RELATIONSHIP BETWEEN BASE FLOW MAGNITUDE AND SPRING FISH

COMMUNITIES

by

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ABSTRACT

Base flow is the portion of stream flow attributed to groundwater, and few studies quantify the pure effects of base flow reductions on stream fish communities. Spring complexes within the karst terrains of the Edwards Plateau Region of central Texas offer a unique opportunity to test hypothesized relationships between base flow and stream fish communities. Spring complexes are numerous within the Edwards Plateau, providing multiple independent observations, stable hydrographs dominated by base flow conditions, similar groundwater sources, and support endemic fishes that are associated with the spring complexes (i.e., spring-associated fishes). Primary objectives of this study were to assess spring-associated fish richness, relative abundances, and densities across a gradient of base flow magnitudes with predictions that metrics of spring-associated fish communities would linearly decrease with reductions in base flow. To control potential confounding variables, additional objectives were to test for the presence and strength of parapatry that is hypothesized to exist between spring-associated fishes and riverine-associated fishes (i.e., fishes with distributions not typically associated with spring complexes). Patterns in richness, relative abundances, and densities indicated parapatric distribution between spring-associated and riverine-associated fishes. Strength of parapatry depended upon base flow magnitude. Correspondingly, differences in spring-associated fish richness, relative abundances, and densities along a base flow gradient were detected, but only densities were linearly related to base flow. Richness and relative abundances of spring-associated fishes were non-linearly related to base

flow, suggesting that spring complexes have a level of buffering capacity against base flow reductions. The relationship between spring-associated fish communities and base flow gradient was used to support the reported parapatry between spring-associated fishes and riverine-associated fishes with in the area and to highlight the conservation value of spring complexes to regional fauna. Predictive models generated in this study can be used to evaluate spring-associated fish community integrity within the Edwards Plateau Region and to predict future changes in Edward Plateau spring complexes related to increases in groundwater extraction.

CHAPTER I

Relationship Between Base Flow Magnitude and Spring Fish Communities

<u>Introduction</u>

Flow is considered the master variable in river ecosystems (Poff et al. 1997). As such, flow regime is viewed as the dominant factor influencing fluvial abiotic parameters and biotic communities. The Natural Flow Paradigm (Poff et al. 1997) states that characteristics of flow regime (i.e. magnitude, duration, timing and rate of change) should be sufficiently similar to historical flow regimes, if the goal of river management is to maintain biological integrity. The importance of water quantity and flow regime has been recognized since the 1970s (Tennant 1976) and is widely accepted among natural resource managers. Experiments, refinement, and applicability of the theory are ongoing, aided by synthesis of sometimes disparate and conflicting stream ecosystem concepts (Humphries et al. 2014) and case-study examples (Ruppel 2014, Vaughn 2014, Olden et al. 2014). Many of the underlying mechanisms relating flow regime to biotic integrity are yet to be resolved and are necessary to understand and evaluate before confidently assigning environmental flow recommendations (Richter et al. 2006) or before refining established environmental flow recommendations.

Base flow is the portion of stream flow attributed to groundwater (Arnold et al. 1995). Heterogeneity in base flow magnitudes and other characteristics of the flow regime are connected to a large number of ecological processes (e.g., physiochemical parameters, sources of nutrients, species richness and trophic guilds) along a longitudinal stream gradient (Vannote et al. 1980). Studies designed to test the ecological services of base flows with the purpose of recommending an environmental flow recommendation

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remain surprisingly rare. In a recent meta-analysis study, Poff and Zimmerman (2010)

evaluated 145 research articles and synthesized the effects of flow alterations. Among

the 145 articles, only three studies assessed the effects of reduced base flows on stream

fish communities and reported decreases in native fish richness and density and shifts

towards more tolerant fishes. Reported reductions in base flows were caused by instream

dams, which likely confound (e.g. shifts in geomorphology, water temperature, turbidity,

and nutrient load) potential effects of reduced base flows on fish communities. Dams

attenuate flow pulses and fragment instream habitats, which also are related to decreases

in native richness and density and shifts towards more tolerant fishes (Baxter 1977,

Perkin and Bonner 2011, Perkin and Gido 2011). Finding stream reaches for sufficient

replication, with sufficient biological information before and after base flow reductions,

and with the reductions not attributed to instream dams is challenging.

     Surface water and groundwater withdrawals also reduce base flows (Freeman and

Marcinek 2006, Roy et al. 2009) and could yield insight into fish community responses

related to reductions in base flow independent of dams (Taylor 2010). Freeman and

Marcinek (2006) assessed stream fish responses to surface water withdrawals

independent of dams and water supply reservoirs in relation to reference conditions (i.e.,

no upstream water withdrawals or water supply reservoirs) in the Piedmont ecoregion of

Georgia and detected an inverse relationship between fluvial-specialist fish richness and

amount of surface water withdrawals.   The authors noted the uncertainties of their

findings, given the potential site differences in abiotic and biotic interactions relating to

stream order and basin size, past and present land uses practices, and geomorphology

processes, which collectively underscore the difficulties in testing pure effects of base

flow reductions with sufficient replication while controlling confounding variables.   One

alternative is to conduct a similar assessment but with an effort to minimize site

differences in basin size, stream order, land use practices, water quality, geomorphology,

and instream habitats.

Spring complexes of the karst Edwards Plateau Region of central Texas provide a

unique opportunity to assess fish responses to changes in base flow conditions.

Numerous spring complexes originate by surface water erosion of aquifer confining

layers enabling artesian spring flow (Abbott and Woodruff 1979, Grimshaw and

Woodruff 1986). Often, the erosive surface water source (e.g., river) migrates away from

the artesian springs because of normal geomorphological processes, leaving the former

channel as a short stream channel for a spring run before joining a larger river. Within a

fairly large and contiguous geographical area (3,200 km^2; Longley 1981), water quality,

hydrology, geomorphology, instream habitats, and drainage basins are similar among

numerous artesian springs and runs (hereafter "spring complexes") with few spatial and

temporal exceptions. Surface water among spring complexes is considered of high

quality, exceptional water clarity, and abiotically stenoecious (Slade et al. 1986,

Groeger et al. 1997, Hubbs 1995). Contributing watersheds are relatively small; hence

hydrology of the first order streams are dominated by base flows with few high flow

events (Kollaus et al. 2014). With flows typically under base flow condition and

stenoecious water quality, spring complexes are often considered relatively stable

environments (Hubbs 1995, Kollaus et al. 2014). Geomorphology and instream habitats

consist of run, riffles, and pools with substrates dominated by limestone gravels, cobbles,

or bedrock and intermediate levels of silt substrates from the surrounding watershed.

Biotic communities, specifically fish communities, are also similar among spring complexes of the Edwards Plateau, though not identical, because of various zoogeographical processes that have influence colonization and isolation of biota in the area. Most recently, Pleistocene glacial events and Holocene aridity have influenced the area's aquatic fauna and flora via species dispersion by interconnectivity of drainages upstream by stream piracy and downstream by changing sea levels and via speciation by episodic interglacial events that restrict gene flow (Abbott and Woodruff 1979, Conner and Suttkus 1986, Al-Rabab'ah and Williams 2004, Maxwell 2012). Given the permanency of water resources since the Pleistocene within the Edwards Plateau, Hubbs (1995) speculated that spring fishes adapted to the stable environments of spring complexes. One possible adaptation is the affinity or necessity of spring-associated fishes to inhabit the spring complexes. Zonation in a riverine landscape is used to describe changes in chemical and physical properties and associated distinct faunal groups found in a particular habitat, altitudinal, or longitudinal zone of a river (Hawkes 1975, Rahel and Hubert 1991, Aarts and Nienhuis 2003). Congruently, Kollaus and Bonner (2012) quantified affinities across several taxa of spring-associated fishes for spring complexes and noted the apparent parapatric distribution between spring-associated fishes for spring complexes and riverine-associated fishes (i.e., fishes with distributions not typically associated with spring complexes; (Hubbs et al. 2008) downstream from spring complexes. The distinction of parapatric assemblages of spring associated fishes as a type of biotic zonation was made by Kollaus and Bonner (2012). Availability of multiple spring habitats driven by base flows with similar geomorphology and physicochemical attributes along with a suite of indicator species (i.e., spring-associated fishes across

several families) reduce some of the confounding factors associated with stream comparisons.

The primary purpose of this study is to test predictions associated with base flow reductions and responses of the fish community. In doing so, this study will also provide greater insight into structuring mechanisms of fish assemblages within the Edwards Plateau. This insight is beneficial not only for the primary purpose of this study but also the role of spring flows in maintain spring-associated fish communities. Municipal and agriculture water demands drive groundwater extractions. Pumping of groundwater has real (Winemiller and Anderson 1997) or perceived (Kollaus et al. 2014) threats to spring complexes. Quantifying the relationships between spring-associated fishes and spring complexes and between riverine-associated fishes and riverine habitats, which only exists now based largely on observational data, will aid in developing environmental flow recommendations for spring complexes. Objectives of this study were to quantify richness (number of species), abundances (% of total fish community), and densities (fish/m^2) of spring-associated fishes and riverine-associated fishes in spring complexes and downstream of spring complexes in riverine reaches (hereafter "river") among six Edwards Plateau spring complexes. Relative abundances of spring-associated fishes were assessed longitudinally along the stream course (i.e., within spring complexes and river using a continuous variable of distance, measured in km downstream from spring source) to test a prediction of parapatric assemblages that spring-associated fishes will be exclusive in spring complexes since some fishes are adapted to these systems as suggested by Hubbs (1995), and riverine associated fishes will dominate downstream when spring influence is lost. Follow up predictions were: a) spring-associated fish

richness, relative abundances, and densities would be greater in spring complexes than river (class variables); b) riverine-associated fish richness, relative abundances, and densities would be greater in river than spring complexes. Follow up predictions may seem simple and intuitive but are necessary to test presence and strength of parapatry, which up to now has only been described by observation. Assuming relationships existed as predicted, additional objectives were to assess relative abundances and densities of the spring-associated fishes and riverine-associated fishes across a base flow gradient from 0.07 to 4.47 cubic meters per second (cms). Here, the prediction is that relative abundances and densities of spring associated fishes will be directly related to base flow conditions, specifically the springs with greater discharge will support greater relative abundances and densities of spring-associated fishes. Predictive models using multiple spring complexes in space, can be used to estimate declines in spring-associated fish relative abundances and densities when base flows decline.

Methods

Spring-associated and riverine-associated fish richness, relative abundances, and densities were obtained from published studies and theses. The six spring complexes and corresponding river reaches were Cypress Creek-Blanco River (Bean et al. 2007), Independence Creek- Pecos River (Watson 2006), Devils River (Kollaus and Bonner 2012), Pedernales River (Shattuck 2010), North Llano-Llano River (Curtis 2012), and the Upper San Marcos-San Marcos River (Behen 2013). These studies were selected because each contained multiple sampling sites along a stream gradient from spring complexes to river, multiple sampling events ($\geq$ 4) across seasons for at least one year,

similar collection techniques, effort, and oversight, data sufficient to calculate densities, and relatively unaltered fish communities. An exception was one site on the Upper San Marcos River, which was reported to a likely altered fish community because of modifications within the system (Behen 2013); this site was dropped from class variable calculations and analyses. Longitudinal river distances were estimated from the spring or the uppermost site nearest the spring. Sites at the spring or nearest the spring were assigned 0 km. Maximum distance downstream from or near the spring used in this study was 63 km. In some of the selected studies, information was available for farther downstream sites but these sites were not included because downstream sites were influenced by another spring sources (Devils River) or downstream sites were similar or had less spring-associated fishes than the site used in our analysis (Llano River, Pedernales River).   Discharges (cms) were calculated from USGS stations, using the median discharge from the available period of record (Table 1). For two of the studies, the spring area (Pedernales River) and uppermost site (North Llano River) were too far upstream from the available USGS station to use median discharge as an appropriate estimate of base flow at the sites. Median discharge was calculated from discharge estimates taken from repeated measurements of the site.

Fishes captured at each site and spring complex-river reach were classified as spring-associated (Table 2) or riverine-associated fish. Spring-associated fishes were defined as fishes with distributions generally restricted to spring complexes. Spring-associated fishes with literature support to establish their affinity for spring complexes were *Cyprinella proserpina* (Hubbs 1995, Edwards et al. 2004), *Dionda argentosa* (Hubbs and Brown 1956, Garrett et al. 2002), *Dionda nigrotaeniata* (Brown 1953, Hubbs

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et al. 1953, Kuehne 1955, Wayne 1979), *Notropis amabilis* (Gilbert 1980), *Notropis chalybaeus* (Texas distribution only; Perkin et al. 2012) *Astyanax mexicanus* (Birkhead 1980), *Ictalurus lupus* (Hubbs et al. 1953, Yates et al. 1984, Sublette et al. 1990), *Gambusia geiseri* (Hubbs et al. 1969, Stevens 1977), *Etheostoma fonticola* (Bonner and McDonald 2005), *Etheostoma lepidum* (Hubbs 1985), *Etheostoma grahami* (Hubbs et al. 2008), *Percina apristis* (Robins and Page 2007), and *Percina carbonaria* (Linam and Kleinsasser 1998).

Diagnostic plots and statistical analyses were used to assess patterns in spring-associated and riverine-associated fishes within spring complexes and river reaches and across spring complexes. Relative abundances of spring-associated fishes were plotted by distance from spring or uppermost site for each site of the six Edwards Plateau spring complexes initially. Two clusters were apparent: relative abundances of spring-associated fishes were greater among the three greater discharge spring complexes (≥0.65 cms) Independence Creek, San Marcos River, and Devils River) than in three lesser discharge spring complexes (≤0.34 cms; North Llano River, Cypress Creek, and Pedernales River). Consequently, subsequent analyses were split between greater discharge and lesser discharge spring complexes. Richness was estimated by counting the total number of spring-associated and riverine-associated fishes reported within a spring complex or in river reach across sites. For example, Independence Creek had seven spring-associated fishes but not necessarily at all six sites taken within Independence Creek. Relative abundances and densities were estimated by averaging site estimates within a spring complex or river reach across sites and species. For example, estimates of all spring-associated fishes, in aggregate and not by individual species,

reported by site within the spring complex of Independence Creek were summed and divided by six. Richness, relative abundances, and densities were calculated for spring-associated fishes for spring complexes and river with greater discharge, for spring complexes and river with lesser discharge, and for riverine-associated fishes for spring complexes and river with greater discharge, and for spring complexes and river with lesser discharge. Hence, each spring represented an independent observation (N = 3) A series of one-tail Student's t-tests was used to assess differences in richness, relative abundances, and density 1) between spring complexes and river reaches for spring-associated fishes within greater discharge springs, 2) between spring complexes and river reaches for riverine-associated fishes within greater discharge springs, 3) between spring complexes and river reaches for spring associated fishes within lesser discharge springs, and 4) between spring complexes and river reaches for riverine-associated fishes with lesser discharge springs. Linear and non-linear models were used to assess relationships between spring-associated and riverine-associated fish relative abundances and median discharge (i.e., an approximation of base flow in hydrologically-stable spring systems) and spring-associated and riverine-associated fish densities and median discharge. Linear or non-linear regression models were applied after viewing each diagnostic plot and determining which model would be most appropriate. Specific models were simple linear regression ($y = a + bx$), exponential rise to maximum ($y = a(1 - e^{(-bx)})$), and exponential decay ($y = ae^{(-bx)}$). Regression models were generated using Systat Software in SigmaPlot for Windows, Version 11.0. Significance level was set at $\alpha = 0.05$ for each pair-wise contrast and regression model.

<center>**Results**</center>

Among six independent spring systems, 13 species of spring-associated fishes and 54 species of riverine-associated fishes occurred within headwater springs and runs and downstream from spring complexes in river reaches. Spring-associated fishes were relatively more abundant among 14 sites within spring complexes (22 – 94%) and less abundant among 10 sites within river reaches (0 – 48%) as spring waters were diluted by confluences (Independence Creek-Pecos River, upper San Marcos River-San Marcos River, Cypress Creek-Blanco River) or influenced by ambient conditions (Devils River, North Llano River, Pedernales River; Figure 1).   Spring-associated fishes dominated (>50% in relative abundance) the fish community up to 20 km downstream from a spring complex in the Devils River, and occurrence of a spring-associated fish extended up to 60 km in the Llano River downstream from spring complex in the North Llano River. Spring complexes with greater discharge (0.65 to 4.47 cms) supported greater abundances of spring-associated fishes (49 to 97%) within the spring runs of Independence Creek, San Marcos River, and Devils River, whereas spring complexes with lesser discharge (0.07 to 0.34 cms) supported lesser abundances of spring-associated fishes (22 to 43%) in North Llano River, Cypress Creek, and Pedernales River. Likewise, spring complexes with high discharge supported greater abundances of spring-associated fishes (28% – 48%) in river reaches than low discharge springs (0% – 15%).

Among greater discharge spring complexes, community metrics (richness, relative abundances, and densities) of spring-associated fishes were generally greater in spring complexes than river reaches, and community metrics of riverine-associated fishes were generally greater in the river reaches than in the spring complexes (Figure 2). Species

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richness of spring-associated fishes ranged from 5.5 to 7 (mean $\pm$ 1 SD: 6.3 $\pm$ 0.75) and did not differ (*t*-statistic: 1.64, df = 4; P = 0.09) from species richness of spring-associated fishes in river reaches (range: 3 - 6; 4.6 $\pm$ 1.53). Relative abundance of spring-associated fishes ranged from 77% to 90% among spring complexes (82% $\pm$ 6.4) and was greater (t-statistic: 5.34, df = 4; P < 0.01) than relative abundance of spring-associated fishes in river reaches (28 - 49%; 41% $\pm$ 11.8). Density of spring-associated fishes ranged from 0.94 to 1.8 within spring complexes (1.2 $\pm$ 0.47) and was greater (t-statistic: 3.27, df = 4; P = 0.02) than densities of spring-associated fishes in river reaches (0.21 - 0.45; 0.37 $\pm$ 0.14). Among riverine-associated fishes, species richness ranged from 13 to 19 within spring complexes (15.6 $\pm$ 5.5) and did not differ (t-statistic: 0.38, df = 4; P = 0.36) from species richness of riverine-associated fishes in river reaches (13 – 22; 17 $\pm$ 4.5). Relative abundance of riverine-associated fishes ranged from 18 to 32% within spring complexes (20.3% $\pm$ 11.1) and was less (t-statistic: 4.08, df = 4; P < 0.01) than relative abundance of riverine-associated fishes in river reaches (52 - 72%; 59% $\pm$ 6.8). Density of riverine-associated fishes ranged from 0.11 to 0.43 within spring complexes (0.16 $\pm$ 0.15) and did not differ (t-statistic: 1.42, df = 4; P = 0.11) from densities of riverine-associated fishes in river reaches (0.38 - 0.84; 0.54 $\pm$ 0.26).

Community metrics (richness, relative abundances, and densities) of spring-associated and riverine-associated fishes were less distinct between spring complexes and river reaches among the three lesser discharge spring systems (Figure 3). Species richness of spring-associated fishes ranged from three to four within spring complexes (3.6 $\pm$ 0.58) and did not differ (*t*-statistic: 1.9, df = 4; P = 0.07) from species richness of spring-associated fishes in river reaches (range: 1.6 – 3.5; 2.5 $\pm$ 0.93). Relative

abundance of spring-associated fishes ranged from 22 to 43% within spring complexes (34% ± 11.1) and was greater (t-statistic: 4.52, df = 4; $P < 0.01$) than relative abundance of spring-associated fishes in river reaches (1 - 7%; 4.4% ± 2.9). Density of spring-associated fishes ranged from 0.07 to 0.25 within spring complexes (0.13 ± 0.1) and did not differ (t-statistic: 1.54, df = 4; $P = 0.1$) from densities of spring-associated fishes in river reaches (0.02 to 0.05; 0.03 ± 0.01). Among riverine-associated fishes, species richness ranged from 9 to 19 within spring complexes (14.7 ± 5.1) and did not differ (t-statistic: 1.26, df = 4; $P = 0.13$) from species richness of riverine-associated fishes in river reaches (16 – 28; 21 ± 6.4). Relative abundance of riverine-associated fishes ranged from 57 to 78% within spring complexes (66% ± 11.1) and was less (t-statistic: 4.52, df = 4; $P < 0.01$) than relative abundance of riverine-associated fishes in river reaches (93 - 99%; 96% ± 2.9). Density of riverine-associated fishes ranged from 0.18 to 0.53 within spring complexes (0.38 ± 0.18) and did not differ (t-statistic: 0.84 df = 4; $P = 0.22$) from densities of riverine-associated fishes in river reaches (0.37 - 0.68; 0.5 ± 0.16).

Across all spring complexes, richness, relative abundances, and densities of spring-associated fishes were related to discharge, whereas same metrics for riverine-associated fishes within spring complexes were inconsistently related to discharge (Figure 4). Positive and non-linear relationships were detected between discharge and spring-associated fish richness (a = 7.08, b = 3.13, $r^2 = 0.83$, $P = 0.04$) and relative abundances (a = 82.53, b = 3.35, $P = 0.03$, $r^2 = 0.87$). Spring-associated fish densities were positively and linearly related to discharge (a = 0.203, b = 0.352, $P < 0.01$, $r^2 = 0.84$). Relationships between richness, relative abundances, and riverine-associated densities and discharge were not detected ($P \geq 0.1$).

Discussion

The initial prediction of spring-associated fish affinity for spring complexes was partially supported. Relative abundances of spring-associated fishes were greater within spring complexes than in the river reaches, and densities of spring-associated fishes were greater in spring complexes than river reaches but only within greater discharge springs. However, spring-associated fishes were not exclusive to spring complexes. Spring-associated fishes were commonly observed downstream from spring complexes, especially among low discharge springs. The prediction that species richness, relative abundances, and densities of spring-associated fishes were positively related to spring discharge was supported. Greater discharge spring systems supported greater species richness, relative abundances, and densities of spring-associated fishes. As spring discharges decreased, spring complexes supported fewer species and lower densities of spring-associated fishes. Predictions about riverine-associated fishes were largely unsupported. Richness, relative abundances, densities of riverine-associated fishes did not differ between spring complexes and river reaches.

Within greater discharge spring complexes, differences in community structure between spring complexes and downstream river reaches reported herein support the occurrence of parapatric distributions between spring-associated and riverine-associated fishes (Hubbs 1995, Kollaus and Bonner 2012) and within riverine-associated fishes (i.e., tributary and mainstem fishes; Winston 1995, Taylor and Lienesch 1996). Complete separation between spring-associated and riverine-associated fishes was not observed, and densities of riverine-associated fishes were not different between spring complexes and rivers. Complete separation between spring-associated and riverine-associated fishes

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is not necessary to define parapatric distributions (Bull 1991). In addition, the degree of

separation of distributions is dependent upon season within the Devils River (i.e.,

seasonal parapatry; Kollaus and Bonner 2012). Overlaps in spring-associated and

riverine-associated fish distributions were observed in the Devils River, more notably

during spring and fall seasons, when water temperatures were similar between spring and

river reaches, and less so (i.e., greater segregation or seasonal paraparty) during winter

and summer seasons, when water temperatures differed the greatest between spring and

river reaches. However, densities of riverine-associated fishes were not different

between spring complexes and rivers in this study are problematic for the distributions to

be defined as parapatry rather than partial sympatry (Weir and Price 2011). Upon further

inspection of the density relationships, densities of riverine-associated fishes were four

times greater in river habitat than in spring complex in the Devils River (0.118 in spring

reach and 0.421 in downstream river reach) and two times greater in river than in spring

complex in the San Marcos River (0.320 in spring reach and 0.691 in downstream river

reach). In both systems, densities of spring-associated fishes were greater in spring

complexes than river; hence, distributional patterns suggest parapatry.   In contrast,

density of riverine-associated fishes was only slightly less in the Pecos River (0.382) than

the spring complex of Independence Creek (0.425). Lack of strong segregation between

spring-associated and riverine-associated fishes within Independence Creek and Pecos

River is attributed to at least two possible factors. One, Pecos River in the area of

Independence Creek confluence is a more degraded system than either the San Marcos

River (Perkin et al. 2012, Kollaus et al. 2014) or the Devils River (Kollaus and Bonner

2012).   Stream discharge regulation by upstream reservoirs (Hoagstrom 2003) and

periodic fish kills attributed to frequent outbreaks of Golden Alga *Prymnesium parvum* (Rhodes and Hubbs 1992) have altered the fish community within a large portion of the Pecos River within Texas. At times of duress, Pecos River fishes seek refuge in spring-influenced tributaries. As such, richness and densities of riverine-associated fishes are lower than historical numbers (Rhodes and Hubbs 1992) and richness and densities of riverine-associated fishes in Independence Creek might be inflated because of conditions in the Pecos River. Two, density differences in lesser discharge springs (<0.65 cms) are not detectable for either spring-associated fishes or riverine associated fishes. Independence Creek discharge (0.65 cms) is the lowest of the greater discharge springs. Independence Creek discharge is sufficient to maintain spring-associated fishes' richness, abundance, and densities similar to those of greater discharge springs but not sufficient to maintain community integrity by excluding riverine-associated fishes. Regardless of the mechanism, riverine-associated fish densities in two of three greater discharge springs were less in spring complexes than in the rivers. As such, I tentatively conclude that spring-associated fishes and riverine-associated fishes are parapatrically distributed with the degree of overlap dependent upon season and quantity of spring discharge.

Parapatric distributions among species exist for fishes, amphibians, reptiles, and mammals and are structured and maintained by abiotic (e.g., physical and chemical tolerances) and biotic mechanisms (e.g., completion, predation) through physiology and behavior (Bull 1991). Water temperature, specifically stenothermal conditions in spring complexes and eurythermal conditions in river reaches, is the oft cited abiotic parameter associated with maintaining spring-associated fish communities from those in river reaches (Hubbs 1995, Kollaus and Bonner 2012), although the mechanism has yet to be

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tested and there are other factors that might wholly or in part maintain the observed parapatry in communities. Nevertheless, water temperature is a likely determinant of spring community composition and is demonstrated to drive selection of physiological variants most fit for a particular water temperature environment. In general, specialist-generalist temperature tradeoffs arise from differences in structure and function of enzymes (Fields 2001). The enzyme lactate dehydrogenase (LDH) is identified in several fish species as an indicator of performance associated with temperature (DiMichele and Powers 1982). The LDH enzyme has been linked to the locus influencing ATP production, which influences blood oxygen affinity and in turn affects overall fitness in fish (e.g., swimming capabilities and respiration rates). Detection and quantification of LDH variants or the manifestation of LDH variant differences in spring-associated and riverine-associated fishes (e.g., competition and predation under stenothermal and eurythermal conditions) would yield insight into the mechanisms of paraparty and greater understanding of spring-associated fish relationships with spring complexes, perhaps even establishing if fishes are "spring-associated" or more specifically "spring-adapted".

Recognition of parapatry and understanding underlying mechanisms of maintaining parapatry provide a framework for understanding zoogeographical history and high rates of endemism in the Edwards Plateau region. Karstification of the limestone began at least 6 MYA (White et al. 2009). With karstification, aquifers formed in the Cretaceous limestone and continued to erode downward in a south and southwest direction (Deike 1990, White et al. 2009). Erosion by streams and rivers often intercept and down-cut confining layers of the aquifer, forming artesian springs (Abbott and Woodruff 1979, Grimshaw and Woodruff 1986) and also accelerates formation of the

vast aquifer (Deike 1990). Spring complexes emerge and provide voluminous spring

discharges, depending on elevation and head pressure, of stenothermal water. However,

the aquifer continues to erode downward, as well as rivers and streams continue to erode

downward, and once high flowing spring complexes evolve into low flowing springs, and

eventually dewater (Abbott and Woodruff 1986), exposing cavernous limestone and

caves. Newly formed cavernous limestone and caves (i.e., hydrologic evolution) parallel

allopatric speciation events in cave spiders within the Edward Plateau (White et al. 2009).

Also, hydrological evolution likely parallels evolution of aquatic organism within the

Edwards Plateau (Wilkens 1986, Langecker and Longley 1993). However, parallelisms

between hydrological evolution and species evolution are poorly understood for surface-

water organisms (Kollaus and Bonner 2012).

The model of parapatry reported herein provides a conceptual framework for

future testing and understanding of high taxa richness and high rates of endemism of

surface-water forms within the Edwards Plateau during the Quaternary Period (Maxwell

2012). Glacial events create more aquatic habitats within the Edwards Plateau by

providing cooler and wetter climates (Toomey et al. 1993, Sylvia and Galloway 2006).

Aquatic organisms, in particular fish, expand from the east to west direction within

western gulf slope drainages of Texas (Conner and Suttkus 1986, Maxwell 2012). As

fish expand into the surface waters of the Edwards Plateau, they encounter spring

complexes with novel water temperature characteristics (i.e., stenothermal), likely

maintaining a parapatric distribution as found today. During inter-glacial periods, areas

at lower latitudes endure more xeric and warmer temperatures, which at times can be

extreme and lead to widespread dewatering such as the Altithermal Period (Toomey et al.

1993, Russ et al. 2000, Al-Rabab'ah and Williams 2004). In theory, fishes would seek

refugia in available aquatic habitats, which likely would be the spring complexes. Fishes

successful at finding refugia would persist until conditions became more favorable for

expansion. Some of the smaller, less mobile fishes, such as darters and minnows, would

be less likely to expand and adapt to the spring conditions (Hocutt and Wiley 1986),

giving rise to fishes with affinities to spring complexes such as the extant forms of today.

Next glacial event would repeat the cycle. Meanwhile, hydrological evolution of the

karst system continues, bypassing higher elevation spring outflows and causing less to no

spring flow. Consequently, lesser discharge holds fewer spring-associated fishes and

more riverine-associated fishes (i.e., loss of parapatry), which could describe patterns

reported herein for the less discharge spring complexes.

Recognition of parapatry and understanding of underlying mechanisms of

maintaining parapatry also benefits conservation of spring-associated organisms through

the protection of base flows. Models generated in this study can be used to evaluate fish

community integrity in other Edwards Plateau spring complexes or used to predict future

changes in Edward Plateau spring complexes related to dewatering (e.g., groundwater

pumping and surface water diversions). The relative abundance model, likely the most

useable model since the reporting of relative abundance is the most common method to

quantify fish communities, was applied to other spring complexes in the Edwards Plateau

region. Ichthyofaunal information from these spring complexes were not used to develop

the models reported herein, because spring complexes had a recorded history of

degradation (Las Moras Creek, Upper San Antonio River) or the information did not

consist of density measurements (i.e., San Felipe Springs, Pinto Creek). Las Moras

Creek (Kinny County, Texas; Las Moras Springs discharge = 0.48 cms) is predicted to have 66% spring-associated fishes. Reported relative abundance of spring-associated fishes is 21%, likely a legacy effect of past chlorination events that were applied to maintain the spring complex as a community recreational area (Garrett et al. 1992). Upper San Antonio River (Bexar County, Texas, historical spring discharge >5.7 cms; current discharge 100% dependent on waste water return = 0.4 cms) is predicted to have 60% spring-associated fishes. Reported relative abundance of spring-associated fishes is 9% (Craig 2014, unpublished data). Low relative abundances of spring-associated fishes in Upper San Antonio River, contained wholly within an urbanized watershed, suggest that water quantity alone is not the only mechanism in maintaining spring-associated fishes through time. Instead, it is likely the character of the water, such as stenothermal conditions, along with water quantity that are related to maintaining expected numbers of spring-associated fishes. San Felipe Creek (Val Verde County Texas; San Felipe Springs = 2.5 cms) is predicted to have 83% spring-associated fishes. Reported relative abundance of spring-associated fishes is 93% (Garrett et al. 1992). Despite concerns of non-native fish introductions and urbanization, San Felipe Creek is considered a healthy fish community and is habitat for several endemic fishes, including the federally-listed Devils River Minnow *Dionda diaboli* (Garrett et al. 1992, López-fernández and Winemiller 2005). Upper Pinto Creek (Kinny County, Texas; Pinto Springs mean discharge in August = 0.32 cms; (Trungale Engineering and Science, unpublished report) was predicted to have 23% of spring-associated fishes. Reported relative abundance of spring-associated fishes is 94% (Garrett et al. 2004). Upper Pinto Creek is an interesting outlier in the model. Relative abundance of spring-associated fishes is considerably

greater than predicted. Pinto Springs and Upper Pinto Creek are the headwaters of Pinto Creek. Groundwater discharge is sufficient to maintain perennial water though not to maintain stenothermal conditions (McMillan 2011), but middle sections of Pinto Creek are intermittent flow and often disconnected from the upper reach until another aquifer supplies spring flow to the lower reaches of Pinto Creek (Garrett et al. 2004). As such, the upper Pinto Creek fish community often is isolated from the middle and lower reaches, which can prevent riverine-associated fishes from immigrating into the area thereby maintaining a predominately spring-associated fish community.

Richness, relative abundances, and densities of spring-associated fishes were directly related to median discharge or, more specifically, base flow conditions. Species richness and relative abundances of spring-associated fishes were asymptotically related to flow, whereas densities were linearly related to flow. The mechanism of the declines related to reductions of base flow could be attributed to reductions of size and volume of available habitat (Bunn and Arthington 2002). Also, mechanisms could be attributed to biotic effects (i.e., exploitative competition; Peres-Neto 2004) by changing abiotic conditions that allow greater movement of riverine-associated fishes into the area. This is consistent with findings from Anderson et al. (2006, Propst et al. 2008) who found an increase in opportunistic fish species with decreased flows. Interestingly, relationships between spring-associated fish richness and relative abundances and discharge were asymptotic, predicting spring-associated fish richness and relative abundances were unaffected by decreases in discharge along a substantial discharge gradient. One potential mechanism of this asymptotic relationship is that a reduction in water volume could reduce the diversity in habitat. Gorman and Karr (1978) noted that the structurally diverse

riverine systems have more buffering capacity against biotic shifts. Another potential

mechanism could be that thermal assimilative capacity decreases as flows decrease

(Poole and Berman 2001).   Regardless, exceptions to the model (Upper Pinto Creek,

Upper San Antonio River) illustrate that maintenance of spring-associated fish

communities is likely regulated by a number of abiotic and biotic factors not fully

understood or captured in the water quantity models developed in this study. As such,

using these models to predict spring-associated fish community changes related to water

quantity reductions can provide expectations of biotic integrity in spring-associated fish

communities with the caveat that various covariables (e.g., connectivity, maintenance of

stenothermal conditions) can potentially confound model predictions.

Table 1. Name of headwater spring source, distance from spring source to first site, USGS gauging station number used, period of record historical flow data was taken, historical discharges of each spring complex for each spring complex and flows calculated from studies taken at time of collection for the Pedernales and Llano rivers. (*) represents flow used in this study.

	Cypress Creek-Blanco	Pedernales	North Lano-Llano	Independence Creek-Pecos	Devils	Upper San Marcos- San Marcos
Name of Headwater Spring	Jacobs Well	several small seeps	Terrett Springs	Caroline Springs and seeps	Hudspeth Spring and seeps	San Marcos Springs
Distance from Spring Source to First Site (km)	6.6	0	24	2.1	7.7	0
USGS Station Number	8170990	8152900	8148500	8447020	8449000	8170500
Distance from spring source to gauge site	3 km upstream	30 km downstream	15 km downstream	within	within	within
Period of Record	2005 - 2014	1915 - 2014	1979 - 2014	1974 - 2014	1925 - 1973	1915 - 2012
Historical Flows						
Mean (cms)	0.17	2.04	1.56	1.08	5.21	5.01
Median (cms)	0.07*	0.54	0.57	0.65*	2.32*	4.48*
Flows calculated from study						
Mean (cms)		0.32	0.37			
Median (cms)		0.19*	0.34*			

Table 2. Presence absence of spring-associated fishes found at each spring complex within the Edwards Plateau, presence is denoted by X, and riverine associated sister taxa with source of phylogenetic and taxonomic relationship.

| Spring-associated Species	Cypress Creek-Blanco	Pedernales	North Llano-Llano	Independence Creek- Pecos	Devils	Upper San Marcos-San Marcos	Riverine associated sister taxa	Source
Cyprinella proserpina				X	X		*C. lutrensis* complex	Broughton and Gold 2000
Dionda argentosa				X	X		*Campostoma*	Schonhuth et al. 2008
Dionda nigrotaeniata	X	X	X			X	*Campostoma*	Schonhuth et al. 2009
Notropis amabilis	X	X	X	X	X	X	*N. athernodies* complex	Bielawski and Gold 2001
Notropis chalybaeus						X	Relict	Perkin et al. 2012
Astyanax mexicanus	X			X	X	X	Central America derived	Tomelleri and Eberle 1990
Ictalurus lupus				X			*Ictalurus punctatus*	Kelsch and Hendricks 1986
Gambusia geiseri				X	X	X	*G. affinis* complex	Lydeard et al. 1995
Etheostoma fonticola						X	*E. proelaire* complex	Ayache and Near 2009
Etheostoma grahami				X	X		*E. spectabile* complex	Ayache and Near 2009
Etheostoma lepidum		X	X				*E. spectabile* complex	Ayache and Near 2009
Percina apristis	X	X				X	*P. sciera* complex	Near et al. 2011
Percina carbonaria		X	X			X	*P. caprodes* complex	Near and Benard 2004

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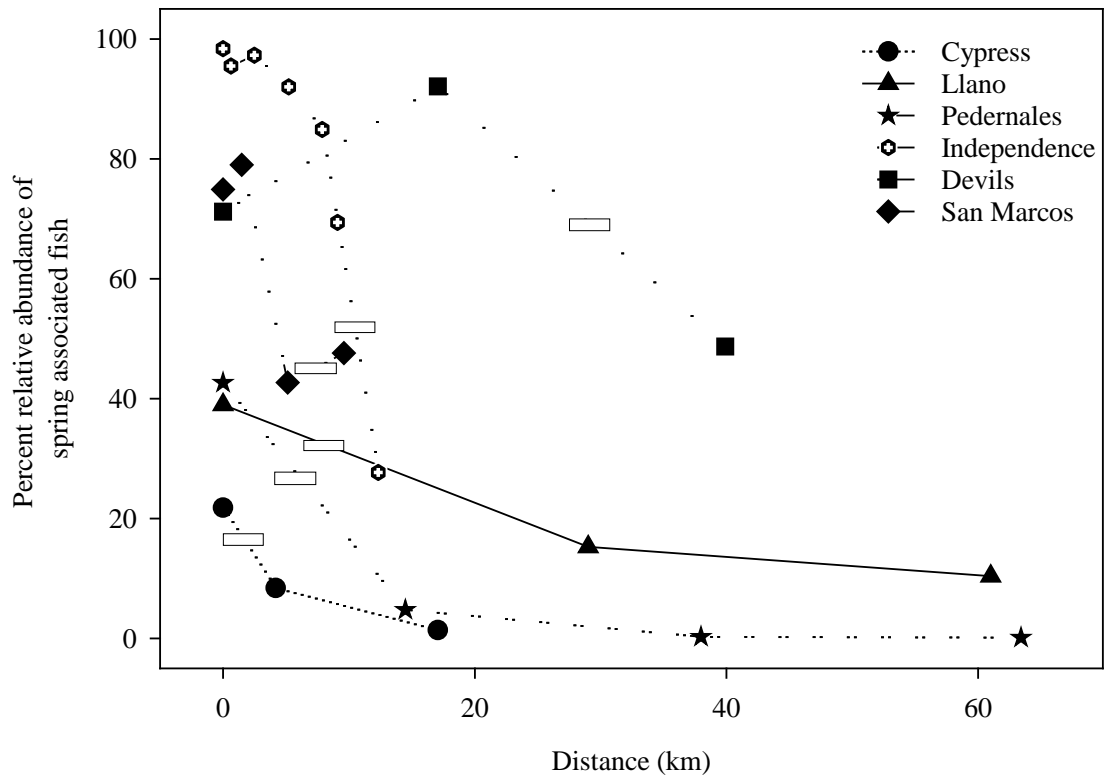
Figure 1. Spring-associated fish abundance plotted against distance downstream from spring for six spring complexes within the Edwards Plateau region. White horizontal bar represents loss of spring influence (i.e. confluence or due to abiotic conditions downstream.
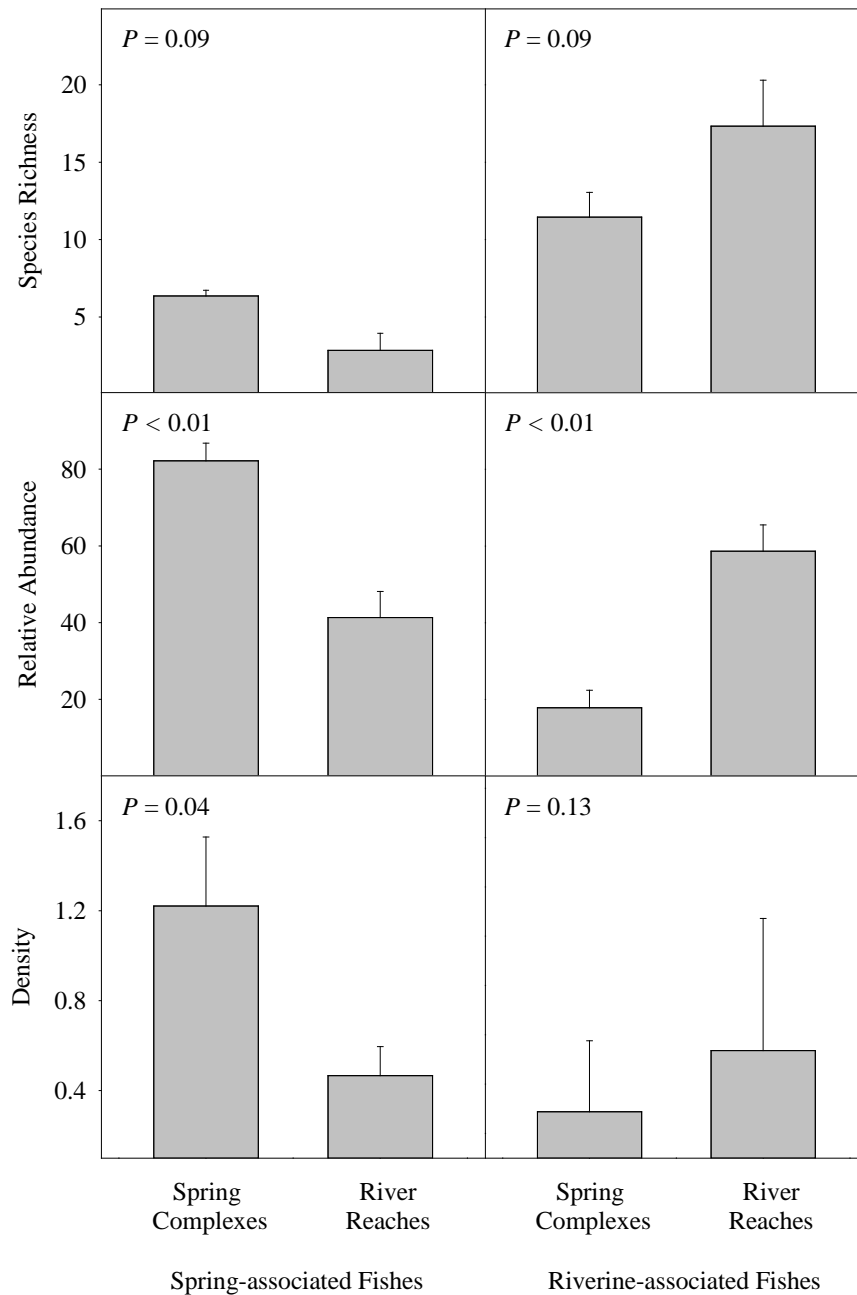
Figure 2. T-tests comparing upstream vs. downstream species richness (n), relative abundance (%), and densities (fish per m^2) for spring associated and riverine associated fishes within larger discharge systems (≥ 0.65 cms).
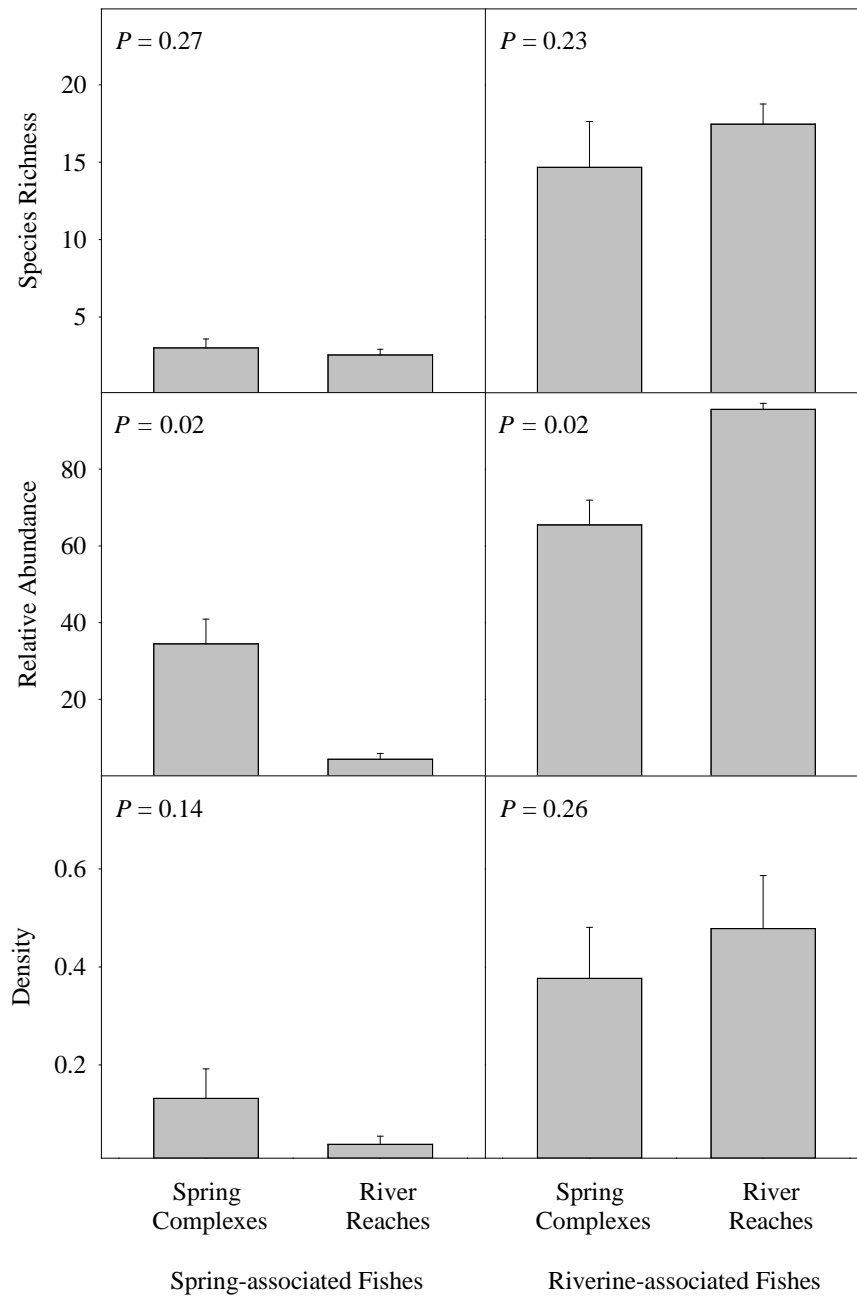
Figure 3. T-tests comparing upstream vs. downstream species richness (n), relative abundance (%), and densities (fish per m^2) for spring associated and riverine associated fishes within smaller discharge systems (≤ 0.65 cms).
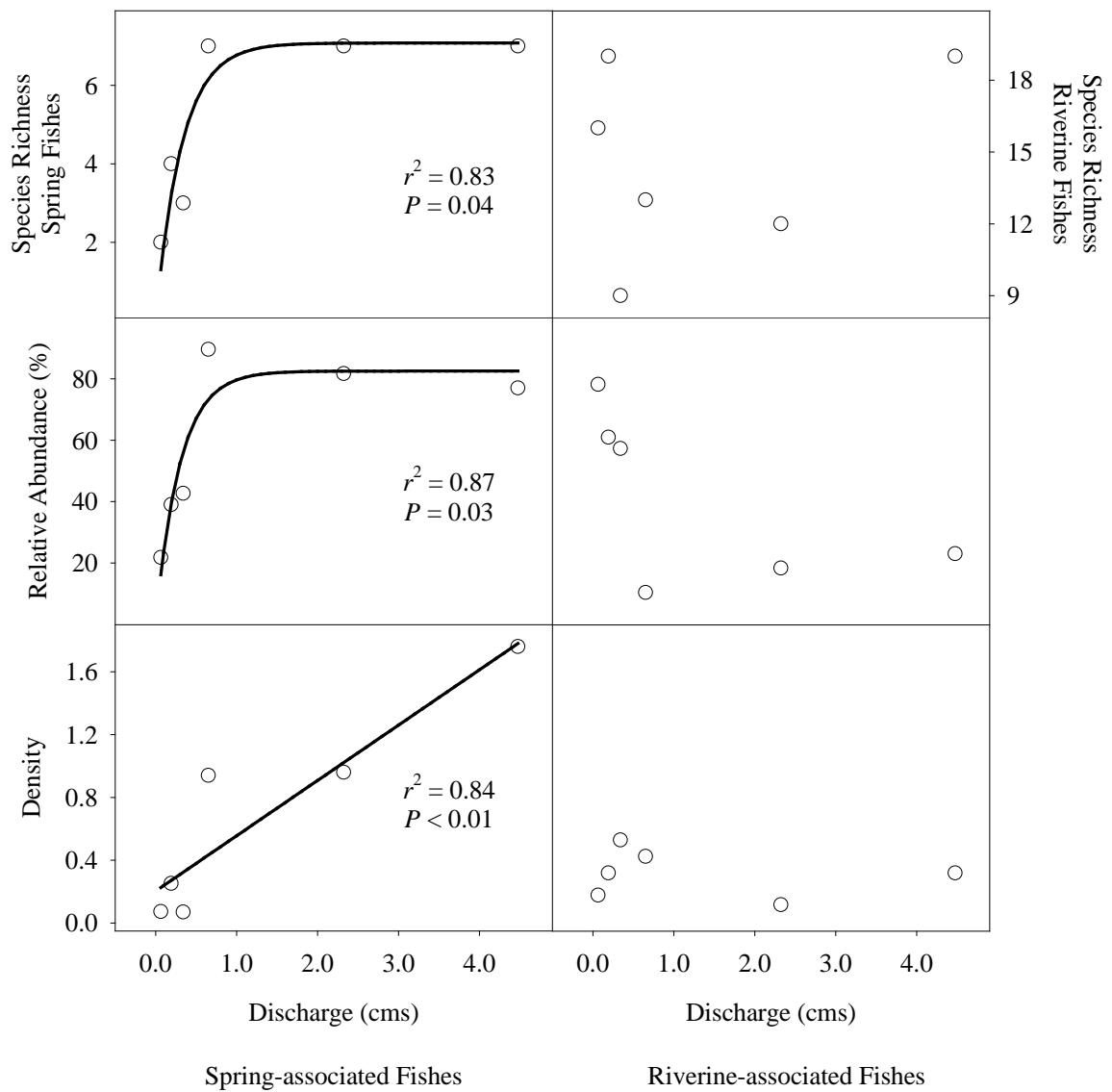
Figure 4. Applied linear and non-linear regressions for discharge vs. species richness (n), relative abundance (%), and densities (fish per m^2) for spring associated and riverine associated fishes. Coefficient of determination (r^2) and p-value are reported, if significant.

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