



Modelling patterns of coexistence of three congeneric headwater fishes

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Abstract

1. Mechanisms driving patterns of occurrence and co-occurrence among North American freshwater fishes are poorly understood. In particular, the influence of biotic interactions on coexistence among stream reaches and their effects on regional species distribution patterns is not well understood for congeneric headwater fishes.
2. Occupancy models provide a useful framework for examining patterns of co-occurrence while also accounting for imperfect detection. Occupancy models may be extended to test for evidence that a dominant species influences the occurrence of a subordinate species and thus evaluate support for the hypothesis that species interactions drive patterns of coexistence.
3. We examined patterns of occurrence and co-occurrence at the stream-reach scale among three species of darters (Percidae: Etheostomatinae) that occupy headwater streams within a Gulf Coastal Plain drainage in the south-eastern U.S.A. We assessed species occurrences at 97 sites in first- to third-order streams on one occasion each and used data from four sub-reaches sampled with equal effort at each site to estimate species-specific detection probabilities. Following sampling, a suite of habitat variables was collected at three equidistant points along each of the three transects established within a sub-reach. Coarse (stream-segment, catchment, network) scale variables were also incorporated using geospatial data. Single-species and two-species occupancy models were used to examine patterns of occupancy and coexistence.
4. The occupancy of each species was influenced by distinct habitat variables. Goldstripe darters (*Etheostoma parvipinne*) were constrained by a stream size gradient, groundwater input appeared to influence the occurrence of Yazoo darters (*Etheostoma raneyi*), and local habitat heterogeneity (e.g. variation in depth and current velocity) appeared to influence the occupancy of redspot darters (*Etheostoma artesiae*).
5. We found no evidence that the presence of one species influenced the occurrence of another within a stream-reach based on two-species occupancy models. Rather, species co-occurrences were best explained as independent occurrences within a stream-reach according to species-specific habitat associations.

6. Occupancy modelling may provide a suitable framework for evaluating the influence of biotic interactions among congeneric stream fishes along species-specific habitat gradients at the stream reach scale. Our study offers insight into how habitat variation can influence coexistence of potential competitors across a large river system.

KEYWORDS

coexistence, freshwater fish, headwater streams

1 | INTRODUCTION

The mechanisms that facilitate the coexistence of sympatric congeners, a group of species within the same genus whose geographic ranges overlap (Heinrich, Elwen, & Bräger, 2010), is widely debated among ecologists (Hochkirch, Gröning, & Bucker, 2007; Schoener, 1974; Sukhikh et al., 2019; Vance, 1972). Often, the coexistence of these species is regulated by a distinct limiting factor (e.g. the size ratio of one morphological character) (Hutchison, 1959). For example, differences in morphological and behavioural traits may facilitate habitat partitioning, effectively allowing species to exploit different resources and enabling long-term coexistence (Schluter, 2000). Such mechanistic differences limit the ability of ecologists to predict if competitive exclusion is at play (Davies, Harrison, Safford, & Viers, 2007). Stable coexistence between two potential competitors is predicted when interspecific competition is lessened (Vergara, Cushman, Urra, & Ruiz-González, 2016). In streams, interspecific competition is reduced by variable abiotic conditions (Meyer et al., 2007), meaning that resident species may share similar ecological, physiological, and morphological traits (Ross, 2013). Thus, abiotic variability may contribute to coarse-scale patterns of co-occurrence in these systems (Giam & Olden, 2016).

Headwater streams (first- to third-order streams) are ubiquitous across a stream network, and are structured in hierarchical mosaics of patches, which are ecologically connected longitudinally (Poole, 2002; Wiens, 2002). However, this longitudinal arrangement of patches is unique and dynamic over time (Rice & Church, 2001). The resulting *branchiness* and hierarchy of these habitat arrangements in stream networks affects patch connectivity and the isolation of metapopulations (Fagan, 2002). Because stream fishes differ in their movement capabilities and habitat preferences, their responses to this diverse, heterogeneous network of patches will be different (Wiens, 2002).

Many headwater fishes exhibit dispersal patterns that adhere to the stream hierarchy model (Meffe & Vrijenhoek, 1988) predicting that hierarchically nested drainages are more likely to exchange organisms. Ecological trait selection within headwater streams is a result of the isolation of unique habitats across a river system (Mundahl & Ingersoll, 1983; Petty & Grossman, 2004; Schmidt & Schaefer, 2018). Morphological adaptations to these unique habitat patches such as small body size and caudal fin shape, both of which

affect swimming performance, may further limit dispersal of headwater specialists (Hudy & Shiflet, 2009; Ovidio, Detaille, Bontinck, & Philippart, 2009; Petty & Grossman, 2004). As a consequence, these species may have disjunct distributions due to the hierarchical arrangement of headwater habitats, thus influencing assemblage composition.

While heterogeneity of available habitat affects coexistence, it is clear that biological interactions (e.g. predation, interspecific competition, facilitation) are important. Biological interactions have been shown at micro and mesohabitat scales (Fausch, Nakano, & Ishigaki, 1994; Grossman et al., 2006; Resetarits, 1997); however, other evidence suggests that facilitation and competition may influence coexistence at more coarse scales (e.g. stream-reach, landscape) (Gilliam, Fraser, & Alkins-koo, 1993; Peoples & Frimpong, 2016; Townsend & Cowl, 1991). Few studies have tested the effects of both biotic and abiotic factors on the coexistence of stream fishes that are congeners or occupy the same trophic guild (Crow, Closs, Waters, Booker, & Wallis, 2010; Fausk et al., 1994; Peoples & Frimpong, 2016; Peres-Neto, 2004; Taylor, 1996) at these coarser scales; however, we are only aware of one study (Peoples & Frimpong, 2016) that accounted for imperfect detection.

The use of occupancy modelling (MacKenzie et al., 2002) provides a framework to better understand how multi-scale abiotic processes influence the coexistence of congeneric, headwater fishes by testing hypotheses explaining whether co-occurrence of species happens more or less than expected by chance (MacKenzie, Bailey, & Nichols, 2004; Miller, Talley, Lips, & Grant, 2012). To that end, we used this method to evaluate multiple working hypotheses to better understand the coexistence of three congeneric darters within the genus *Etheostoma* (Percidae: Etheostominae, Near et al., 2011) at the stream-reach scale in a Gulf Coastal Plain drainage located within the south-eastern U.S.A. The south-eastern U.S.A. is the centre of diversity for darters; a diverse group of benthic, freshwater fishes which are often headwater specialists (i.e. functional trait databases place 87 of 250 species in springs, or headwater habitats, Frimpong & Angermeier, 2009). If competition influences occupancy of these headwater fishes, we predict that a species occupancy or detectability will be lower when another congener is present or detected within a stream reach. If competition does not influence occupancy of these congeners, we predict that a species occupancy or detectability will be

unaffected when another congener is present or detected within a stream-reach. Assessing the influence of biotic interactions at the stream-reach scale aids in our understanding of how abiotic and biotic processes regulate distributional patterns of aquatic biota at a more coarse spatial extent.

2 | METHODS

2.1 | Study-system and species

We conducted our study in the Little Tallahatchie River system (henceforth LTR), which is positioned within the upper Yazoo River basin in North-Central Mississippi. The LTR consists of the Little Tallahatchie and Tippah River drainages, and is isolated by the presence of a large (398 km²) reservoir, Sardis reservoir (Figure 1). The Yazoo darter *Etheostoma raneyi*, goldstripe darter *Etheostoma parvipinne*, and redspot darter *Etheostoma artesiae* all occur within the LTR and all three species are most abundant in small to medium sized streams (Ross & Breneman, 2001; Smiley, Dibble, & Schoenholtz, 2006; Sterling, Warren, & Henderson, 2013). These species are members of separate subclades (Yazoo darter: *Adonia*; goldstripe darter: *Fuscatelum*; redspot darter: *Vexillapinna*) within a large genus (Near et al., 2011). While the goldstripe darter (Bart & Taylor, 1999) and redspot darter (Piller, Bart, & Walser, 2001) are broadly distributed across the south-eastern U.S.A., the Yazoo

darter is endemic to the Upper Yazoo River basin (Suttkus et al., 1994; Thompson & Muncy, 1986) and is listed as vulnerable by the Southeastern Fishes Council (Warren et al., 2000) and the American Fisheries Society (Jelks et al., 2008).

2.2 | Datasets

Habitat and associated fish assemblage stability in this system (Schaefer, Clark, & Warren, 2012, Table S1) allowed us to model the occupancy and coexistence of redspot and goldstripe darters with data collected at 53 historic (1999–2003; Sterling et al., 2013) and 44 contemporary (2015–2016) sites (97 sites total, Table S2) (Figure 1). Of the 44 currently surveyed sites, 39 had never been previously sampled. Because Yazoo darters are not known to occupy the eastern portion of the LTR (i.e. the headwaters of the LTR, see Hubbell and Schaefer 2017), we used a subset of sites (52 historic, 13 contemporary) to model occupancy and co-occurrence of Yazoo darters in relation to redspot and goldstripe darters (Figure 1). We used 12-digit hydrological unit codes (HUCs, U.S. Geological Survey) to delineate catchments within the LTR. We randomly selected one to five sites per HUC (mean area \pm SD = 82.8 \pm 27.4 km²) to reduce historical sampling bias (i.e. site densities were much higher for historically sampled drainages which flow through public land). Due to a lack of accessibility, some HUCs were not able to be sampled.

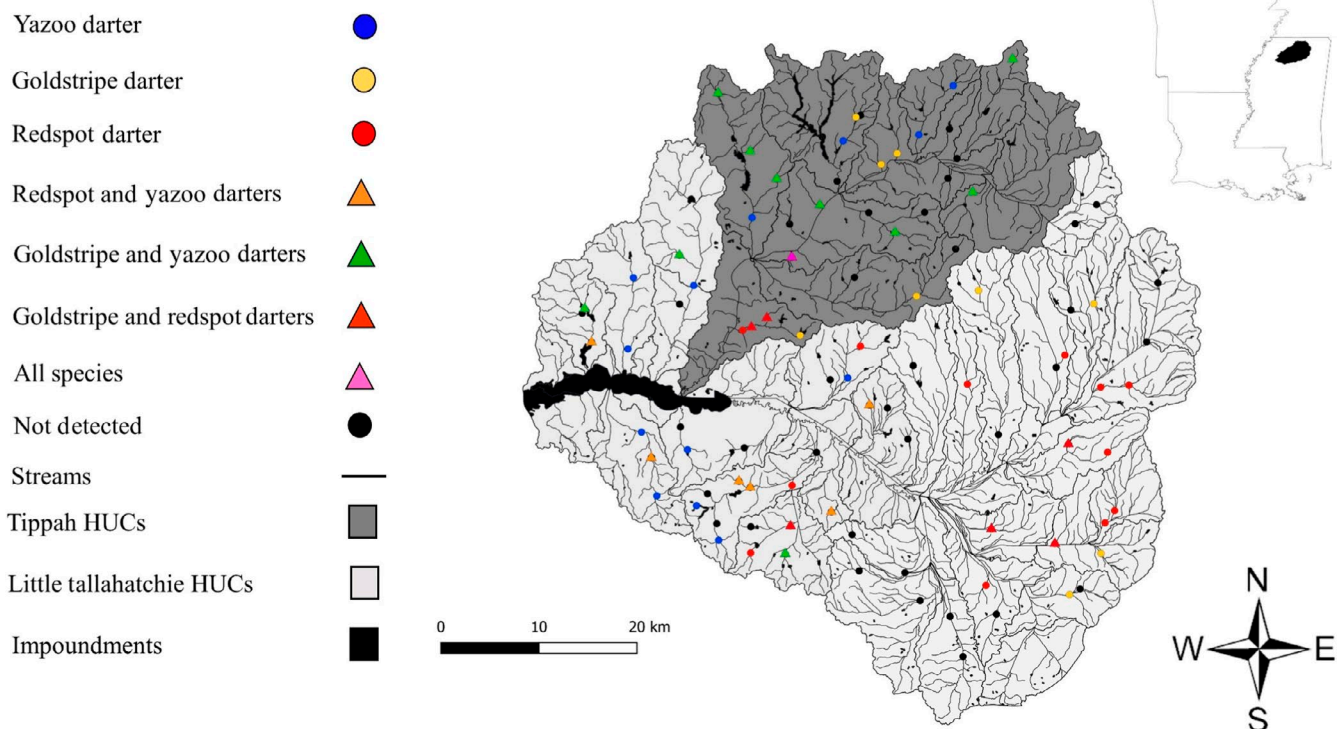


FIGURE 1 Map of detections, co-detections, and absences for each darter and darter pairing for all 97 localities distributed across the Tippah and upper Little Tallahatchie River systems included in our analyses. Inset map identifies the locality of the upper Yazoo River basin. Colour (red, orange, yellow, teal, pink) and shape (Δ , \circ) combinations distinguish which darter or darter pairing was detected at a given locality. All black circles indicate sites where none of the target species were detected [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Field methods

Sub-reaches were used as an alternative to re-sampling over time to generate detection histories (Albanese, Peterson, Freeman, & Weiler, 2007) for both historic and contemporary sites (sampled May–September). All sites were divided into four evenly sized sub-reaches. In this study, we assumed that the occupancy state of a sub-reach did not change during the survey period, all species were correctly identified, and that all species detections were independent. Reach lengths were calculated by multiplying the average stream wetted width by 30, with minimum and maximum lengths of 120 and 300 m, respectively. We performed backpack electrofishing and seining surveys to sample each sub-reach with equal effort. Two seine hauls were performed within each sub-reach, and an attempt was made to sample all available habitats. Electrofishing effort was set at 5 s/m of stream length. We preserved fishes using 10% formalin, and later transferred to 70% ethanol, for cataloguing and counting (University of Southern Mississippi Ichthyological Collection). To prevent over-sampling of Yazoo darter populations, we only vouchered two individuals per site. Before pooling presence–absence generated by the two gear types for modelling, these data were initially kept separate to assess how detection varied as a result of these two sampling methods; however, because presence–absence data were pooled in the final datasets, we do not present these results here (see Table S3). All sampling protocols were approved by the University of Southern Mississippi's Animal Care and Use Committee (IACUC 09–007). Within each sub-reach, we established three evenly spaced transects perpendicular to flow. At three equidistant points (i.e. interval based on wetted width) along each transect we measured depth (cm), current velocity (m/s), dominant substrate size (modified Wentworth scale, Cummins, 1962), and the presence (binary variables) of woody structure or aquatic vegetation. Substrate types were divided into six categories: 1 = silt, 2 = sand, 3 = gravel, 4 = cobble, 5 = boulder, 6 = bedrock. We quantified the coefficient of variation of current velocity (CVCV), substrate size (CVSUB), and depth (CVD) to serve as proxies of habitat heterogeneity. We also calculated mean depth, mean current velocity, mean substrate size, woody structure (WS), and aquatic vegetation.

2.4 | Data processing

We compiled stream size and network variables (drainage area, confluence link) from the National Hydrography Dataset Plus (USEPA & USGS, 2006); all data processing was performed in ArcGIS 10.0 (ESRI, 2011). Confluence link (C-Link) is the number of confluences downstream from each stream segment (Fairchild, Horwitz, Nieman, Boyer, & Knorr, 1998). We defined a stream-segment as an individual segment when using the NHDPlus flowline vector layer. C-Link values decrease in a given catchment from extreme headwaters to the base of a stream network. We quantified C-Link as the number of confluences downstream from a site to the furthest downstream stream-segment on the main stem of the LTR. Drainage area (DA) is

the total drainage area in km² upstream of each site. We included well depth (WD) (MDWQ, 2015) as a surrogate measure of water table depth to infer stream permanence and relative groundwater input. Well depth is known to correlate with water table depth across a catchment (Rosenberry, LaBaugh, & Hunt, 2008). We used nearest neighbour interpolation to assign WD vector point data to all sites within the LTR. Nearest neighbour interpolation (implemented using the Spatial Analysis Toolbox; ESRI, 2011) selects the value of the nearest point and does not consider the values of other points at all. We obtained land cover data (19 classes) for the years 2002 and 2012 from the U.S. conterminous wall-to-wall anthropogenic land use dataset (Falcone, 2015). These time periods were used because they represented the closest approximations of land use when fish assemblages were sampled. We reclassified the land cover data into five broad land cover types: forested, urban, wetland, open water, and agricultural for both time periods. We conducted a principal components (PC) analysis on the relative area of each cover type within each site's DA. The first axis of this PC analysis explained 45.5% of the variation (with forested land having the highest loading) and was used (PC1) in our occupancy models.

2.5 | Modelling of occupancy and co-occurrence

We used single-species models to characterise important habitat covariates associated with the probability of occurrence (Ψ) and the probability of detection (p) of each headwater darter. Because spatial replicates may not represent truly independent surveys and lead to the inflation of occupancy estimators (Kendall & White, 2009), we also developed spatial dependence models (Hines et al., 2010). Spatial dependence models allow the probability that a spatial segment may or may not be occupied based upon whether the previous segment was occupied (θ') or not (θ) (Hines et al., 2010) where parameters are modelled as a first-order Markov process. We modelled detection as constant and as a function of sampling covariates to distinguish if p varied among sites. We used untransformed β estimates to infer relationships (positive or negative) between covariates and parameters. To assess the relative fit of our single-species occupancy models, we used the MacKenzie–Bailey goodness of fit test (MacKenzie & Bailey, 2004), in which overdispersion (\hat{c}) is estimated by calculating the χ^2 goodness of fit statistic for a global model and then dividing it by the mean test statistic of 10,000 bootstrap samples.

Two-species occupancy models using the Ψ^{Ba} parameterisation (Richmond, Hines, & Beissinger, 2010), an extension of the model described by MacKenzie et al. (2004), were used to test whether species occupancy was influenced by the occupancy or detectability of another congener at the stream-reach scale. This parameterisation allows for the estimation of Ψ^A (probability of occupancy of the dominant species), Ψ^{Ba} (i.e. probability of co-occurrence), and Ψ^{Ba} (probability of occupancy of the subordinate species given the dominant species is absent) (Richmond et al., 2010). This parameterisation allows for the incorporation of covariates, the direct estimation of the species interaction factor (SIF), and sets Ψ^B

conditional upon Ψ^A . The SIF represents the probability that the two species co-occur no more or no less than what would be expected if all occurrences of the species were random (MacKenzie et al., 2004). We only calculated SIF if the competition model (i.e. $\Psi^{BA} \neq \Psi^{Ba}$) was included among the best models for each darter pair. When using this parameterisation, the dominant species and subordinate species must be established a priori (Richmond et al., 2010). Because Yazoo darters are likely to be more habitat-limited, we assigned redspot and goldstripe darters as Ψ^A when examining coexistence with Yazoo darters (designated Ψ^B). Because of its restriction to smaller streams, we designated goldstripe darters as Ψ^B and redspot darters as Ψ^A when modelling coexistence of these two fishes. We constructed models that assumed occupancy of Ψ^B would (i.e. $\Psi^{BA} \neq \Psi^{Ba}$) or would not (i.e. $\Psi^{BA} = \Psi^{Ba}$) be influenced by the presence of Ψ^A . For detection probability, we estimated p^A (probability of detecting species A given species B is absent), p^B (probability of detecting species B given species A is absent), r^A (probability of detecting species A, given both species are present), r^{BA} (probability of detecting species B, given both species are present), and r^{Ba} (probability of detecting species B given species A is present but was not detected). We modelled all detection parameters within our two-species models as both independent (i.e. $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$), and dependent (i.e. $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$). Similar to single-species models, we used untransformed β estimates to infer relationships (positive or negative) between covariates and parameters. We only included the top ranked occupancy covariates and detection covariates ($w_i > 0.10$) from our single-species occupancy models in the two species models to account for habitat preferences and imperfect detection. We constructed all single and two-species models using the software program PRESENCE (vers. 12.7) (Hines, 2006).

2.6 | Covariates

We included four spatial scales of abiotic variables (network, catchment, stream-segment, stream-reach) in our occupancy models using the logit link transformation to model all parameters as a function of covariates (MacKenzie et al., 2002) (Table S4). Network scale variables captured variation occurring at the largest spatial extent (i.e. the river network), catchment scale variables elucidated variation within distinct drainages (i.e. 12-digit HUCs), stream-segment variables were indicative of variation among stream-segments, and stream-reach scale variables were indicative of variation among individual sites. C-Link was the only variable included at the network scale, while the PC1 score for land cover was the sole variable included at the catchment scale. At the stream segment scale, we included DA, and WD to estimate the influence of hydrological and geological variables. To assess the effects of stream-reach scale variation on occupancy, we included mean depth, mean current velocity, mean substrate size, CVCV, CVSUB, CVD, WS, and aquatic vegetation as covariates within our occupancy models. Sub-reach means for current velocity, substrate size, and depth were included as sampling covariates to estimate p . To evaluate

the relative influences of each covariate, we standardised all variables by subtracting the mean and dividing by twice the standard deviation. Prior to modelling, we tested for the correlation between covariates. Any two covariates with a Pearson correlation greater than the absolute value of 0.5 were not included in the same model. However, correlated variables were used as separate covariates for detection and occupancy within the same model.

2.7 | Model selection

We used Akaike information criterion for small sample sizes (AIC_C) to assess the quality of competing models (Burnham & Anderson, 2002). Models with small ΔAIC_C and large Akaike weights (w_i) indicate the greater parsimony (Burnham & Anderson, 2002). We only interpreted models with $w_i > 0.10$. To prevent the inclusion of uninformative parameters, models which only differed in ΔAIC_C by 1–2 units from the best models and possessed similar log-likelihood values were removed (Burnham & Anderson, 2002). As an alternative to using a single best-supported model, we applied model averaging to quantify unconditional model average estimates of Ψ and p , and associated standard errors (bounded between 0 and 1.0) for all occupancy and detection parameters within models with $w_i > 0.001$ (Burnham & Anderson, 2002). To infer coexistence patterns, we considered estimated parameters (i.e. Ψ^A , Ψ^{BA} , Ψ^{Ba} , p^A , r^A , p^B , r^{BA} , r^{Ba}) and the relationships among them based on the top ranked model for each species pair.

3 | RESULTS

3.1 | Species occupancy and co-occurrence

The three study species were detected in less than half of the surveyed sites. Of the 39 new sites, goldstripe darters were detected at 10, redspot darters were detected at 13, and Yazoo darters were not detected at any of these new localities. Out of the 65 sites sampled occurring within the range of the species, Yazoo darters were detected at 27 sites (naïve occupancy estimate = 0.42). Out of the 97 total sites sampled, goldstripe darters were detected at 30 sites (naïve occupancy estimate = 0.31), and redspot darters were detected at 30 sites (naïve estimate = 0.31). Darter species occurred together at rates closer to those expected given independent occurrences. Of the three darter pairings, Yazoo and goldstripe darters were co-detected at 14 of 65 sites (naïve occupancy estimate = 0.22), Yazoo and redspot darters at 8 of 65 sites (naïve estimate = 0.12), and redspot and goldstripe darters at 11 of 97 sites (naïve estimate = 0.11).

Detection was best modelled as a function of different covariates across the three darter species. Detection of Yazoo darters was best modelled by depth ($w_i = 0.96$), goldstripe darters by current velocity and depth ($w_i = 0.84$), and redspot darters by current velocity and depth ($w_i = 0.78$). Detectability of Yazoo darters was negatively correlated with depth (β estimate, -0.28 ± 0.12). Detection of goldstripe darters, was positively related to current velocity (0.26 ± 0.12), and

negatively related to depth (-0.74 ± 0.21). Detection of redspot darters was positively related (0.17 ± 0.07) to current velocity, but negatively related to depth (-0.23 ± 0.08). Unconditional, model average estimates for p (i.e. unconditional estimates for detection across all sample sites) for all models with $w_i > 0.001$ for each species were as follows; Yazoo darter: 0.53 ± 0.09 for p ; goldstripe darter: 0.33 ± 0.18 ; redspot darter: 0.35 ± 0.13 .

Single-season null models were ranked higher than spatial dependence null models for all three darters (Table 1), and initial model weights (redspot darter, $w_i = 0.78$; Yazoo darter, $w_i = 0.90$, goldstripe darter, $w_i = 0.79$) suggested that detections were not spatially autocorrelated, justifying the use of spatial replicates for p . All single-species occupancy models converged. Global models for all darters indicated no evidence of a lack of model fit (Yazoo darter: $p = 0.26$, $\hat{c} = 1.19$; goldstripe darter: $p = 0.62$, $\hat{c} = 0.83$; redspot darter: $p = 0.36$, $\hat{c} = 1.08$).

The occupancy of each darter species was associated with distinct habitat variables. Goldstripe and Yazoo darters were both associated with one model which had $w_i > 0.10$ when modelling occupancy (ψ), whereas two models had $w_i > 0.10$ when modelling ψ of redspot darters (Table 1). Occupancy of Yazoo darters declined in relation to well depth (β estimate, -0.26 ± 0.12), and we estimated Ψ at 0.46 ± 0.05 which is a 9.5% increase from the naïve estimate (0.42). Goldstripe darter occupancy was negatively related to DA (β estimate, -0.93 ± 0.37), and an average model estimate signified that Ψ for this species was 0.35 ± 0.05 , which is a 12.9% increase from the naïve estimate (0.31). Redspot darter occupancy was positively related to CVD (0.39 ± 0.17), negatively related to WS (-0.26 ± 0.13), and negatively related to CVCV (-0.30 ± 0.16). Model averaging revealed that Ψ for the redspot darter was approximately 0.36 ± 0.06 which is a 16.2% increase from the naïve estimate (0.31).

Rankings and parameter estimates for all two-species models suggest that the dominant species did not influence the occupancy of the

subordinate species (i.e. $\Psi^{BA} = \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$, Tables 2 and 3). Detection parameters were best modelled as a function of depth for all three species pairs (Table 2). For the first species pairing, the best model ($w_i = 0.62$) assumed that there was a slight negative effect of stream permanence (i.e. WD, β estimate, -0.21 ± 0.12) on the probability of Yazoo darter occupancy regardless of the presence of goldstripe darters (i.e. $\Psi^{BA} = \Psi^{Ba}$) at the reach-scale, but also indicated that there was a strong negative effect of stream size (i.e. DA, β estimate, -0.90 ± 0.42) on the probability of goldstripe darter occupancy (i.e. Ψ^A ; Table 2). For the second species pairing, the best model ($w_i = 0.41$) only signified that Yazoo darter occupancy at the reach-scale was not influenced by the presence of redspot darters (i.e. no habitat covariates appeared in this model, Table 2). For the third species pairing, the best model ($w_i = 0.46$) assumed that there was a negative effect of stream size (i.e. DA, β estimate: -0.93 ± 0.37) on the probability of goldstripe darter occupancy regardless of the presence of redspot darters at the reach-scale (i.e. $\Psi^{BA} = \Psi^{Ba}$), but also implied that there was a slight positive effect of heterogeneity in depth (i.e. CVD, β estimate, 0.38 ± 0.17) on the probability of redspot darter occupancy (i.e. Ψ^A , Table 2).

4 | DISCUSSION

Multi-scale observational studies help ecologists to better understand how fine and large-scale processes influence non-random species co-occurrence. However, distinguishing between mechanisms that influence patterns of non-random coexistence is difficult because both biotic and abiotic processes shape species distributional patterns. Imperfect species detection may further limit any inferences made. In this study, occupancy modelling was used to integrate habitat covariates and heterogeneous detection probabilities into an investigation of co-occurrence patterns

Species	Model	K	AIC _C	ΔAIC _C	w _i
Yazoo darter	p (Depth), Ψ (WD)	5	234.33	0	0.36
	p (.), Ψ (.)	2	243.88	11.29	0
	p (.), Ψ (.), θ (.) θ' (.)	5	249.17	16.58	0
Goldstripe darter	p (Depth + Velocity), Ψ (DA)	7	261.98	0	0.68
	p (.), Ψ (.)	2	292.09	34.08	0
	p (.), Ψ (.), θ (.) θ' (.)	4	519.63	32.15	0
Redspot darter	p (Depth + Velocity), Ψ (CVD)	5	274.23	0	0.50
	p (Depth + Velocity), Ψ (WS)	5	276.59	2.57	0.14
	p (Depth + Velocity), Ψ (CVCV)	5	277.21	3.19	0.10
	p (.), Ψ (.)	2	282.99	9.07	0
	p (.), Ψ (.), θ (.) θ' (.)	5	287.29	13.37	0

TABLE 1 Top single-species occupancy models and intercept-only models for occurrence of three sympatric darter species sampled in the Little Tallahatchie River system, MS, USA.

Note: Values are shown for the number of parameters (K), AIC_C, ΔAIC_C, and model weights (w_i). Intercept-only models are designated by periods in place of covariates. Models with parameters θ and θ' indicate spatial dependence models.

TABLE 2 Co-occurrence occupancy models used to evaluate the role of interspecific interactions on the habitat use of three sympatric darter species sampled in the Little Tallahatchie River system, MS, U.S.A.

Species	Model	K	AIC _C	ΔAIC _C	w _i
Yazoo and goldstripe darters	Ψ^A (DA), $\Psi^{BA} = \Psi^{Ba}$ (Well), $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	8	443.42	0	0.62
	Ψ^A (DA), $\Psi^{BA} \neq \Psi^{Ba}$ (Well), $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	9	445.42	2.50	0.18
	Ψ^A (DA), $\Psi^{BA} = \Psi^{Ba}$ (DA), $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	8	446.60	3.18	0.13
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	7	461.24	17.79	0
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	8	462.19	19.22	0
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	9	464.46	21.37	0
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	9	466.62	22.74	0
Yazoo and redspot darters	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	6	429.66	0	0.41
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	4	431.57	1.91	0.16
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	9	432.44	2.78	0.10
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	9	433.91	4.25	0.05
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	9	435.0	5.34	0.03
Goldstripe and redspot darters	Ψ^A (CVD), $\Psi^{BA} = \Psi^{Ba}$ (DA), $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	8	531.93	0	0.46
	Ψ^A (CVD), $\Psi^{BA} = \Psi^{Ba}$ (DA), $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$ (Depth)	14	532.90	0.97	0.28
	Ψ^A (CVD), $\Psi^{BA} \neq \Psi^{Ba}$ (DA), $p^A = r^A$ (Depth), $p^B = r^{BA} = r^{Ba}$ (Depth)	8	534.32	2.39	0.14
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	4	555.98	18.84	0
	Ψ^A , $\Psi^{BA} = \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	7	556.38	20.13	0
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A = r^A$, $p^B = r^{BA} = r^{Ba}$	5	557.95	20.66	0
	Ψ^A , $\Psi^{BA} \neq \Psi^{Ba}$, $p^A \neq r^A$, $p^B \neq r^{BA} \neq r^{Ba}$	8	559.17	22.51	0

Note: Values are shown for the number of parameters (K), AIC_C, ΔAIC_C and model weights (w_i).

TABLE 3 Occupancy and detection probabilities (p and r) estimated from co-occurrence occupancy models of three sympatric darter species sampled in the Little Tallahatchie River system, MS, U.S.A.

Species pair	Ψ^A	Ψ^{BA}	Ψ^{Ba}	r^A	p^A	p^B	r^{BA}	r^{Ba}
Yazoo and goldstripe darters	0.39	0.46	0.46	0.39	0.39	0.53	0.53	0.53
Yazoo and redspot darters	0.35	0.46	0.46	0.40	0.40	0.53	0.53	0.53
Redspot and goldstripe darters	0.36	0.35	0.35	0.35	0.35	0.33	0.33	0.33

(MacKenzie et al., 2004). Coexistence of headwater fishes is mediated by multi-scale variation, with some studies documenting conflicting results regarding the importance of species interactions within these systems (Grossman, Ratajczak, Crawford, & Freeman, 1998; Peoples & Frimpong, 2016; Taylor, 1996; Townsend & Crowl, 1991). Evidence from our results suggests that (1) competition does not influence the occupancy or detectability of these congeners at the stream-reach scale, and (2) patterns of coexistence at the stream-reach scale may be mediated by habitat preference differences. We therefore suggest that competition probably does not influence the coexistence of these headwater congeners at the stream-reach scale.

The influence of competition on the distributional patterns of small-bodied, stream fishes is inconsistent, and may differ as a consequence of biotic and/or abiotic factors. Several studies have successfully documented the negative influence of an invasive species on the distribution of native game fish, in which both species are members of the same family (e.g. Salmonidae; Hoxmeier & Dieterman, 2016; Wagner, Deweber, Detar, & Sweka, 2013). However, the extent to which competition affects the distribution of small-bodied fishes is less clear. Because competition among many small-bodied, stream fishes is often restricted to the microhabitat and mesohabitat scales (Holomuzki, Feminella, & Power, 2010; Resetarits, 1997; Taylor, 1996), phenotypic clustering may allow for

the presence of ecologically similar species within a stream-reach (Olden & Kennard, 2010). Many stream fishes have small, restrictive home ranges (Minns, 1995), in particular headwater specialists (Meyer et al., 2007; Skalski & Gilliam, 2000); thus, there may be a higher probability of interspecific competition at the microhabitat scale. For example, Resetarits (1997), using experimental streams revealed that life stages (juvenile versus adult) influenced the type of biotic interaction (facilitation or competition) displayed by two benthic strategists at the microhabitat scale. Because headwaters are species depauperate, if competition were important, one might expect ecological release to occur (i.e. a species should exhibit higher abundances in the absence of its competitor, Schoener, 1988). Such a pattern is referred to as density compensation (Crowell, 1962; MacArthur, Diamond, & Karr, 1972) and is associated with intense competition for resources (Angermeier & Schlosser, 1989). Given our results, we suggest that ecological release, as a biotic process, may only be observed among small-bodied, headwater fishes at the mesohabitat and microhabitat scales. To date, Taylor (1996) is the only other study of which we are aware to examine the influence of interspecific competition on the coexistence of a headwater benthic fish guild at multiple sample sites across a river system. Although Taylor (1996) found support that small scale interspecific interactions could contribute to the structure of a benthic fish guild (e.g. fish density), his results did not yield significant complementary occurrences. Taylor's finding of nonsignificant complementary occurrences are supported by another coarse-scale, natural experiment (Peres-Neto, 2004), and the findings of this study. Finally, we also recognise the influence of variation in hydrologic regime on our findings. Extreme hydrologic variability within headwater streams alters demographic patterns, thereby reducing competition for resources within a given stream-reach (Grossman et al., 1998; Poff & Allan, 1995). Thus, hydrologic variability diminishes the influence of biotic interactions at a fine scale in shaping species distributional patterns at the stream-reach and landscape scales. Therefore, the influence of competition should be assessed across multiple hydrologic regimes.

Coexistence of these headwater congeners may be mediated by distinct habitat preferences. All three of the species assessed in this study are representatives of distinct clades within a large genus (Near et al., 2011), and our results suggest, at the spatial extent examined, habitat use by these three fishes was best explained by distinct habitat parameters (Yazoo darter: groundwater input; goldstripe darter: stream size; redspot darter: variation in depth). One speculation for the distinctive habitat preferences of these fishes is that they may be clade specific. Streams inhabited by the redspot darter and other darters in *Vexillapinna* are often characterised by strong riffle-pool structure (Scalet, 1973; Taylor, 2000; Stearman, Adams, & Adams, 2015), and may range in size from small headwaters to larger third- and fourth order streams (Echelle, Echelle, Smith, & Hill, 1975; Taylor, 2000; Stearman et al., 2015; Matthews & Turner, 2019). In opposition, in *Fuscatelum*, the rush darter *Etheostoma phytophilum* and the goldstripe darter both appear to be mostly constrained to small headwater tributaries (first order) within their respective ranges (Howell, Drennen, & Aarons, 2016; Mettee,

O'Neil, & Pierson, 1996; Robinson & Buchanan, 1988; Smiley et al., 2006). While it seems that the habitat preferences of the redspot darter and goldstripe darter may be clade specific, it is difficult to make such a proposition for the Yazoo darter. Characterising commonalities in habitat preference in *Adonia* is difficult due to the large number of species (19, Near et al., 2011), and widespread distribution (Porter, Cavender, & Fuerst, 2002) of this group. Our proposition for clade-specific habitat preferences may be indicative of niche conservatism, a classical concept that was recently detected among several clades of stream fishes, including a darter clade (McNyset, 2009). Coexistence of two of the three species pairs was best described as a function of stream size and groundwater input (Yazoo and goldstripe darter) or habitat heterogeneity and stream size (redspot and goldstripe darters). Given our results, coexistence among Yazoo and goldstripe darters at the stream-reach scale seems most probable in small, perennial headwaters, whereas the coexistence of redspot and goldstripe darters at this scale appears to be most likely in headwater streams with consistent riffle-pool structure (i.e. high depth heterogeneity). Coexistence of Yazoo and redspot darters was best described by a null model in which species occurrences were modelled as independent. Such a result may indicate that at the stream-reach scale, habitat preferences of these two species may be so dissimilar that coexistence at this spatial extent is rare.

While it appears that coexistence of these congeners at the stream-reach scale may be habitat mediated, other factors cannot be ignored. To further elucidate the extent to which habitat preferences influence the coexistence of a local species pool, Kraft et al. (2015) suggest a multi-step process, focusing on dispersal, persistence, competitive exclusion, source-sink dynamics, and their contribution to species distributional patterns. Because observational studies are limited in scope, a more thorough test would require manipulative experiments. Such designs assess the coexistence of local guilds through the direct manipulation of inter and intraspecific densities. If species do interact, the extent to which the interaction directly or indirectly affects each species resource usage and acquisition, behaviour and other interactions with other species may be assessed (Martin & Martin, 2001).

Although it is beyond the scope of this study, it is worth noting that the occupancy of Yazoo darters was best explained by variability in groundwater input (approximated by the variation in well depths in this study) in relation to all of the other habitat covariates assessed. The influence of groundwater input on shaping stream fish assemblages is well documented (Adams & Warren, 2005; Driver & Hoeinghaus, 2016; Mollenhauer, Zhou, & Brewer, 2019). Spring or groundwater-fed streams are characterised by predictable flow patterns, thus there is limited variation in stream discharge and water temperature (Gordon, McMahon, Finlayson, Gippel, & Nathan, 2004); however, the availability, quality, and connectivity of refugia vary within a stream-reach and in relation to drought intensity forming a mosaic of temporally dynamic habitat patches (Magoulick & Kobza, 2003). Thus, aquatic-obligate species occupying ephemeral drainages have often evolved to persist or rapidly recolonise as these habitats fluctuate between flowing and non-flowing states (Dodds, Gido, Whiles, Fritz, & Matthews, 2004). Adams and Warren (2005) indicate that recolonisation probabilities

are lower for Yazoo darters in relation to redspot and goldstripe darters following a drought within ephemeral drainages. Wider niche breaths may allow eurytopic species (e.g. redspot and goldstripe darters) to recolonise ephemeral aquatic habitats more rapidly whereas stentopic species (e.g. Yazoo darter) may be locally extirpated.

Our results provide further support that biotic interactions may not be meaningful in describing patterns of co-occurrence of stream fishes; the influence of these interactions on species occupancy may only be detectable at specific spatial extents. There is much support for the regulation of co-occurrence within a stream-reach as a consequence of habitat preferences at the stream-reach and landscape scales (Giam & Olden, 2016; Grossman et al., 1998; Jackson, Pedro, & Olden, 2001; Peres-Neto, 2004); however, there is also limited support that stream fishes may be structured by biotic interactions at the stream-reach scale as well (Lamothe, Dextrase, & Drake, 2019; Peoples & Frimpong, 2016). In our study, we sought to examine the influence of biotic and abiotic factors on non-random patterns of co-occurrence of three headwater congeners at the stream-reach scale using a method that accounts for imperfect detection. While many studies have detailed the influence of intra and interspecific competition of headwater fishes using experimental streams, these study designs do not provide an appropriate means for extrapolation to the stream-reach scale, due to a lack of variation in physical setting. Natural study designs that use large datasets and robust analytical tools provide insight into the significance of how both biotic and abiotic processes structure the coexistence of potential competitors.

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AUTHOR CONTRIBUTIONS

Conceived and designed the investigation: J.P.H., J.F.S. Performed field and/or laboratory work: J.P.H., M.L.W., K.A.S. Analysed the data: J.P.H. Contributed materials, reagents, and/or analysis tools: J.P.H. Wrote the paper: J.P.H.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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