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Increased landscape disturbance and streamflow variability threaten fish biodiversity in the Red River catchment, USA

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Abstract

Aim: Stream fish distributions are hypothesized to be strongly associated with landscape characteristics at multiple scales. Variation in flow regimes and intensity of landscape disturbance are associated with stream fish distributions; however, relationships are poorly understood in many high-diversity regions. Our objective was to identify occurrence relationships between fish distributions and streamflow and landscape characteristics in the south-central United States.**Location:** Our study area was the central Red River catchment in Oklahoma, Texas and Arkansas, USA.**Methods:** We used existing fish surveys to model the occurrence of a diverse, warm-water assemblage among hydraulic response units (HRUs). We used multispecies occupancy modelling to identify variation in occurrence probability among 111 stream fishes in relation to landscape disturbance and flow regime characteristics.**Results:** We found occurrence relationships with landscape disturbance and 11 metrics comprising all flow-regime components. The relationships varied within both major species groups and some genera. Frequency and duration were the most common metrics underlying flow regime relationships. More common stream fishes tended to be positively associated with higher levels of landscape disturbance and flow regime metrics representing variability; conversely, narrow-ranged fishes tended to be negatively associated. Occurrence relationships with flow metrics representing high-flow events were predominately negative. As expected, many species were strongly associated with ecoregion with landscape disturbance and flow relationships held constant.**Main conclusions:** Our study informs land use and water management decisions and stream fish conservation at multiple spatial scales. Collectively, the findings suggest potential homogenization of the Red River fish assemblage with increased landscape disturbance and streamflow variability. A reduction in landscape disturbance and maintenance of natural flow patterns at coarser scales may benefit endemic and narrow-ranged fishes. Our findings also help guide finer-scale land use and water

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management decisions by identifying stream network areas with a high occurrence probability of less tolerant fishes.

KEYWORDS

Bayesian, existing data, flow regime, landscape disturbance, multispecies occupancy modelling, stream fishes

1 | INTRODUCTION

Identifying drivers of species distributions (i.e. occurrence) is an essential aspect of both ecological research and conservation planning. Species occurrence is a fundamental state variable used to identify critical habitat, describe assemblages, and understand colonization and extinction processes (Begon et al., 1986; Kéry & Royle, 2016; MacKenzie et al., 2017). Stream fish distributions are hypothesized to be strongly associated with coarse-scale landscape characteristics. Climate and geology are primary constraints that influence vegetation, geomorphology and instream habitat at finer scales (Frissell et al., 1986; Hynes, 1975; Wiens, 2002). For example, temperature not only limits species ranges (Eaton & Scheller, 1996; Sharma et al., 2007; Shuter & Post, 1990), but also influences distributions among stream segments (Brewer, 2013; Smith & Kraft, 2005), reaches (Ebersole et al., 2001; Mollenhauer et al., 2020) and microhabitats (Grossman & Freeman, 1987). Streams with different underlying lithology are also associated with distinct fish assemblages at different spatial scales (Neff & Jackson, 2012; Sharpe et al., 1987). Predator–prey dynamics and other biotic interactions also influence stream fish distributions (Jackson et al., 2001; Lake, 2000; Pont et al., 2005); however, the nature of these relationships is dependent on abiotic constraints (Fausch et al., 2002; Horwitz, 1978; McManamay et al., 2013).

Streamflow characteristics, which are largely defined by the surrounding landscape, are integrally linked to fish distributions (Poff & Allan, 1995; Schlosser, 1991). Stream discharge (hereafter discharge) provides a “currency” that characterizes flow patterns in numerous ways. The flow regime paradigm hypothesizes that the magnitude, duration, timing, frequency and rate of change of discharge are primary drivers of ecological processes (Poff et al., 1997; Rolls et al., 2012; Sofi et al., 2020). Kennard et al. (2007) showed relationships between long-term flow regimes and fish assemblage structure in river basins of Australia. Iwasaki et al. (2012) found that both low and high flow characteristics explained variation in fish species richness among river basins in various regions. Flow regimes globally have been altered due to human activities, particularly damming (Poff & Zimmerman, 2010; Sofi et al., 2020; Xenopoulos et al., 2005).

Flow-regime alteration can change the structure of fish assemblages. Most commonly, researchers have documented a shift from fishes with specialized life histories to those more opportunistic (e.g. invasive and cosmopolitan species). Jumani et al. (2018) showed a decrease in species richness associated with a loss of rarer fishes after a reduction in flow magnitude following dam construction.

In contrast, Anderson et al. (2006) did not find decreased species richness in relation to flow reduction, but instead reported a loss of fishes with more complex reproductive requirements (also see Schlosser, 1985). Flow-regime alteration after dam construction is also associated with increased prevalence of lentic fishes. Taylor et al. (2014) found a fish assemblage shifted from lotic to lentic species after changes in flow magnitude, frequency, timing and rate of change post damming. Similarly, Taylor et al. (2008) reported increased abundances of lentic-adapted fishes, including an invasive species, after changes in flow magnitude and duration following dam construction. Flow-regime alteration is also particularly detrimental to fishes sensitive to environmental change or perturbations (e.g. McClain et al., 2014; Papadaki et al., 2016; Travnicek et al., 1995).

Land use is an additional coarse-scale constraint on stream species distributions (Allan, 2004; Schlosser, 1991; Stevenson, 1997). Landscape disturbance associated with land use has negatively affected stream habitat (e.g. reductions in water quality and degradation) and altered the structure and function of many ecosystems (Allan, 2004; Maloney & Weller, 2011; Ward, 1998). Effects of landscape disturbance, even at lower intensities, have been largely detrimental to stream fishes (Brown et al., 2005; Murdoch et al., 2020; Sala et al., 2000). However, landscape disturbance has also been associated with increased fish species diversity at higher trophic levels (Johnson & Angeler, 2014) and a higher prevalence of cosmopolitan (Li et al., 2018; Scott, 2006) and invasive (Cooper et al., 2013; Ferreira et al., 2017) fishes.

Long-term effects of flow regime alteration and landscape disturbance on stream fishes remain poorly understood in most regions (Murdoch et al., 2020; Sofi et al., 2020). The majority of stream fishes, especially non-game species, are listed as “data deficient” on the International Union for Conservation of Nature Red List (www.iucnredlist.org). This conservation status is often due to a lack of research associated with environmental drivers of distributions, particularly at coarser spatial scales. These understudied species relationships prevent advances in aquatic ecology and hinder effective stream fish conservation and habitat restoration (Palmer & Ruhi, 2019). Our objective was to identify relationships between stream fish distributions and streamflow and landscape characteristics in the south-central United States. We used existing fish surveys to model the occurrence of a diverse, warmwater assemblage among hydraulic response units (HRUs) of the Red River catchment. Hydraulic response units are 10-digit hydrologic units with refined boundaries for flow modelling based on local characteristics (Markstrom et al., 2015). The HRUs in the Red River catchment were primarily delineated

using topography and homogenous surface water patterns derived from the National Hydrography Dataset (NHD) stream segments (U.S Geological Survey, 2020a). Our study provides insight into how flow regimes and landscape disturbance relate to species occurrence across a large river catchment. The findings inform assemblage-level fish conservation at broad scales and regional water management and land use strategies.

2 | METHODS

2.1 | Study area

Our study area was the central Red River catchment in Oklahoma, Texas and Arkansas, USA (Figure 1). The study area represented a range of flow regimes and landscape characteristics, with a diverse warmwater fish assemblage. The area mostly comprised the Cross Timbers and Ouachita Mountains level-three ecoregions (hereafter

ecoregions), but also included small portions of the Arkansas Valley, East Central Texas Plains (ECTP) and Texas Blackland Prairies (TBP). Following Woods et al. (2005), the Cross Timbers separates the forested eastern portion of the catchment from the more-arid western portion. A mix of savanna, woodland and prairie grassland is native to the Cross Timbers. The most common land use is farming and livestock, with some urban development and oil and gas production. Gravel- and cobble-bed streams are common in upstream reaches, with wide, shallow sand-bed streams in some downstream reaches. The Cross Timbers has more streamflow variability and drying than other ecoregions. Following Griffith et al. (2007), the ECTP's dominant vegetation cover was historically oak savanna; however, the majority has been converted to croplands and pasture. The TBP is tallgrass prairie-dominated, with less agriculture than the ECTP. Streams of the ECTP and TBP are primarily sand- and silt-bed with low to moderate gradient. Historically, ECTP and TBP streams were characterized as clear, but runoff from agriculture has increased turbidity. Following Woods et al. (2004, 2005), the Ouachita Mountains

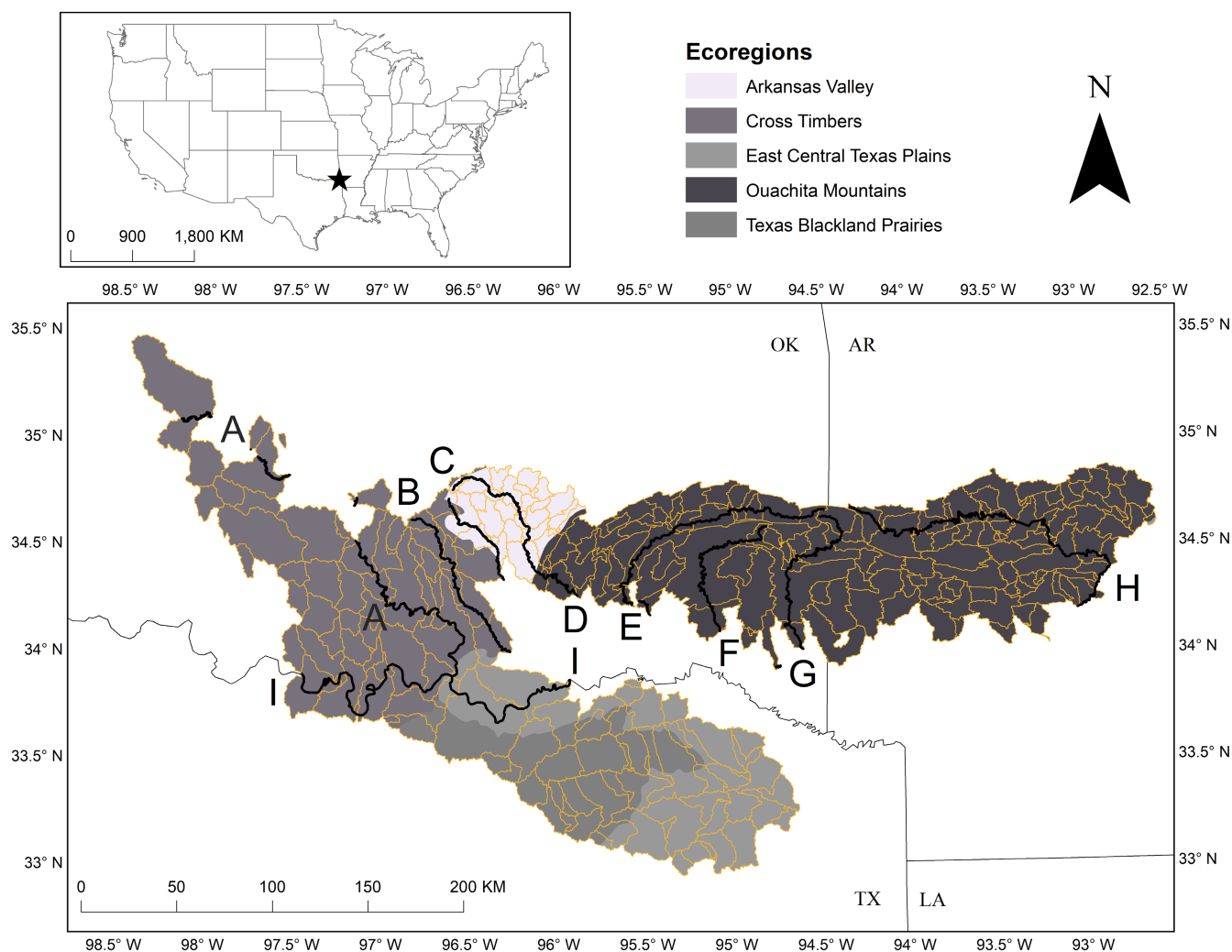


FIGURE 1 Study area in the central Red River catchment with delineation of hydraulic response units (HRUs) and level-three ecoregions. Letters indicate the Red River mainstem (I) and select major tributaries (black lines). A is the Washita River, B is the Blue River, C is Clear Boggy Creek, D is Muddy Boggy Creek, E is the Kiamichi River, F is the Little River, G is Mountain Fork and H is the Ouachita River

is the most vegetated ecoregion, with native oak-hickory-pine forest cover. Land use remains primarily forest, although pastureland, hayland and livestock grazing occur. Ouachita Mountain streams are predominantly high gradient with gravel and cobble beds. Streamflow is least variable among the ecoregions; however, some stream drying occurs. Water quality is generally good in the Ouachita Mountains, with reductions in some streams due to agriculture. The Arkansas Valley is a transitional ecoregion with diverse native vegetation including mixed forest, oak savanna and prairie grasslands. Land use is similar to the Ouachita Mountains, but with increased livestock grazing and some urban development. Streams of the Arkansas Valley also resemble the Ouachita Mountains, but with higher variability and increased drying.

The central Red River stream fish assemblage comprises >100 warmwater species (Woods et al., 2004, 2005; Griffith et al., 2007, Table S1). The assemblage is predominantly smaller-bodied fishes including darters (*Etheostoma* and *Percina*), madtoms (*Noturus*), topminnows (*Fundulus*) and members of Leuciscidae (hereafter small-bodied minnows, e.g. *Cyprinella*, *Notropis* and *Pimephales*). Larger-bodied fishes include sunfishes (Centrarchidae, e.g. *Lepomis*, *Micropterus* and *Pomoxis*), creek chub (*Semotilus atromaculatus*), suckers (Catostomidae) and redhorses (*Moxostoma*). Catfishes (flathead catfish *Pylodictis olivaris* and *Ictalurus*), freshwater drum (*Aplodinotus grunniens*, and gars (*Lepisosteus*) are common fishes in higher-order streams. Most fish species occur throughout the study area, with a general increase in diversity from west to east.

2.2 | Climatic periods and fish surveys

Our study period was 1980–2014. We divided the study years into relatively wet (1980–1998) and relatively dry (1999–2014) climatic periods (hereafter period one and period two). The periods were determined with a lowess smoothing line (Cleveland, 1979) in the software Python (version 2.7.10, <https://www.python.org/>) using precipitation records from 1895 to 2015 (Smith et al., 2017). We used data from Oklahoma climate division eight (Oklahoma Climatological Survey, 2020) to represent the study area because it was centrally located. Precipitation records were bias corrected and quality assured using data from the U.S. Historical Climatology Network (National Climatic Data Center, 2020).

We compiled stream fish assemblage surveys from agencies and online databases (Table S2). For databases, we used the terms “fish” and “fishes” to search all Arkansas, Oklahoma and Texas counties within the study area from 1981 to 2015. Each unique survey was spatially referenced to an HRU nested in an ecoregion based on the latitude and longitude. We treated repeat surveys within an HRU and climatic period as spatial replicates with replacement (Kendall & White, 2009), which assumes surveys were independent (also see Section 4). In addition to species capture histories (i.e. one for detection and zero for nondetection), we also compiled the survey date, collector (i.e. agency or individual) and sampling gear type for

each survey. We assumed seining for surveys that did not report the gear type because it is considered the most common warmwater stream fish sampling method (Rabeni et al., 2009) and was the predominant sampling method among the fish surveys where gear was reported (Table S3). Fishes were grouped by genera if identification was consistently not to species-level (e.g. redhorses) or nomenclature changes (i.e. species splitting) occurred after the beginning of the study period (e.g. stoneroller *Camptostoma*, or there were inconsistencies in species-level identification between duplicate surveys (e.g. *Menidia*, Table S1).

2.3 | Streamflow metrics and landscape disturbance

We characterized the flow regime of each HRU in each climatic period using a suite of metrics (Kennen et al., 2007; Olden & Poff, 2003). We calculated 171 flow metrics using EflowStats (version 5.0.1, median option, U.S. Geological Survey, 2019a) based on mean daily discharge estimates at the outlet of each HRU mainstem (Roland, 2020). The discharge estimates were obtained from a precipitation-runoff modelling system (PRMS, Markstrom et al., 2015) adapted from the National Hydrologic Model (Viger & Bock, 2014) for the Red River catchment. The flow modelling was part of a larger U.S. Geological Survey project for the entire Red River catchment (U.S. Geological Survey, 2019b). The PRMS model from the Red River catchment predicted daily discharge at 1614 NHD stream segments associated with outlets of HRUs. The model was calibrated using discharge data from 202 U.S. Geological Survey stream gages from 1980 to 2016. The accuracy of the estimates was assessed using Nash-Sutcliffe Efficiency (NSE), the ratio of the root mean square error to the standard deviation (RSR) and percent bias (P_{bias}). The passing threshold for model performance was $NSE > 0.5$, $RSR < 0.7$, and $P_{bias} \pm 10.0$ (Moriassi et al., 2007). The daily discharge estimates were considered satisfactory if they passed at least two of the three performance metrics. For stream segments with no suitable calibration gage, estimates were adjusted using the QPPQ method described by Farmer et al. (2018). The QPPQ method simulates and maps daily discharge values to a non-exceedance probability and rescales the estimates using a regional flow duration curve. Some daily discharge estimates were deemed unsatisfactory, but none for HRUs in our study area. The unsatisfactory estimates were primarily in the more arid upper portion of the Red River catchment due to inaccurate estimates of water withdrawals for irrigation and power generation.

As expected, flow metrics were highly correlated. We retained flow metrics based on the pairwise correlation coefficient (r) to achieve a comprehensive set with a minimal number of variables (Table S4). We also considered the drainage area of each HRU outlet a flow metric because it provided a surrogate for flood-return intervals (Interagency Advisory Committee on Water Data, 1982). We chose not to include both drainage area and median daily discharge

TABLE 1 Summary statistics by climatic period for streamflow metrics and the landscape disturbance index used to model occurrence probability among hydraulic response units (see Table 2 for disturbance index summaries by level-three ecoregion)

Metric (EflowStats code)	Climatic period one Mean \pm SD (range)	Climatic period two Mean \pm SD (range)
Date of annual maximum flow (TH1) ^{a,b}	106.36 \pm 87.19 (1.00–365.00)	96.05 \pm 47.82 (19.00–358.00)
Date of annual minimum flow (TL1) ^{a,b}	240.46 \pm 119.58 (23.00–360.00)	199.22 \pm 146.83 (2.00–365.00)
Drainage area ^{a,b}	6676 \pm 19,860 (13–102,145)	5887 \pm 18,364 (28–102,145)
Flood frequency (FH10) ^a	1.56 \pm 0.57 (1.00–5.50)	1.46 \pm 0.69 (1.00–8.50)
High flow discharge index (MH17) ^{a,b}	2.21 \pm 0.70 (1.17–5.03)	2.17 \pm 0.70 (1.06–4.68)
High flow duration (DH17) ^{a,b}	18.06 \pm 10.15 (5.35–48.32)	19.32 \pm 10.39 (6.17–50.57)
Median of the coefficients of variation for each year (MA3) ^b	186.91 \pm 81.34 (44.56–550.34)	188.56 \pm 73.92 (38.27–521.01)
Number of day rises (RA5) ^a	0.27 \pm 0.05 (0.16–0.40)	0.27 \pm 0.06 (0.14–0.40)
Low flow pulse duration (DL16) ^b	10.47 \pm 5.51 (0.00–28.27)	10.69 \pm 4.97 (0.00–29.63)
Skewness in annual maximum flows (MH19)	0.24 \pm 0.59 (–1.95–1.73)	0.02 \pm 0.68 (–1.92–1.13)
Variability in annual maximum daily flows (DH6) ^{a,b}	56.00 \pm 16.05 (34.75–101.29)	68.14 \pm 25.00 (35.72–179.48)
Variability in low flow pulse count (FL2) ^{a,b}	52.96 \pm 26.41 (21.10–165.54)	64.17 \pm 23.77 (33.55–123.33)
Variability in reversals (RA9) ^a	9.92 \pm 3.06 (4.81–18.79)	10.13 \pm 2.87 (4.25–18.05)
Variability in timing of annual maximum flow (TH2)	66.86 \pm 6.89 (34.58–80.15)	61.47 \pm 7.97 (40.46–79.03)
Variability in timing of annual minimum flow (TL2) ^a	50.45 \pm 11.81 (24.18–71.80)	45.20 \pm 9.85 (24.19–77.48)
Disturbance index – all ecoregions ^{a,b}	1.50 \pm 0.45 (1.00–3.25)	1.47 \pm 0.31 (1.02–2.73)

Note: The three-character alphanumeric codes correspond to EflowStats flow regime metrics flow metrics (see appendix 7 of Kennen et al., 2007 for detailed descriptions). Climatic period one is relatively wet (1980–1998), and climatic period two is relatively dry (1999–2014). The landscape disturbance index was calculated by multiplying the proportion of each land use type by a weighted coefficient and summing the values (see Methods).

Abbreviation: SD, Standard deviation.

^aVariables that had at least one species coefficient with an HDI that did not overlap zero.

^bMetrics that were natural-log transformed for the analysis due to right-skewed distributions.

(MA2) in the occurrence model due to the high correlation level ($r = .84$, also see Section 4). We retained drainage area because it was highly correlated ($r > .80$) with more metrics than median daily discharge (i.e. drainage area provided a surrogate for a greater number of metrics). The reduced variable set comprised 15 metrics that represented all five flow regime components (Table 1). The r was $< .60$ for all pairwise comparisons between flow metrics and $> .50$ for only 9 of 105 comparisons (Table S4). We also quantified the relative flow magnitude of each HRU at the time of the fish survey to account for associated variation in detection probability. Relative flow magnitude was calculated as median monthly discharge/drainage area.

We calculated a disturbance index for each climatic period to represent levels of development intensity. We obtained land use coverage for 1989 (U.S. Geological Survey, 2020b; Sohl et al., 2016) and 2006 (Multi-Resolution Land Characteristics Consortium, 2020) for period one and two, respectively (i.e. the median year of each period). The land use layers were spatially referenced to HRUs using ArcMap (version 10.6.1, ESRI, Redlands, CA). We calculated the disturbance index by multiplying the proportion of each land use type by a weighted coefficient and summing the values. Coefficients were initially developed by Brown and Vivas (2005) to represent landscape development intensity based on human energy use within various land uses. We modified

the coefficients following Mouser et al. (2019) for use with National Land Cover Database (Table 2).

2.4 | Occupancy modelling

We used occupancy modelling (MacKenzie et al., 2002; Tyre et al., 2003) in a hierarchical multispecies framework (Dorazio et al., 2006; Dorazio & Royle, 2005; Kéry & Royle, 2016) to examine landscape and streamflow occurrence relationships. In this modelling framework, species-specific occurrence and detection coefficients are modelled as variation around the group mean hyperparameter μ . The species coefficients represent a trade-off between individual fit and μ (i.e. coefficients shrink towards a central tendency) and are assumed to follow a probability distribution (see linear model equations below). A meaningful colonization-extinction model (e.g. MacKenzie et al., 2003) was not possible with only two periods and 45% of the HRUs sampled in only one period (see Section 3). Thus, we allowed the occurrence state at HRUs sampled in both periods to change as a function of covariates and random processes. The latent occurrence state for species i at HRU j was treated as partially observed ($z_{ij} = 1$ if the species was truly present and $z_{ij} = 0$ if the species was truly absent). Each z_{ij} followed a Bernoulli distribution with occurrence probability Ψ :

$$z_{ij} \sim \text{Bernoulli}(\Psi_{ij}).$$

The detection of species i at HRU j for survey k was conditional on both the true occurrence state and detection probability p , where y_{ijk} followed a Bernoulli distribution:

$$y_{ijk} \sim \text{Bernoulli}(z_{ij} \times p_{ijk}).$$

We modelled variation in Ψ and p as a function of predictor variables using linear equations (MacKenzie et al., 2002). Detection covariates comprised relative flow magnitude, drainage area and time of year (month of the survey). Drainage area characterized stream size at HRU mainstems to account for variation in p associated with species abundance. We natural-log transformed relative flow magnitude and drainage area due to right-skewed distributions. A time of year covariate represented photoperiod and general trends in water temperature using the integers 1–6 (1 = January and December, 2 = November and February, 3 = October and March, 4 = September and April, 5 = August and May, and 6 = June and July). We treated climatic period as a dummy (indicator) variable, with period one as the reference level, to account for variation in p . We also allowed each species detection intercept to vary by both sampling gear type (1–7) and collector (1–17) using a grouping factor (i.e. “random intercept,” Wagner et al., 2006; Tables S2 and S5). We used a t -distribution, rather than a normal distribution, for species coefficients and grouping factors. The t -distribution introduces a normality parameter v to account for heavy tails and improve model fit (Kruschke, 2013; Lee & Thompson, 2008).

The detection component can be written as:

$$\text{logit}(p_{ijk}) = \alpha_i + \alpha_{1ijk} + \sum_{n=1}^3 \beta_{n[i]} X_{n[jk]} + \sum_{g=1}^7 \gamma_g[jk] + \sum_{c=1}^{17} \tau_c[jk],$$

$$\text{for } i = 1, 2 \dots N, \text{ for } j = 1, 2 \dots J, \text{ for } k = 1, 2 \dots K,$$

$$\alpha \sim t(\mu_\alpha, \sigma_\alpha^2, v_\alpha), \alpha_1 \sim t(\mu_{\alpha_1}, \sigma_{\alpha_1}^2, v_{\alpha_1}), \beta_n \sim t(\mu_{\beta_n}, \sigma_{\beta_n}^2, v_{\beta_n}),$$

$$\gamma_g \sim t(0, \sigma_{\gamma_g}^2, v_{\gamma_g}), \tau_{ck} \sim t(0, \sigma_{\tau_c}^2, v_{\tau_c}),$$

where α is the detection intercept, α_1 is period two, β_n is the slope for associated detection covariate X_n , γ is the grouping factor for sampling gear g , τ is the grouping factor for collector c and σ^2 is variance. Occurrence covariates comprised the disturbance index and 15 flow metrics (Table 1, also see Section 2.3). The absolute value of r was <0.44 between the disturbance index and the flow metrics (Table S4). Climatic period and ecoregion were treated as dummy variables. Ecoregion provided a surrogate for climate, geology and other landscape characteristics (Omernik, 1995, 2004). Sampling in the Arkansas Valley, ECTP and TBP were sparse (Figure S1). Thus, we made two groups from the five ecoregions (reference group A: ECTP, TBP and Cross Timbers, group B: Arkansas Valley and Ouachita Mountains) based on similarities in vegetation, landforms and streambed characteristics (see Section 2.1). The occurrence component can be written as:

$$\text{logit}(\Psi_{ij}) = \alpha_i + \alpha_{1ij} + \alpha_{2ij} + \sum_{n=1}^{16} \beta_{n[i]} X_{n[j]},$$

TABLE 2 Weighted coefficients used for the landscape disturbance index

Land use category	Coefficient
Reference	1.00
Urban development	5.14
Pasture and hay agriculture	2.99
Cultivated crop agriculture	4.54

Note: Values for coefficients represent levels of landscape development intensity relative to reference conditions (i.e. least disturbed). The reference comprised open water, barren land, forest (all types), shrub and scrub, herbaceous, and wetlands. Coefficients for different land uses were derived for use with the National Land Cover Database following Mouser et al. (2019). Low-intensity urban development was low-density single family residential in Brown and Vivas (2005). Medium-intensity urban development was the mean of medium- and high-density single family residential in Brown and Vivas (2005). High-intensity urban development was the mean of low-density commercial, institutional, and industrial, multi-family residential, and high-density commercial in Brown and Vivas (2005). Oil and natural gas development were combined with high-intensity urban development. A mean value of low-, medium- and high-density was used for urban development because the 1989 land use layer did not differentiate densities. Pasture and hay agriculture was the average of woodland pasture with livestock, improved pasture without livestock, and improved pasture with livestock in Brown and Vivas (2005). Cultivated crop agriculture was the same as for row crops in Brown and Vivas (2005).

$$\text{for } i = 1, 2 \dots N, \text{ for } j = 1, 2 \dots J,$$

$$\alpha \sim t(\mu_\alpha, \sigma_\alpha^2, v_\alpha), \alpha_1 \sim t(\mu_{\alpha_1}, \sigma_{\alpha_1}^2, v_{\alpha_1}), \alpha_2 \sim t(\mu_{\alpha_2}, \sigma_{\alpha_2}^2, v_{\alpha_2}), \beta_n \sim t(\mu_{\beta_n}, \sigma_{\beta_n}^2, v_{\beta_n}),$$

where α is the occurrence intercept, α_1 is period two, α_2 ecoregion group B and β_n is the slope for associated occurrence covariate X_n . All detection and occurrence covariates were standardized to a mean of zero and standard deviation (SD) of one to improve interpretation of coefficients and model convergence.

We fit models using the program JAGS (Plummer, 2003) called from the statistical software R (version 3.5.3, R Development Core Team, 2019) using the package jagsUI (Kellner, 2018). We used vague normal priors for coefficients and vague gamma priors for associated SDs (Kéry & Royle, 2016). Posterior distributions for coefficients were estimated with Markov chain Monte Carlo methods using four chains of 80,000 iterations each after a 40,000 iteration burn-in phase (thinning = 100). We assessed model convergence using a potential scale reduction factor (\hat{R} , Brooks & Gelman, 1998) and trace plots. We considered adequate convergence an $\hat{R} < 1.05$ and a “grassy” trace plot for all coefficients (Kéry & Royle, 2016).

We simplified the model using a two-step backward selection process. We began by fitting the full model and examining detection coefficients. We removed detection parameters (i.e., all coefficients for the covariate) when 95% highest density intervals (HDIs) for all species coefficients overlapped zero. We then refit the model and used the same criteria to simplify the occurrence component of the model. Our approach supports credibility for either a positive or negative

TABLE 3 Landscape disturbance index among hydraulic response units (HRUs) used to model stream fish occurrence for level-three ecoregions in climatic periods one (relatively wet, 1980–1998) and two (relatively dry, 1999–2014)

	Climatic period one Mean \pm SD (range)	Climatic period two Mean \pm SD (range)
Arkansas Valley	1.56 \pm 0.20 (1.28–1.92); $n = 8$	1.44 \pm 0.14 (1.14–1.67); $n = 21$
Cross Timbers	1.77 \pm 0.39 (1.08–3.25); $n = 35$	1.57 \pm 0.19 (1.25–2.22); $n = 34$
ECTP and TBP	2.39 \pm 0.39 (1.67–2.78); $n = 11$	1.93 \pm 0.38 (1.15–2.73); $n = 14$
Ouachita Mountains	1.27 \pm 0.23 (1.00–2.23); $n = 82$	1.34 \pm 0.27 (1.02–2.53); $n = 75$

Note: Values indicate intensity of landscape development relative to reference conditions of 1.0 (Table 2). The ECTP and TBP values were pooled due to their geographic proximity, limited spatial extent, and small number of fish surveys (see Section 2.1).

Abbreviations: ECTP, East Central Texas Plains; SD, standard deviation; TBP, Texas Blackland Prairies.

occurrence relationship (i.e. species occurrence probability increases or decreases in relation to the covariate) based on the decision rule cut-off (Kruschke & Liddell, 2018). The mode for each species coefficient among the retained parameters is the most plausible value, and the HDI contains credible values from the posterior distribution with a total probability of 95%. An HDI for a species coefficient that overlapped zero was interpreted as no relationship with the associated covariate. Removing these species coefficients would result in a loss of information and bias remaining species relationships. The decision rule is analogous to traditional hypothesis testing with confidence intervals; however, an interval that does not overlap zero is not interpreted as rejecting the null hypothesis of a slope equal to zero. Rather, HDIs provide support for a range of plausible estimates (Kruschke & Liddell, 2018).

We examined model fit with a posterior predictive check. Fit was assessed using a Bayesian p -value from a goodness-of-fit (GOF) test (Kéry & Royle, 2016). A Bayesian p -value near .5 supports adequate fit, with extreme values (i.e. $<.05$ or $>.95$) indicate a lack of fit (Conn et al., 2018; Kéry & Royle, 2016).

3 | RESULTS

3.1 | Fish surveys

The final dataset included 1338 surveys (climatic period one: $n = 548$, climatic period two: $n = 790$) for 111 stream fishes across 180 HRUs (climatic period one: $n = 136$, climatic period two: $n = 144$, Figure S1). Sampling was done predominately in the Oklahoma and Arkansas portions of the study area. One hundred HRUs were sampled in both periods. The species list included 34 small-bodied minnows, 21 darters, 15 sunfishes, 7 madtoms, 4 topminnows, and 3 suckers (Table S1).

3.2 | Streamflow metrics and landscape disturbance

The flow metrics and disturbance index were variable among HRUs, but generally similar between climatic periods (Table 1). There were no notable differences in the range of values between the periods

for any flow metrics. The mean and range of the disturbance index across all HRUs were similar in both seasons.

Land use was predominately categorized as undisturbed in both climatic periods (74% and 78% of HRUs in period one and period two, respectively), with some variation in agriculture and urban development between periods and ecoregions. Among ecoregions, the mean disturbance index was lowest in the Ouachita Mountains and highest in the ECTP and TBP (Table 3). Except for the Ouachita Mountains, the mean disturbance index was lower in period two. Although the lower and upper extent of the disturbance index tended to be higher in the Cross Timbers, ECTP and TBP, there was considerable overlap in values among the ecoregions. The landscape disturbance differences between periods may not reflect land use changes but may instead be associated with different fish survey locations.

3.3 | Occupancy modelling

Model diagnostics indicated good convergence and adequate fit. \hat{R} was <1.05 for all coefficients with well-mixed chains. The Bayesian p -value from the GOF test was 0.43.

We did not remove any detection parameters because at least one species coefficient HDI did not overlap zero for period two and all three detection covariates (Table S6). The most common p relationship was with drainage area ($n = 42$ fishes), and the least common relationship was with relative flow magnitude ($n = 10$ fishes). Unexplained variability in p (as SD) was more attributed to gear type than collector.

Seventy-two fishes had an HDI that did not overlap zero (hereafter relationship) with at least one occurrence predictor variable including 21 of 33 small-bodied minnows, 17 of 21 darters, 6 of 15 sunfishes, 4 of 7 madtoms and all topminnows ($n = 4$) and suckers ($n = 3$, Table S7). The most common relationship was with ecoregion ($n = 38$ fishes), which also had the most variation in Ψ (as group mean SD) among fishes (Table S7). Occurrence probability was higher in ecoregion group B (Ouachita Mountains and Arkansas Valley) for 29 fishes and lower for 9 fishes (Figures 2–5). Species Ψ relationships with flow metrics comprised all flow regime components (Table 1 and Table S7). The most common flow regime relationship was

FIGURE 2 Occurrence relationships among small-bodied minnows determined using species coefficients with an HDI that did not overlap zero (Tables S3 and S7). A plus sign (+) indicates a positive occurrence relationship. A minus (-) sign indicates a negative occurrence relationship. Colours associated with + or - indicate black for ecoregion relationships, red for landscape disturbance relationships, purple for flow magnitude relationships, green for flow duration relationships, brown for flow frequency relationships, orange for flow rate of change relationships and blue for flow timing relationships. OM is ecoregion group B (Ouachita Mountains and Arkansas Valley), DI is landscape disturbance index and M1 is drainage area. See Table 1 for description of three-character alphanumeric codes for flow regime metrics

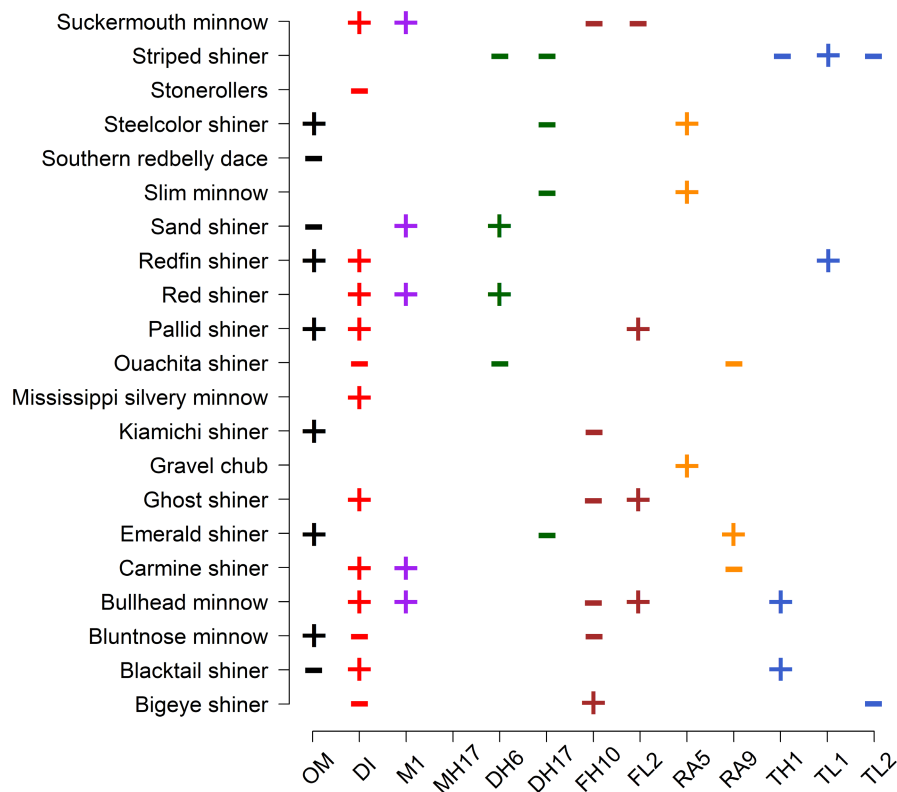
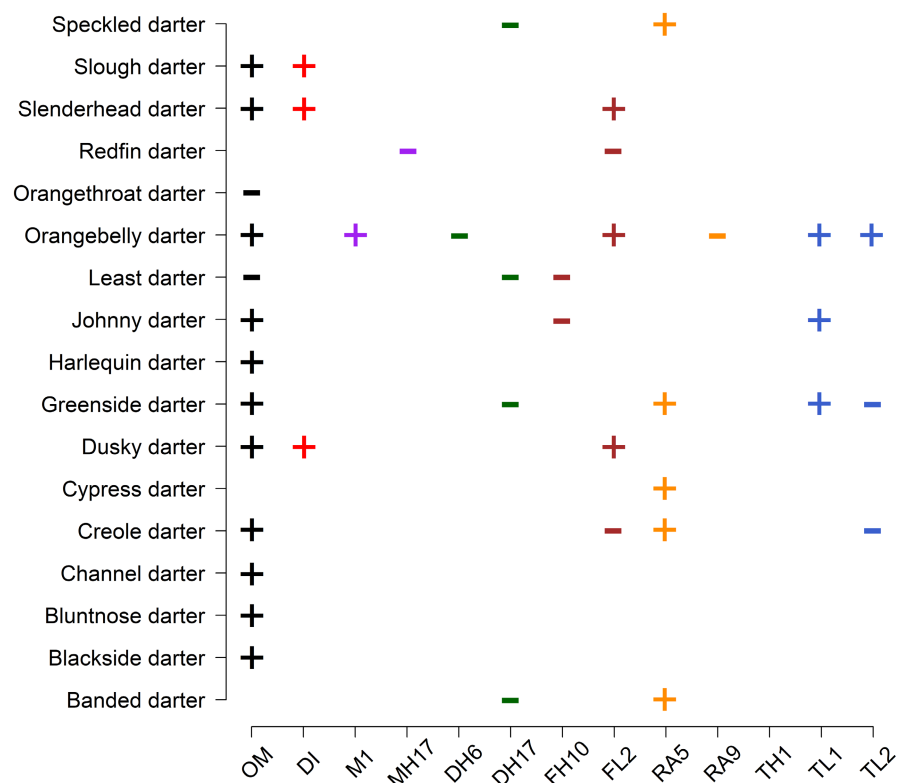


FIGURE 3 Occurrence relationships among darters determined using species coefficients with an HDI that did not overlap zero (Tables S3 and S7). A plus sign (+) indicates a positive occurrence relationship. A minus (-) sign indicates a negative occurrence relationship. Colours associated with + or - indicate black for ecoregion relationships, red for landscape disturbance relationships, purple for flow magnitude relationships, green for flow duration relationships, brown for flow frequency relationships, orange for flow rate of change relationships and blue for flow timing relationships. OM is ecoregion group B (Ouachita Mountains and Arkansas Valley), DI is landscape disturbance index and M1 is drainage area. See Table 1 for description of three-character alphanumeric codes for flow regime metrics



frequency ($n = 24$ fishes), and the least common relationship was magnitude ($n = 12$ fishes). Orangebelly darter (*Etheostoma radiosum*, $n = 6$), striped shiner (*Luxilus chrysocephalus*, $n = 5$) and northern studfish (*Fundulus catenatus*, $n = 5$) had the most Ψ relationships with flow metrics (Figures 2–5). Occurrence probability was higher

in climatic period two for only 4 fishes and was not higher in period one for any fishes (Table S7).

Nineteen fishes had a positive Ψ relationship with landscape disturbance, and 8 fishes had a negative Ψ relationship (Table S7). The direction of the relationships varied among small-bodied minnows

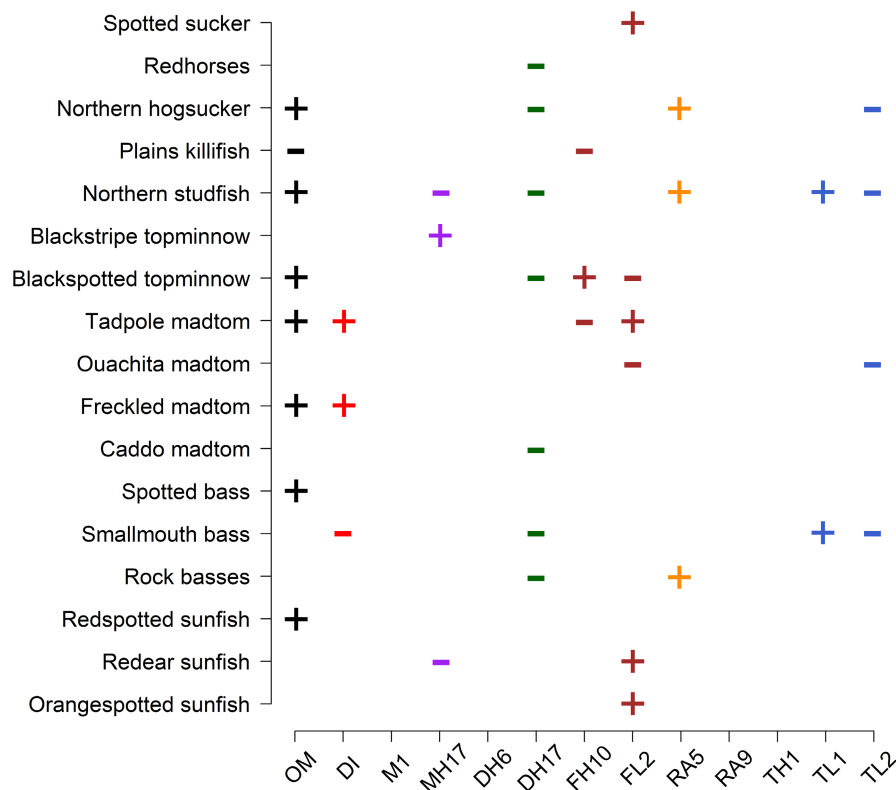


FIGURE 4 Occurrence relationships among sunfishes, madtoms, topminnows and suckers determined using species coefficients with an HDI that did not overlap zero (Tables S3 and S7). A plus sign (+) indicates a positive occurrence relationship. A minus (-) sign indicates a negative occurrence relationship. Colours associated with + or - indicate black for ecoregion relationships, red for landscape disturbance relationships, purple for flow magnitude relationships, green for flow duration relationships, brown for flow frequency relationships, orange for flow rate of change relationships and blue for flow timing relationships. OM is ecoregion group B (Ouachita Mountains and Arkansas Valley), DI is landscape disturbance index and M1 is drainage area. See Table 1 for description of three-character alphanumeric codes for flow regime metrics

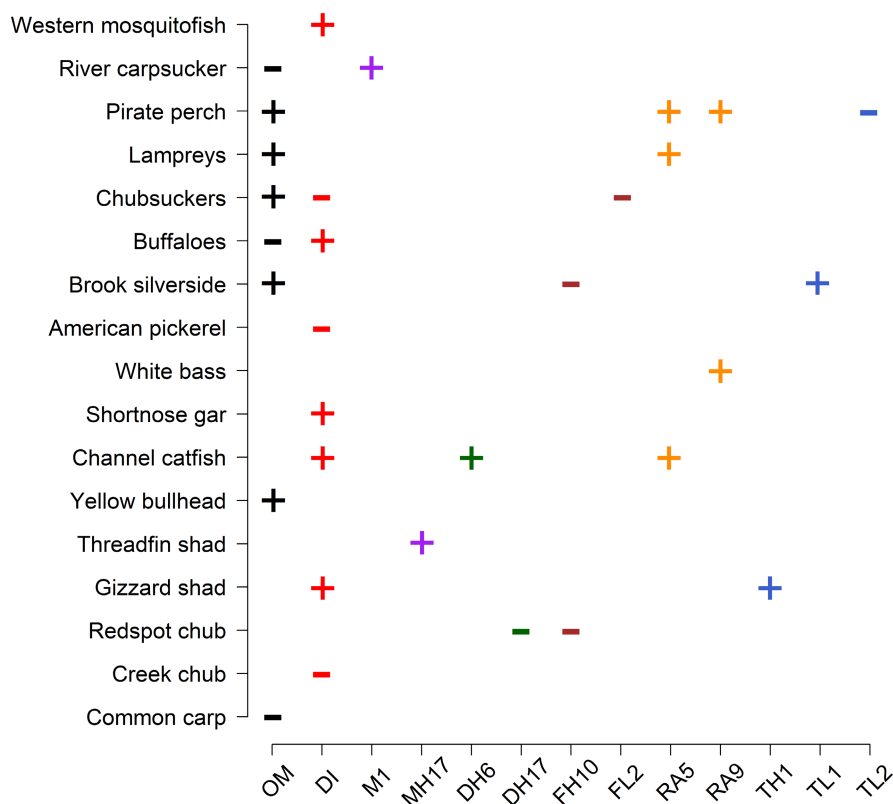


FIGURE 5 Occurrence relationships among remaining stream fishes determined using species coefficients with an HDI that did not overlap zero (Tables S3 and S7). A plus sign (+) indicates a positive occurrence relationship. A minus (-) sign indicates a negative occurrence relationship. Colours associated with + or - indicate black for ecoregion relationships, red for landscape disturbance relationships, purple for flow magnitude relationships, green for flow duration relationships, brown for flow frequency relationships, orange for flow rate of change relationships and blue for flow timing relationships. OM is ecoregion B (Ouachita Mountains and Arkansas Valley), DI is landscape disturbance index and M1 is drainage area. See Table 1 for description of three-character alphanumeric codes for flow regime metrics

($n = 13$), including within members of *Notropis* and *Pimephales* (Figure 2). All relationships with the disturbance index were positive for darters ($n = 3$) and madtoms ($n = 2$, Figures 3 and 4). Smallmouth bass (*Micropterus dolomieu*) was the only sunfish associated with the disturbance index, with a negative relationship (Figure 4). No

suckers or topminnows were associated with the disturbance index. Disturbance index relationships varied among remaining fishes ($n = 8$, Figure 5). Disturbance index had more variation in Ψ among fishes than retained flow metrics, except for variability in low flow pulse count (FL2, Table S7).

Species Ψ relationships with frequency comprised flood frequency (FH10, $n = 13$ fishes) and low flow pulse count ($n = 16$ fishes, Table S7). Relationships varied with both frequency metrics among small-bodied minnows ($n = 6$ and $n = 4$ for flood frequency and variability in low flow pulse count, respectively, Figure 2). Among darters, relationships were all negative with flood frequency (Johnny darter *Etheostoma nigrum* and least darter *E. microperca*) but varied with variability in low flow pulse count ($n = 5$, Figure 3). Tadpole madtom (*Noturus gyrinus*) was associated with both frequency metrics (a negative and positive relationship with flood frequency and variability in low flow pulse count, respectively, Figure 4). Ouachita madtom (*N. lachneri*) had a negative relationship with variability in low flow pulse count. Orangespotted sunfish (*Lepomis humilis*), redear sunfish (*L. microlophus*) and spotted sucker (*Minytremma melanops*) had a positive relationship with variability in low flow pulse count (Figure 4). No sunfishes or suckers were associated with flood frequency. Blackspotted topminnow (*Fundulus olivaceus*) was associated with both frequency metrics (a positive and negative relationship with flood frequency and variability in low flow pulse count, respectively). Plains killifish (*F. zebrinus*) had a negative relationship with flood frequency. Brook silverside (*Labidesthes sicculus*) and redspot chub (*Nocomis asper*) had a negative relationship with flood frequency (Figure 5). Chubsuckers (*Erimyzon* spp.) had a negative relationship with variability in low flow pulse count. The most variation in Ψ among fishes for flow metrics was with variability in low flow pulse count (Table S7).

Twenty-one fishes had a Ψ relationship with flow duration, comprising high flow duration (DH17, $n = 16$) and variability of annual maximum flow (DH6, $n = 6$, Table S7). Among small-bodied minnows, relationships were all negative with high flow duration ($n = 4$) but varied with variability of annual maximum flow ($n = 2$ for both positive and negative relationships, Figure 2). Striped shiner was the only species negatively associated with both duration metrics. Relationships were all negative with both frequency metrics among darters ($n = 4$ and orangebelly darter for high flow duration and variability of annual maximum flow, respectively, Figure 3). Relationships were also negative with high flow duration among sunfishes (rock basses *Ambloplites* spp. and smallmouth bass), madtoms (Caddo madtom *Noturus taylori*), topminnows (blackspotted topminnow and northern studfish) and suckers (northern hogsucker *Hypentelium nigricans* and redhorses, Figure 4). No sunfishes, madtoms, topminnows or suckers were associated with variability of annual maximum flow. Redspot chub had a negative relationship with high flow duration (Figure 5). Channel catfish (*Ictalurus punctatus*) had a positive relationship with variability of annual maximum flow. There was more variation in Ψ among fishes with high flow duration than variability of annual maximum flow (Table S7).

Nineteen fishes had a Ψ relationship with rate of change, comprising number of day rises (RA5, $n = 14$) and variability in reversals (RA9, $n = 6$, Table S7). Relationships among small-bodied minnows were all negative with number of day rises ($n = 3$) but varied with variability in reversals ($n = 3$, Figure 2). Relationships were all

positive with number of day rises among darters ($n = 5$, Figure 3). Orangebelly darter was the only darter associated with variability in reversals, with a negative relationship. Rock basses, northern studfish and northern hogsucker also had a positive relationship with number of day rises (Figure 4). No sunfishes, topminnows or suckers were associated with variability in reversals. No madtoms were associated with either rate of change metric. Among remaining fishes, two had a positive relationship with number of day rises, and three had a positive relationship with variability in reversals (Figure 5). Pirate perch (*Aphredoderus sayanus*) was the only species associated with both rate of change metrics. There was more variation in Ψ among fishes with variability in reversals than number of day rises (Table S7).

Species Ψ relationships with timing ($n = 16$ fishes) comprised variability in date of annual minimum flow (TL2, $n = 10$), date of annual minimum flow (TL1, $n = 8$) and date of annual maximum flow (TH1, $n = 4$, Table S7). Timing had the greatest number of fishes associated with more than one metric ($n = 5$). Among small-bodied minnows, relationships were all positive with date of annual minimum flow ($n = 2$) and all negative with variability in date of annual minimum flow ($n = 2$) and varied with date of annual maximum flow ($n = 3$, Figure 2). Striped shiner was the only species associated with all three timing metrics (a positive relationship with date of annual minimum flow and a negative relationship with both variability in date of annual minimum flow and date of annual maximum flow). Relationships were all positive with date of annual minimum flow among darters but varied with variability in date of annual minimum flow ($n = 3$ for both metrics, Figure 3). Smallmouth bass and northern studfish had a positive relationship with date of annual minimum flow and a negative relationship with variability in date of annual minimum flow (Figure 4). Freckled madtom (*Noturus nocturnus*) and northern hogsucker also had a negative relationship with variability in date of annual minimum flow. No darters, sunfishes, or topminnows were associated with date of annual maximum flow (Figures 3 and 4). No madtoms or suckers were associated with any timing metric (Figure 4). Pirate perch had a negative relationship with variability in date of annual minimum flow (Figure 5). Brook silverside and gizzard shad (*Dorosoma cepedianum*) had a positive relationship with date of annual minimum flow and date of annual maximum flow, respectively. There most variation in Ψ among fishes for timing flow metrics was with variability in date of annual minimum flow and the least was with date of annual minimum flow (Table S7).

Species Ψ relationships with magnitude comprised drainage area ($n = 7$ fishes) and high flow discharge index (MH17, $n = 5$ fishes, Table S7). Magnitude was the only flow regime component with no fishes associated with more than one metric. Relationships were all positive with drainage area among small-bodied minnows ($n = 5$, Figure 2). No small-bodied minnows were associated with high flow discharge index. Orangebelly darter also had a positive relationship with drainage area (Figure 3). Redfin darter (*Etheostoma whipplei*) had a negative relationship with high flow discharge index. Redear sunfish (*Lepomis microlophus*) and northern studfish also had a negative relationship with high flow discharge index, but blackstripe

topminnow (*Fundulus notatus*) had a positive relationship (Figure 4). No sunfishes or topminnows were associated with drainage area. No madtoms or suckers were associated with either magnitude metric. River carpsucker (*Carpionodes carpio*) and threadfin shad (*Dorosoma petenense*) had a positive relationship with drainage area and high flow discharge index, respectively (Figure 5). There was more variation in Ψ among fishes with high flow discharge index than drainage area (Table S7).

4 | DISCUSSION

Our findings support flow-regime characteristics and land use as drivers of stream fish distributions in the central Red River catchment. Relatively few studies have examined relationships of a large number of fishes with environmental variables at the catchment scale (but see Kennard et al., 2007; Snelder & Lamouroux, 2010; Iwasaki et al., 2012). We found stream fish occurrence relationships with all five flow-regime elements. Contrasting occurrence relationships were common within major species groups and genera with both landscape disturbance and all flow regime components (also see Section 4.1). Endemic or environmentally sensitive fishes had opposite relationships with landscape disturbance and flow-regime metrics representing variability taxonomically similar species.

The occurrence relationships indicate increased landscape disturbance and streamflow variability may result in a loss of species diversity in the central Red River catchment. Small-bodied minnows positively associated with either flow regime metrics representing variability or landscape disturbance (or both) included species common to the upper portion of the catchment (bullhead minnow, red shiner, sand shiner and suckermouth minnow, Taylor et al., 1993; Starks et al., 2018). The upper Red River catchment has harsher environmental conditions and increased streamflow variability (Woods et al., 2004, 2005). Other fishes positively associated with landscape disturbance or streamflow variability were cosmopolitan species (e.g. channel catfish and western mosquitofish *Gambusia affinis*, www.iucnredlist.org/) or have extensive North American ranges (e.g. dusky darter, slenderhead darter, freckled madtom and tadpole madtom). Conversely, fishes with narrow ranges (e.g. creole darter, redbfin darter, Ouachita madtom), that perform key ecosystem functions (e.g. stonerollers, Gelwick & Matthews, 1997; Reisinger et al., 2011), or are good water-quality indicators (e.g. big-eye shiner, Eley et al., 1981 and creek chub, Nagrodski et al., 2013) were negatively associated with landscape disturbance and streamflow variability. For example, Ouachita shiner and the Ouachita strain of smallmouth bass, which are endemic to the eastern portion of the study area, had negative relationships with both, but were not associated with ecoregion. This suggests lower levels of human disturbance and flow variability in the Ouachita Mountains strongly influence their distributions. Collectively, these relationships suggest a risk of increased prevalence of common fishes and associated loss of species richness and diversity with increases in

agriculture, urbanization and streamflow variability. Research at the stream reach-scale in basins nearby the Red River have shown altered fish assemblage structure after changes in environmental and flow-regime characteristics associated with anthropogenic pressure. Miyazono et al. (2015) found a reduction in reach-scale native fish relative abundance and species diversity in the Rio Grande River sub-basin following a decrease in flow magnitude and increase in salinity. Similarly, Taylor et al. (2019) reported changes in the fish assemblage in reaches of the Pecos River subbasin and homogenization in the Rio Grande River subbasin following reduction in flow magnitude and water quality. The homogenization of fish assemblages due to landscape development has been documented globally in both freshwater (Scott & Helfman, 2001; Villéger et al., 2014) and marine systems (Magurran et al., 2015; Richardson et al., 2018). Lower species richness and diversity are also associated with higher streamflow variability in other regions (e.g. Herbert & Gelwick, 2003; Poff & Allan, 1995). In contrast, Sánchez-Pérez et al. (2020) found a decrease in diversity in Mediterranean rivers with increased hydrologic stability due to native species adaptations to flow variability.

In contrast to streamflow variability, central Red River fishes were predominately negatively associated with a greater frequency of high flow events. Small-bodied minnows that were positively associated with landscape disturbance had a negative relationship with flood frequency. Thus, a change in precipitation patterns resulting in increased flooding may also threaten fishes more tolerant to other environmental changes. Studies in other regions had similar findings. For example, Thomaz et al. (2007) found that increased flooding was associated with a homogenization of fish assemblages. However, these high-flow event relationships are also dependent on the scale of observations. Espínola et al. (2020) found flooding increased the spatial variability of fish assemblages at the reach scale.

The lack of occurrence relationships with flow magnitude differed from similar studies. Both average daily discharge and drainage area are associated with stream fish distributions in various catchments globally (Iwasaki et al., 2012; Kennard et al., 2007). However, our findings suggest flow magnitude has minimal influence on stream fish distributions in the central Red River catchment. Although confounded in our study due to the high correlation level, daily discharge and drainage area have different functional roles in fish distributions. Daily discharge is a more accurate measure of water availability, while drainage area provides a better surrogate of flow diversity (Hugueny et al., 2010; Iwasaki et al., 2012).

Datasets combined from numerous existing sources provide important information about ecological relationships and associated species distributions by expanding the spatial and temporal extent of studies. However, existing data are inherently “messy,” with numerous sources of detection error (MacKenzie et al., 2017) and incomplete survey coverage across space and time (Farley et al., 2018; Hampton et al., 2013). We also found a high prevalence of duplicate fish surveys among publicly available databases (i.e. surveys tended to be overreported). Although removing duplicates requires careful attention and additional time requirements, ignoring this aspect

when organizing amalgamated datasets can lead to incorrect conclusions about both ecological and detection processes. Obstacles are, of course, common when using existing historical data, but approaches exist to overcome the variety of sampling gears and managing data (also see Sleezer et al., 2021). We used occupancy modelling, which allowed us to account for differences in species detection probability associated with relative flow, the timing of the survey and sampling biases. Detection probability is typically ignored in multispecies studies (e.g. correspondence analyses), which misrepresent assemblage structure and species diversity (Benoit et al., 2018; Dorazio & Royle, 2005). Spatially replicated surveys come with caveats concerning occupancy model assumptions (Kendall & White, 2009). However, we feel trade-offs are reasonable given the nature of the data (e.g. numerous species and multiple gear types and collector) and temporally replicating entire HRUs across a catchment for decades is not realistic even with a priori design. Independence among surveys was a reasonable assumption, given we eliminated duplicates and no surveys in space were performed at the same time. The detection covariates also allowed for some degree system openness, which addresses cautions of using spatial replicates described by Kendall and White (2009). The time of year and drainage area covariates allowed species abundance, as it relates to detection, to vary in time and space, respectively. Similarly, the relative flow magnitude covariate allowed species abundance to vary in both time and space in relation to flow conditions. The nature of the data also prevented examining abundance because counts were seldom reported in the surveys and, if so, associated effort or site size was rarely reported. Though, occurrence provided a more-appropriate state variable with the coarse HRU spatial scale. Abundance cannot be realistically measured at a subbasin scale due to inherent logistical constraints and extrapolating based on subsamples may not be ecologically meaningful (e.g. subsamples may not encompass all habitat types or species) or reasonably accurate. Abundance at the subbasin scale is also not typically of conservation and management interest. The stream reach (e.g. variation in reach-scale abundance within subbasins) is a more-natural scale to examine population size (Fausch et al., 2002; Frissell et al., 1986). Further, discharge estimates were only available at HRU mainstem outlets. The broad-scale approach also does not capture finer-scale variation in Red River stream fish populations within the long time periods (e.g. Hargrave & Taylor, 2010; Starks et al., 2018; Taylor et al., 1993). There are also some trade-offs of using a hierarchical multispecies model. In addition to model complexity, the compromise of species-specific fit and estimating the group mean can result in missing some individual relationships (Gelman & Hill, 2007). However, we feel a hierarchical multispecies model was particularly advantageous here given the large fish assemblage. Individual species models would have been unwieldy with poor fit likely for rarer species. Also, a more-traditional multispecies model (i.e. dummy variable approach) would also likely have fit issues and interpreting relationships as differences from a reference species would have been cumbersome. We depicted the results as simple positive and negative relationships to summarize occurrence relationships among

a large number of species. However, a Bayesian modelling approach also provides intuitive measures of effect size and relative uncertainty (i.e. the mode and HDI of the posterior distribution) to compare the magnitude of relationships both within and among species groups (Table S7).

4.1 | Conservation implications

Our findings inform proactive, long-term strategies, but also highlight the challenges of stream fish conservation across a river catchment (e.g. actions that may benefit some species may be detrimental to others). Small-bodied minnows, in particular, had contrasting relationships with landscape disturbance and various flow metrics. Reducing landscape disturbance is one strategy that may benefit several species including an endemic sportfish, the Ouachita strain of smallmouth bass. Because the spatial extent of our observations is relatively coarse, areas with higher HRU disturbance have both higher and lower species occurrence probabilities could set the stage for opportunities to mitigate disturbance effects at finer spatial extents or identify areas for protection. For example, if smallmouth bass were historically common in an area where occurrence probability is now low, improving riparian corridors, stabilizing banks, adding sediment traps or other strategies could mitigate land use effects in targeted HRUs. Building on our findings, investigations directed at determining the mechanisms by which landscape disturbance affects these populations would be beneficial. Mixed relationships among fishes with flow regime characteristics is common among similar studies (e.g. Iwasaki et al., 2012; McManamay et al., 2013; Whiterod et al., 2015). Nevertheless, our findings can also guide land use and water management decisions by identifying areas with a high occurrence probability of less-tolerant or narrow-range species and help managers understand potential changes in stream fish assemblages under different scenarios. A positive occurrence relationship with higher flows later in the year was also common among study fishes. Thus, a shift in precipitation patterns, in addition to increased landscape disturbance and streamflow variability, could result in a change in the Red River fish assemblage. Moreover, the Red River catchment is central to water-management debates (Burch et al., 2020) where water diversions and dam operations could benefit from an understanding of how these fishes respond to flows. In particular, the relationships between flow, disturbance and species of conservation concern (e.g. Kiamichi shiner and Ouachita shiner) could be used to provide initial guidance on strategies for water transfers. However, we caution that follow up surveys are necessary as the HRU relationships may not mimic those found at stream segment scales. Ignoring coarse-scale constraints on stream fish distributions can hamper conservation efforts and confound ecological research at finer scales (Fausch et al., 2002). The occurrence of numerous stream fishes was also associated with an ecoregion, with other variables held constant. As would be expected, this relationship suggests other landscape characteristics (e.g. underlying lithology and coarse-scale geomorphology) also influence Red River

stream fish distributions. We primarily included ecoregion to control for unexplained variation among species. However, these relationships do highlight that occurrence is associated with numerous variables and not all can be captured in a model (e.g. biogeography associated with the opportunity for a species to colonize).

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CONFLICT OF INTEREST

The authors do not have any conflicts of interests or competing interests that need disclosed.

DATA AVAILABILITY STATEMENT

Availability of data and material: All data were acquired from publicly available sources. The authors provide the data sources for the fish surveys as supplemental information (Table S2). The Red River fish survey dataset compiled by the authors is available at [10.22488/okstate.22.000006](https://doi.org/10.22488/okstate.22.000006). The hydrology data generated in this study are available as a USGS data release (Roland, 2020).

PEER REVIEW

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BIOSKETCH

The authors' research is focused on identifying relations and mechanisms related to rare, declining or economically important aquatic species for which the causes and corresponding management responses are unclear. They conduct applied research on a wide range of lotic species to address specific conservation and management questions. Activities central to their efforts include determining population size, occupancy, demographics, distributions and providing a scientific basis to guide conservation and management actions. V. Roland is a hydrologist with the Lower Mississippi Gulf Water Science Center and is focused on water quality and quantity. A complete list of publications can be found at: <https://www1.usgs.gov/coopunits/staff/478971> and <https://www.usgs.gov/staff-profiles/victor-l-roland>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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