	26	1
Notropis bairdi	83	P	3	29, 30	1
Notropis buccula	71	P	4	31, 32, 33	3
Notropis girardi	80	P	2	26, 27	2
Notropis jemezanus	76	P	8	42, 49	2
Notropis oxyrhynchus	65	P	4	32, 33	2
Notropis simus pecosensis	100	P	8	42	1
Spring endemics					
Dionda argentosa	64	D	8	50, 51, 52	3
Satan eurystomus	137	?	6		0
Trogloglanis pattersoni	104	?	6		0
Gambusia amistadensis	50	L	8		0
Gambusia clarkhubbsi	58	L	8	51	1
Gambusia geiseri	44	L	6		0
Gambusia georgei	50	L	6		0
Gambusia heterochir	54	L	5	34	1
Gambusia nobilis	64	L	8	43, 45, 47, 48	4
Cyprinodon bovinus	58	A	8	47	1
Cyprinodon elegans	62	A	8	48	1
Etheostoma fonticola	43	A	6		0
Euryhaline endemics					
Fundulus kansae	111	D	1, 2	8, 9, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28	15
Fundulus zebrinus	102	D	3–5, 8	29, 31, 32, 35, 42, 43, 44, 46, 49	9
Cyprinodon eximius sp.	50	A	8	50	1
Cyprinodon pecosensis	60	A	8	42, 43, 44, 46	4
Cyprinodon rubrofluviatilis sp.	58	A	4	31, 32	2
Cyprinodon rubrofluviatilis sp.	58	A	3	29	1

Macrhybopsis marconis, *Notropis amabilis*, *Fundulus zebrinus*, *Micropterus treculii*, *Etheostoma lepidum*, and *Percina carbonaria*. Also, the Smoky Hill and upper Salina rivers were transferred from the Missouri River drainage to the Arkansas River drainage and back again (Hunt, 1974; Hoagstrom and Berry, 2006), corresponding with presence of *Notropis stramineus missuriensis*, *Hybognathus placitus*, *Fundulus kansae*, and *Etheostoma spectabile pulchellum* in both drainages. Of these taxa, only *F. kansae* is restricted to these two drainages. Broader distributions of *H. placitus*, *N. s. missuriensis*, and *E. s. pulchellum* could reflect more recent dispersal among drainages, lower rates of divergence, or unrecognized, cryptic diversity. Long-distance dispersal through downstream regions via the Mississippi River, along with stream captures (described above) could explain their presence in the Missouri, Arkansas, and Red river drainages, but occurrence in the Brazos, Colorado, and San Antonio Bay drainages (not directly connected to the Mississippi River) must reflect inter-drainage stream connections, lower rates of divergence, or cryptic diversity. The phylogeography of these fishes has been studied (Al-Rawi and Cross, 1964; Tanyolaç, 1973; Bossu and Near, 2009), but detailed molecular

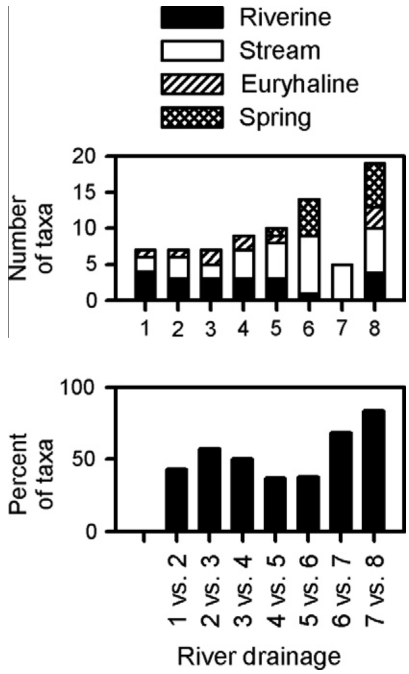

Fig. 2. Number of endemic fishes in the plains of North America by river drainage grouped by habitat type (top, drainage numbers are given in Table 2) and endemic species turnover (percent of endemic species unshared) between adjacent river drainages (bottom).

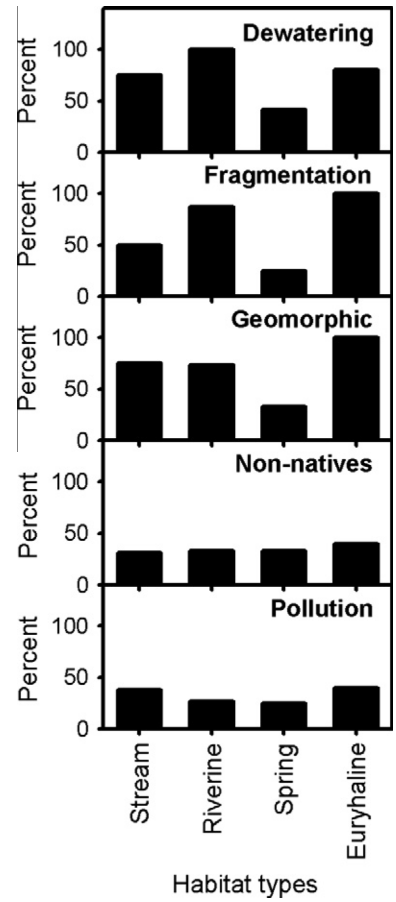

Fig. 3. Percentage of endemic fish taxa of four habitat types in the plains of North America that is declining in association with the stressors: habitat dewatering, habitat fragmentation, geomorphic degradation, non-native taxa, and water pollution.

analyses of trends within the plains are lacking. Future recognition of cryptic diversity would reinforce the general trend of endemism by drainage, whereas absence would suggest widespread dispersal events or slower rates of divergence. Inter-drainage dispersal, though noteworthy, is peripheral to the general pattern of diversification among drainages, but correspondence to inter-drainage distributions supports the significance of regional boundaries downstream for limiting dispersal of endemic fishes among drainages.

Habitats suitable for riverine, euryhaline, and stream endemics were widespread throughout the plains and distributed as a mosaic within natural riverine landscapes (e.g. Cross et al., 1985; Hoagstrom and Brooks, 1999). Mountainous headwaters with high annual precipitation and geographically extensive drainages ensured riverine habitats persisted in the plains despite climatic shifts, although they were more widespread in wet periods. Downstream river sections with larger drainages were likely refugia during warm, dry periods. Extension of plains-like conditions to the east would have allowed riverine endemics to retreat farther than at present. Downstream reaches of the largest plains rivers were likely climatic refugia for riverine endemics, but divergence among major drainages indicates regional boundaries limited downstream dispersal among major plains rivers.

Euryhaline habitats can be evaporative pools formed via floods and flow pulses, terminal wetlands fed by freshwater springs, or saline springs fed by brine aquifers (e.g. Hoagstrom and Brooks, 1999). Populations of euryhaline endemics are often patchy and transient depending on the abundance, distribution, and persistence of euryhaline habitats, so dispersal is important for maintaining broad distributions (Cross et al., 1985; Fausch and Bestgen, 1997; Hoagstrom and Brooks, 1999). Euryhaline endemics tolerate freshwater habitats, which they use to colonize disjunct saline habitats (Hoagstrom and Brooks, 1999; Ostrand and Wilde, 2004; Hoagstrom et al., 2009), but rely on saline habitats as refuge from competition with freshwater fishes (e.g. Echelle et al., 1972) and stable substrates of stagnant, saline waters are needed for egg deposition or attachment. Saline springs likely were climatic refugia during cool, wet periods when euryhaline habitats were rare. Isolated populations of euryhaline endemics persist in saline springs of adjacent, less-arid regions to the east (Pflieger, 1997; Miller and Robison, 2004), presumably as relicts from warm, dry periods when euryhaline fishes were more widespread. Freshwater spring-fed wetlands were likely important climatic refugia during warm, dry periods, when transient euryhaline habitats were hypersaline or desiccated. Warm springs may have provided thermal refugia in the northern plains during cool, wet periods (Hoagstrom et al., 2009).

Spring and spring-fed stream habitats represent a continuum of habitats reliant on spring flow. Spring endemics depend on local habitats and supporting aquifers (Hubbs, 1995, 2001), with dispersal limited to spring-fed corridors (e.g. Echelle et al., 1989, 2003). In contrast, stream endemics depend on groundwater discharge but also employ broader dispersal to maintain populations (Fausch et al., 2002; Falke, 2009). Spring brooks—a natural feature in riverine landscapes of the plains—provided abundant habitats for stream endemics and facilitated their dispersal (Cross et al., 1985). Stable substrates of springs and spring-fed streams facilitate various types of egg deposition or attachment and more intense biological interactions in these environmentally stable habitats favor energetically expensive reproductive behaviors and spawning modes (Kodric-Brown, 1981; Constantz, 1981). However, association with more stable environments may limit the northern

Table 3
Taxonomic diversity (genus with number of species in parentheses) and spawning mode (C = crevice spawning adhesive eggs; D = broadcast demersal adhesive or non-adhesive eggs; N = nesting; A = egg attachers; B = egg burier; P = broadcast pelagic, non-adhesive eggs; L = livebearer), of endemic fishes in four habitat types of the plains of North America – smaller streams, major rivers (open water), springs and spring runs, and saline habitats (euryhaline).

Mode	Stream	Riverine	Spring	Euryhaline
C	*Cyprinella* (3)			
D	*Dionda* (4)		*Dionda* (1)	*Fundulus* (2)
N	*Micropterus* (1)			
A	*Etheostoma* (2)		*Cyprinodon* (2) *Etheostoma* (1)	*Cyprinodon* (4)
B	*Etheostoma* (2) *Percina* (2)			
P		*Hybognathus* (3) *Macrhybopsis* (6) *Notropis* (6)		
L			*Gambusia* (6)	

distribution of spring and stream endemics. All but two are restricted to the southern plains in association with major spring systems (Stevens and Meretsky, 2008) and a milder climate (McAllister et al., 1986).

4.2. Conserving regional endemism

Analysis of regional endemism reveals habitats that maintain biodiversity over large spatial and temporal scales. For example, endemic fishes of the plains occupy characteristic habitats with ample climatic refugia. Characteristic habitats of the region facilitated divergence from related taxa in adjacent regions. Taxa of plains habitats became restricted to the plains such that regional boundaries limited dispersal among major drainages. Thus, perpetuation of endemic plains fishes relies on maintenance of characteristic habitats including refugia. Human disturbances have impacted endemic fishes of the plains by degrading characteristic habitats (dewatering, fragmentation, geomorphic and flow regime degradation, non-native introductions, pollution) and restricting dispersal (fragmentation). Similarly, endemic species elsewhere are threatened by habitat fragmentation and degradation, including loss of climatic refugia (e.g. Attorre et al., 2007; Lees and Peres, 2008; Ford et al., 2009).

Our analysis represents an early step in assessing long-term status of regional endemics. Its accuracy relies on identification of endemics and existing refuges via taxonomic studies (Cook et al., 2008; Hendry et al., 2010) and field surveys (Rosenberg and Muratov, 2005). For example, endemic fish diversity in the plains may be underestimated because new taxa continue to be discovered (Garrett and Edwards, 2003). Unknown populations of endemic fishes also continue to be discovered (Garrett et al., 2004). Thus, our analysis is preliminary in the sense that future phylogenetic studies may reveal additional endemism and future field surveys may discover more refuges. Despite this, it provides the benefit of identifying endemic taxa in need of more detailed study (e.g. *H. placitus* and *E. s. pulchellum*) and areas in need of more field surveys (e.g. Nueces River drainage).

A next step would be to determine refuge viability and population status of resident endemics (Moyle, 1995; Winston and Angermeier, 1995). Determining extinction debt (Tilman et al., 1994) would help identify refuges needing rapid conservation action and avoid overly optimistic estimates of endemic taxon status. Yet, evaluating extinction debt is a challenge (Olden et al., 2010). Extinction debts are highest where habitat destruction is geographically varied (Loehle and Li, 1996), disturbance disrupts metapopulation dynamics (Bulman et al., 2007), taxa disperse to track dynamic habitats (Thuiller et al., 2005), and disturbance is recent or ongoing (Hanski and Ovaskainen, 2002; Ford et al., 2009). In the plains, all of the above criteria pertain to contemporary refuges (e.g., Luttrell et al., 1999; Falke and Fausch, 2010). Refuges with extinction debt may be unsuitable for long-term conservation unless it includes or restoration. Drought and habitat fragmentation are believed to have eliminated historic populations of endemic fishes (Winston et al., 1991; Kelsch, 1994; Luttrell et al., 1999; Wilde and Ostrand, 1999), cumulative effects of periodic droughts may erode population viability (Turner et al., 2006), droughts more severe than historical ones are evident from prehistoric records, indicating relatively severe droughts may occur in the future (Forman et al., 2001; Cook et al., 2004), and human disturbances may also increase severity of future droughts (Muhs and Maat, 1993; Seager et al., 2007). Further, some studies have already anticipated future declines of endemic fishes (Echelle et al., 1989; Hesse, 1994; Wilde and Ostrand, 1999; Lienesch et al., 2000; Ostrand and Wilde, 2002). Hence, future drought combined with effects of past and ongoing disturbance could result in rapid, widespread losses of endemic fish populations, similar to concerns in adjacent regions (Deacon et al., 2007; Williams et al., 2009a).

Large-scale assessments of refuges are increasingly feasible via emerging technologies and associated new approaches (Buchanan et al., 2008), but these still rely on basic biological information. For example, the distribution and environmental limits of remnant populations of endemic *Oncorhynchus clarkii* are relatively well understood in the Rocky Mountain region of North America, which facilitates large-scale assessment of refuge viability (Williams et al., 2009a). In the adjacent plains region, case studies have quantified characteristics of viable refuges for spring (e.g. Echelle et al., 1989; Hubbs, 2001), stream (e.g. Labbe and Fausch, 2000; Falke and Fausch, 2010), euryhaline (e.g. Higgins and Wilde, 2005; Echelle et al., 2006), and riverine (e.g. Polivka, 1999; Dudley and Platania, 2007; Hoagstrom et al., 2008b) endemics, but criteria have not been synthesized within habitat types or among river drainages and ecological thresholds (sensu Catalan et al., 2009) are undetermined. Hence, it is not yet possible to conduct a regional assessment of refuge viability in the plains. Case histories indicate high-quality refuges suffer less water withdrawal (Bonner and Wilde, 2000; Hoagstrom et al., 2008a), incorporate larger habitat areas (Labbe and Fausch, 2000; Dudley and Platania, 2007), and have less degraded flow regimes, uplands, and stream channels (Polivka, 1999; Dieterman and Galat, 2004; Quist et al., 2004; Perkin and Bonner, 2010). Available data indicate high-quality refuges have maintained consistent streamflow regimes for at least 50 years.

Ultimate conservation of global biological diversity partly relies on viable refuges nested within human-dominated landscapes (Rosenzweig, 2003). This is particularly evident for aquatic biota of river systems in semi-arid, arid, or heavily populated regions where water development for human use results in appropriation of water supplies (Deacon et al., 2007), fragmentation and degradation of natural habitats (Dynesius and Nilsson, 1994), alteration of natural processes (Poff et al., 2007), and invasion of non-native species (Johnson et al., 2008). Analogous examples affecting terrestrial endemics are (for example) associated with deforestation (Sánchez-Cordero et al., 2005; Buchanan et al., 2008) and urbanization (Bond et al., 2006; Mcdonald et al., 2008). Preservation,

Table 4
Preliminary list of aquatic refuges for endemic fishes in the plains of North America from literature based on post-1989 surveys with the number of native extant endemic fishes (Taxa). Refuges harbored endemic fishes of stream (St), riverine (R), spring (Sp), or euryhaline (E) habitats. Drainage numbers (in parentheses) are used in Table 2.

Water body	Taxa	Niches	References
Missouri River drainage (1)			
1. Powder River	4	St, R	10, 45
2. Yellowstone/Missouri River: Lower Yellowstone Diversion to Lake Sakakawea	3	R	39, 41, 46
3. Upper Little Missouri River	2	St, R	10, 45
4. Lower Little Missouri River	3	St, R	4, 16
5. Moreau River	3	St, R	20
6. Belle Fourche River upstream of Keyhole Reservoir	2	St, R	10, 45
7. Belle Fourche River: Keyhole dam to Belle Fourche dam	2	St, R	10, 14, 56
8. Cheyenne River upstream of Angostura Reservoir	3	St, R, E	10, 40, 45, 56
9. Belle Fourche/Cheyenne River: Belle Fourche/Angostura dams to Lake Oahe	5	St, R, E	22, 40, 55, 56
10. Bad River	3	St, R	56
11. White River downstream of Nebraska border	4	St, R	56
12. Missouri River: Fort Randall Dam to Lewis and Clark Lake	1	St	38, 60
13. Keya Paha River	1	St	43
14. Missouri River downstream of Gavins Point Dam	4	St, R	3, 38, 39
15. North Platte River: Guernsey Dam to Lake McConaughy	4	St, R, E	1, 5
16. North Platte River downstream of Kingsley Dam	3	St, E	5
17. Horse Creek	1	E	57
18. Lower South Platte River	3	St, R, E	5
19. Central Platte River	4	St, R, E	7, 37
20. Lower Arikaree River	3	St, E	36
21. Republican/Smoky Hill/Kansas rivers downstream of Kanopolis & Milford dams	2	St	2, 29, 63
Arkansas River drainage (2)			
22. Lower Purgatoire River	2	St, E	9
23. Ninnescah River upstream of Cheney Reservoir	2	St, E	52
24. Upper Cimarron River	2	St, E	18
25. Ute Creek	3	St, R, E	11
26. South Canadian River: Ute Dam to Lake Meredith	5	St, R, E	21, 26, 50, 59
27. South Canadian River: Sanford Dam to Lake Eufala	4	St, R, E	23, 26
28. Deep Fork Canadian River	2	St, E	15
Red River drainage (3)			
29. Red River upstream of Lake Texoma	6	St, R, E	6, 48
30. Buncombe Creek	3	St, R	27
Brazos River drainage (4)			
31. Double Mountain Fork Brazos River upstream of Lake Alan Henry	4	R, E	25
32. Brazos River upstream of Possum Kingdom Lake	5	R, E	30, 44
33. Middle Brazos River	2	R	50
Colorado River drainage (5)			
34. Clear Creek	3	St, Sp	17
35. Pedernales River	3	St., E	59
San Antonio Bay drainage (6)			
36. Blanco River	7	St, R	58
37. Guadalupe River upstream of Canyon Lake Reservoir	5	St, R	64
38. Guadalupe River downstream of Canyon Lake Reservoir	6	St, R	64
39. San Marcos River	6	St, Sp, R	64
40. Cibolo Creek	1	St	17
41. San Antonio River	2	St	17
Rio Grande drainage (8)			
42. Pecos River: Fort Sumner Irrigation District Diversion to Brantley Reservoir	5	R, E	19, 49, 62
43. Bitter Lake	5	St, Sp, E	19
44. Bottomless Lakes	2	E	19
45. Blue Spring	3	St, Sp	24, 34
46. Salt Creek	2	E	53
47. Diamond Y Spring	2	Sp	8, 31, 32, 35
48. San Solomon Springs	2	Sp	13, 31, 32, 34, 35
49. Independence Creek/Lower Pecos River	7	St, R, E	33, 35, 47
50. Devils River	6	St, Sp, E	12, 35
51. San Felipe Creek	5	St, Sp	32, 54
52. Sycamore Creek	3	St, Sp	28
53. Pinto Creek	2	St	42

1: Patton and Hubert (1993); 2: Wenke et al. (1993); 3: Hesse (1994); 4: Kelsch (1994); 5: Lynch and Roh (1996); 6: Taylor et al. (1996); 7: Chadwick et al. (1997); 8: Echelle and Echelle (1997); 9: Lohr and Fausch (1997); 10: Patton (1997); 11: Pittenger and Schiffmiller (1997); 12: Valdes Cantu and Winemiller (1997); 13: Winemiller and Anderson (1997); 14: Doorenbos (1998); 15: Pigg et al. (1998); 16: Barfoot and White (1999); 17: Edwards (1999); 18: Hargett et al. (1999); 19: Hoagstrom and Brooks (1999); 20: Loomis et al. (1999); 21: Luttrell et al. (1999); 22: Newman et al. (1999); 23: Polivka (1999); 24: Propst (1999); 25: Wilde and Ostrand (1999); 26: Bonner and Wilde (2000); 27: Lienesch et al. (2000); 28: Garrett and Edwards (2001); 29: Fritz et al. (2002); 30: Ostrand and Wilde (2002); 31: Echelle et al. (2003); 32: Garrett (2003); 33: Hoagstrom (2003); 34: Hubbs (2003); 35: Karges (2003); 36: Scheurer et al. (2003); 37: Yu and Peters (2003); 38: Berry and Young (2004); 39: Dieterman and Galat (2004); 40: Duehr (2004); 41: Everett et al. (2004); 42: Garrett et al. (2004); 43: Harland and Berry (2004); 44: Ostrand and Wilde (2004); 45: Quist et al. (2004); 46: Welker and Scarnecchia (2004); 47: Bonner et al. (2005); 48: Higgins and Wilde (2005); 49: Hoagstrom and Brooks (2005); 50: Zeug et al. (2005); 51: Durham and Wilde (2006); 52: Durham et al. (2006); 53: Echelle et al. (2006); 54: Edwards and Garrett (2006); 55: Hoagstrom et al. (2006a); 56: Hoagstrom et al. (2006b); 57: Quist et al. (2006); 58: Bean et al. (2007); 59: Birnbaum et al. (2007); 60: Kaemingk et al. (2007); 61: Durham and Wilde (2008b); 62: Hoagstrom et al. (2008a); 63: Eitzmann and Paukert (2010); 64: Perkin and Bonner (2010).

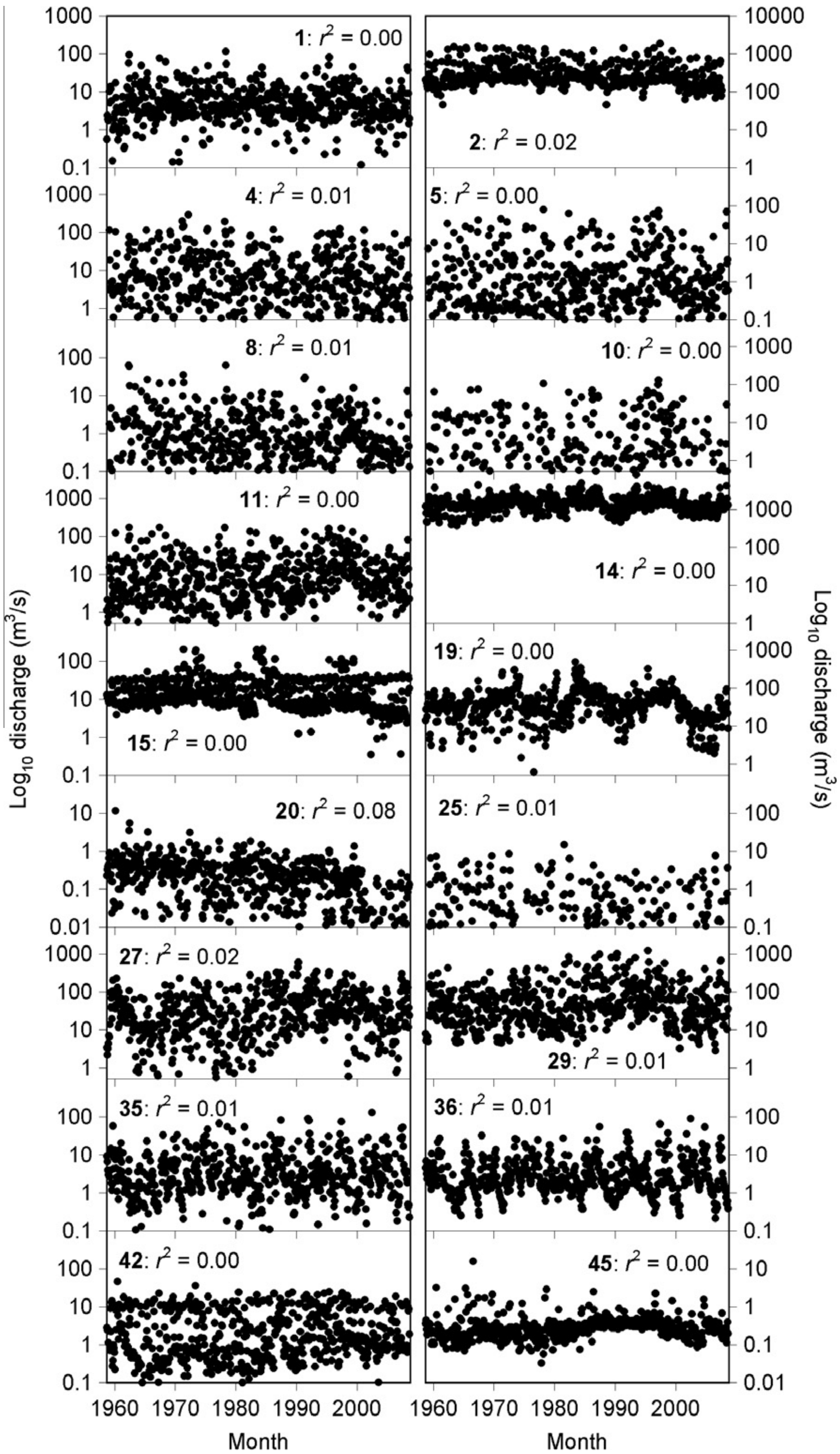

Fig. 4. Mean monthly discharge for a 50-year period (1959 through 2008) for high-quality refuges (harboring three or more endemic fishes) in the plains of North America. Proportion of variation attributable to month and year (r^2, based on a simple linear regression) is provided. Refuges are listed in Table 4.

management, or restoration of viable refuges in human-dominated landscapes requires integration of conservation activities with all aspects of human resource management (Minckley et al., 2003). More rigorous conservation strategies and better conservation planning are needed if conservation is to succeed at a large scale (Olden et al., 2010). For example, freshwater protected areas can be integrated with terrestrial ones (Amis et al., 2009). In the plains, humans make increasing use of the limited water supply (Ojima et al., 1999; Loáiciga et al., 2000) and water resource planners are already considering long-term strategies in the event of future droughts (Woodhouse, 2001; Sauchyn et al., 2003). Water management is challenging in its own right (e.g. Sophocleous, 2000), so unless planning explicitly includes measures to preserve or restore endemic fish refuges and lower extinction debts, extinction risk will likely increase and extinctions will likely continue.

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