



SPECIAL SECTION: ALLIGATOR GAR

Occurrence and Co-Occurrence Patterns of Gar in River–Floodplain Habitats: Methods to Leverage Species Coexistence to Benefit Distributional Models

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Abstract

Habitat segregation and hypothesized biotic interactions among coexisting gar species may confound attempts to describe the distributions of these species by using only macrohabitat availability in the presence of conspecifics. However, the strength of interactions among gar species and the spatial scale at which they occur are largely unknown. We used an existing data set to evaluate the co-occurrence patterns (i.e., random assemblages versus species co-occurring more or less than expected at random) of three gar species in 62 dynamic river–floodplain habitats associated with the lower Mississippi River and its major tributaries. A novel parameterization of a multispecies occupancy model was utilized to examine the spatial relationships among the full array of possible gar assemblages across a gradient of floodplain habitats. Spotted Gar *Lepisosteus oculatus* were the most abundant and frequently encountered species (~78% of samples). Shortnose Gar *L. platostomus* (~27% of samples) and Longnose Gar *L. osseus* (~12% of samples) were relatively uncommon, and no Alligator Gar *Atractosteus spatula* were captured in over 600 electrofishing transects. Estimated detection probabilities of the encountered species varied (range = 0.27 [Longnose Gar] to 0.80 [Spotted Gar]), and five species-specific environmental and sampling covariates predicted detection. Relatively strong co-occurrence patterns between Shortnose Gar and Longnose Gar were significantly influenced by the proximity of a floodplain lake to a river (i.e., river : lake elevation change and linear distance) and by lake latitude. In contrast, the occurrence patterns of Spotted Gar were largely independent of the other species and had minor influences on the relationship between Longnose Gar and Shortnose Gar. We demonstrate how species co-occurrence patterns can be leveraged to reduce uncertainty associated with species-specific occupancy estimates and how species distribution models can be improved by utilizing abiotic and biotic features of the target ecosystems.

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A prevalent paradigm suggests that local fish assemblage structure exists as a result of nonrandom temporal and spatial patterns developed through a series of environmental filters and interactions among species (Poff 1997; Angermeier and Winston 1999; Jackson et al. 2001). As such, the occurrence of particular taxa and distinct assemblages reflects historic processes, such as speciation and dispersal (Rahel and Hubert 1991; Lyons 1996); local habitat suitability and physical and chemical attributes (Taylor et al. 1993); and interactions among individuals (Gilliam et al. 1993; Bronstein 1994). Although the role of environmental conditions in regulating fish occurrence is well understood and often applied to conservation actions (Jackson et al. 2001), the influence of biotic interactions on co-occurrence patterns is less understood (Wisiz et al. 2013; Peoples and Frimpong 2016a; Arnhold et al. 2019). Small-scale experimental and field studies have demonstrated the occurrence of positive and negative interactions among fishes in specific microhabitats and have provided evidence that assemblages can be described as a result of species interactions (Hoeinghaus et al. 2007; Afkhami et al. 2014; Arnhold et al. 2019). Further research is required to designate the spatial and temporal context in which species interactions have strong effects on assemblage structure in order to target future management efforts (Jackson et al. 2001; Chamberlain et al. 2014; Peoples and Frimpong 2016b). Novel methods to quantify the relative importance of both abiotic and biotic components for influencing the occurrence patterns of fish species may provide new evidence for their relative importance in structuring local assemblages (Jackson et al. 2001; Olden and Jackson 2002).

Few analytical approaches are available to evaluate the nonrandom biotic mechanisms that may regulate species distributions and structure fish communities (Olden et al. 2002; Peres-Neto 2004). Although models that investigate co-occurrence patterns of species pairs are relatively common (Farris et al. 2014, 2015; Arnhold et al. 2019), analytical approaches for describing all of the possible interactions among larger assemblages are rare (Rota et al. 2016) and, to our knowledge, have yet to be applied to aquatic species. Recent advances in multispecies co-occurrence modeling procedures provide an objective method with which to evaluate hypotheses about assemblage structure and inform conservation decision making and monitoring (Farris et al. 2014; Rota et al. 2016; Arnhold et al. 2019; Lamothe et al. 2019).

Worldwide, there are only seven extant species of gar (Alfaro et al. 2008), four of which occur in floodplain habitats associated with the Mississippi River and its larger tributaries in the southeastern USA (Baker et al. 1991; Snedden et al. 1999; Echelle and Grande 2014). Although most gar species are relatively common and can become abundant in diverse freshwater habitats (Snedden et al.

1999; Robertson et al. 2008; Boothroyd et al. 2016), populations of Alligator Gar *Atractosteus spatula* are thought to be in decline throughout their native range (Warren et al. 2000; Ferrara 2001; O'Connell et al. 2007). Historically, gar species have been targeted for eradication due to largely unfounded concerns about competition with and predation upon game fish species (Scarnecchia 1992). More recently, gars have been recognized as important components of aquatic ecosystem function and as valuable recreational species (Scarnecchia 1992; Quinn 2010), but to date this lineage has received relatively little attention in the ecological literature, leaving many aspects of their ecology poorly understood (Echelle and Grande 2014).

Anecdotal evidence suggests that coexisting gar species segregate spatially and that dominant individuals within species may exclude related species from optimal habitats (Vokoun 2000; Robertson et al. 2008; Walker et al. 2013). Differences in jaw structure and body morphology likely equate to differences in foraging behaviors and may result in the partitioning of prey (Goodyear 1967; Kammerer et al. 2006; Walker et al. 2013) and/or habitat (Robertson et al. 2008) among gar species. Relatively little is known about the strength of interactions among gar species (Solomon et al. 2013; Walker et al. 2013), and whether these interactions can regulate species' occurrence patterns, such as other piscivore communities, remains unknown (Ross 1986; Winemiller 1989). It is suspected that the magnitude of these interactions is greatest between the closely related Longnose Gar *Lepisosteus osseus*, Shortnose Gar *L. platostomus*, and Spotted Gar *L. oculatus*; however, the unique characteristics of Alligator Gar are thought to make this species less vulnerable to displacement via biotic interactions (Buckmeier et al. 2013; Kluender et al. 2017).

Observations of habitat segregation and potential interactions among gar species may confound attempts to describe the distributions of these species by using macro-habitat availability alone. Moreover, strong co-occurrence patterns could be exploited to reduce uncertainty in future distribution models for relatively uncommon species. Herein, we describe the co-occurrence patterns (i.e., random assemblages versus species coexistence/avoidance) of gar species in dynamic river-floodplain habitats associated with Mississippi River tributaries in northwestern Mississippi and southeastern Arkansas. We extend the two-species co-occurrence models developed by Richmond et al. (2010) to three species and evaluate relationships among each of the possible gar species assemblages across a gradient of suitable habitats. Using co-occurrence occupancy modeling, we (1) estimated the occurrence probabilities of each species and the probability that each species is present in a floodplain habitat conditional on the presence of each of the other species, (2) estimated the direction and magnitude of species' relationships based on the species

interaction factor (SIF); and (3) linked these estimates and species relationships to environmental covariates that are thought to influence gar detection and occupancy. To inform future monitoring and potentially improve attempts to delineate gar distributions in the region, we used estimated detection probabilities to advise the number of electrofishing transects that would be needed to reliably characterize the gar assemblage and we evaluated the benefit of accounting for species co-occurrence when predicting species distributions.

METHODS

Study area.—The fish assemblages in floodplain and oxbow lakes ($N = 62$) associated with major tributaries to the lower Mississippi River were sampled in Mississippi and Arkansas (Figure 1). Hundreds of floodplain lakes are located along these tributary systems, most of which are oxbows that resulted from river channel abandonment due to sediment deposition or anthropogenic channel alterations (Biedenharn et al. 2000). Fish species richness is relatively high in the region, and these tributaries maintain the greatest diversity of gar species in the world (i.e., 57% of all extant gar species). Floodplain lakes in the area are thought to support populations of Longnose Gar, Shortnose Gar, Spotted Gar, and Alligator Gar (Baker et al. 1991). Efforts were made to select lakes along environmental gradients, including depth, surface area, and degree of connectivity with the nearest river system (Table 1). The lakes were situated at varying distances from the closest river (range = 0.0–13.5 km) and were morphologically distinct (depth [mean \pm SE] = 2.7 ± 0.21 m; length : width ratio = 38.8 ± 6.9) and chemically diverse (turbidity = 27.4 ± 2.6 NTU; conductivity = 145.1 ± 14.0 μ S/m).

Gar assemblage sampling.—Each waterbody was sampled periodically during the summer or early fall of 2006–2012 to describe the fish assemblages and physical and chemical characteristics of floodplain ecosystems in the region (Miranda 2011; Dembkowski and Miranda 2012, 2014). Fish species were sampled using spatially replicated boat electrofishing transects that each approximated 15 min of “on time” (mean \pm SE = 14.95 ± 0.04 min). Shorter periods were rare and occurred when weather conditions or habitats precluded additional sampling. The number of transects per lake varied, but generally the complete shoreline of each system was sampled. We collected 2–16 samples/lake depending on lake area. In total, 604 distinct fish samples were collected from the 62 floodplain lakes. All captured fish species were identified and counted before release near the site of capture. No Alligator Gar were captured in any electrofishing transects, so this species was removed from all analyses.

Environmental sampling and predictor variables.—Several environmental variables were measured to characterize the

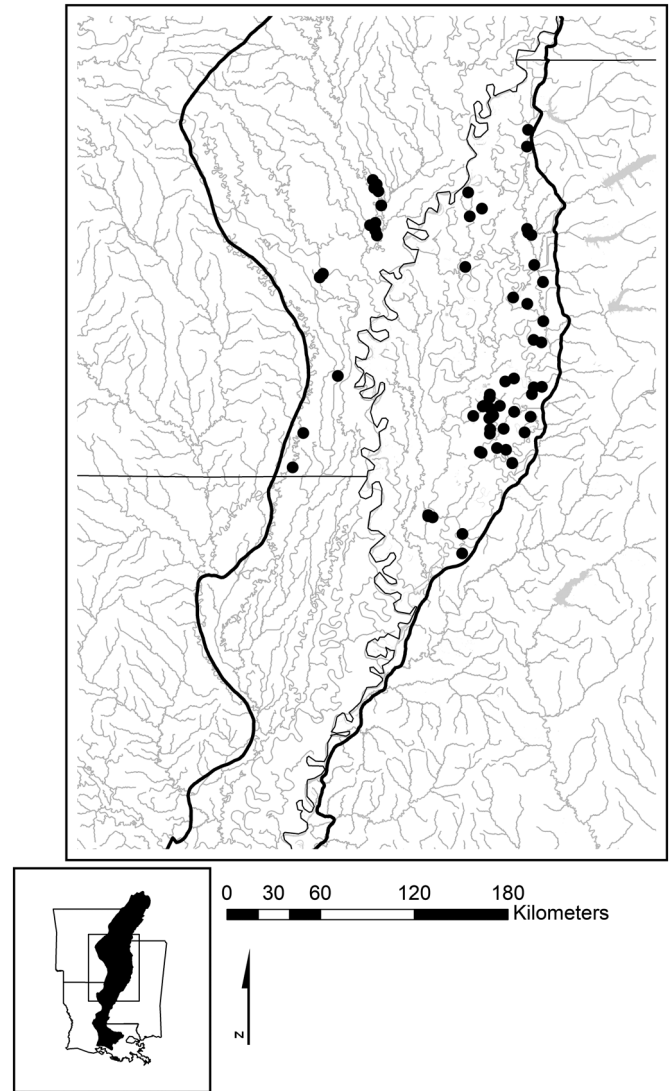


FIGURE 1. Floodplain lakes ($N = 62$) associated with major tributaries of the lower Mississippi River, Mississippi–Arkansas, that were sampled to describe the coexistence patterns of gar species (Lepisosteiformes: Lepisosteidae).

physical morphology, water quality, and primary productivity of each lake. In total, seven candidate environmental variables were used to predict gar occupancy and six candidate variables were used to predict gar species detection (Table 1). In addition to conductivity (μ S/m), we selected turbidity (NTU) and water transparency (cm) to represent lake water quality; however, these variables were autocorrelated ($r > 0.60$) and only turbidity was retained for analysis. Environmental variables were measured twice at each lake during daytime hours in the summer (June–August) from the epilimnion at a single location near the deepest point in the lake. Turbidity and conductivity were measured in situ using a Eureka Manta multi-probe (Eureka Environmental

TABLE 1. Mean (SE in parentheses) and range of values for each candidate variable used to predict the detection and occupancy probabilities of gar species in floodplain lakes associated with the lower Mississippi River and its larger tributaries in Mississippi and Arkansas.

Covariate	Value			Model inclusion	
	Mean (SE)	Minimum	Maximum	Detection	Occupancy
Maximum depth (m)	2.74 (0.22)	0.5	8.6	X	X
Conductivity ($\mu\text{S/m}$)	146.5 (14.2)	38	567	X	
Turbidity (NTU)	26.5 (2.6)	4.7	106.7	X	X
Length : width ratio	38.5 (7.0)	0.73	309.3	X	X
Lake surface area (km^2)	0.76 (0.16)	0.01	5.7	X	X
Sampling effort (min)	14.95 (0.04)	5.00	15.00	X	
River : lake elevation change (m)	1.72 (0.37)	-4.38	6.71		X
Distance to river (km)	2.82 (0.47)	0.00	13.48		X
Lake latitude	33.63 (0.07)	32.67	34.67		X

Engineering, Austin, Texas). Water transparency was measured using a Secchi disk (20-cm diameter). Maximum depth was defined as the deepest point detected by soundings taken with either a handheld depth finder (DF2200PX; NorCross Marine Products, Stuart, Florida) or a boat-mounted depth finder (X126 DF Sonar; Lowrance Electronics, Tulsa, Oklahoma). The depth finders were operated from a boat navigating in a zig-zag pattern along the former thalweg between the two ends of each lake. Maximum depth was selected over mean depth because it better characterizes the cross-sectional morphology of channel remnants (Dembkowski and Miranda 2012). Lake surface area and lake length : width ratio were estimated using spatial analysis tools available in the ArcGIS software package.

Modeling gar species co-occurrence.—Occupancy models were developed to evaluate lake-level gar co-occurrence patterns using hierarchically dependent species detections (i.e., transects within lakes; Table 2). Gar occupancy was estimated using the conditional occupancy rates (ψ) developed by Richmond et al. (2010) but extended to evaluate three species (Table 2). Specifically, occupancy rates were conditioned on the presence or absence of specific gar species. The ordinate-subordinate approach was used in the conditional specification, with the order of interactions reflecting the relative abundances of the species. The Spotted Gar was the ordinate species, followed by Shortnose Gar, and the Longnose Gar was the last subordinate species. Seven conditional occupancy rates were needed to estimate the eight possible gar assemblages (Figure 2). Lake-level assemblage of the three gar species was modeled as

$$\text{Assemblage}_{lake} \sim \text{Multinomial}(\gamma_{1:8,lake}), \quad (1)$$

where Assemblage_{lake} is the lake-specific gar assemblage, which takes a value of 1–8, representing the eight possible

TABLE 2. Possible gar assemblage occupancy states and the generalized equations used to calculate the unique unconditional occupancy probabilities. Specific equations that were used to describe the probability of each gar assemblage are provided in Figure 2.

Unconditional occupancy	Equation
$\Psi_{\text{Spotted Gar}}$	$\text{Pr}(111) + \text{Pr}(110) + \text{Pr}(101) + \text{Pr}(100)$
$\Psi_{\text{Shortnose Gar}}$	$\text{Pr}(111) + \text{Pr}(110) + \text{Pr}(011) + \text{Pr}(010)$
$\Psi_{\text{Longnose Gar}}$	$\text{Pr}(111) + \text{Pr}(101) + \text{Pr}(011) + \text{Pr}(001)$
$\Psi_{\text{Spotted Gar, Shortnose Gar}}$	$\text{Pr}(111) + \text{Pr}(110)$
$\Psi_{\text{Spotted Gar, Longnose Gar}}$	$\text{Pr}(111) + \text{Pr}(101)$
$\Psi_{\text{Shortnose Gar, Longnose Gar}}$	$\text{Pr}(111) + \text{Pr}(011)$
$\Psi_{\text{Spotted Gar, Shortnose Gar, Longnose Gar}}$	$\text{Pr}(111)$

gar assemblages identified in Figure 2; $\gamma_{1:8,lake}$ is a lake-specific vector of eight probabilities for each gar assemblage; and $lake$ indexes each lake. Lake-specific conditional species occupancy rates ($\psi^i = [\psi^a, \psi^{aB}, \psi^{aB}, \psi^{ABC}, \psi^{AbC}, \psi^{aBC}, \psi^{abC}]$; Figure 2) were estimated as

$$\text{logit}(\psi_{lake}^i) = \beta_{0,i} + \beta_{k,i} \cdot \mathbf{X}_{lake,k}, \quad (2)$$

where ψ_{lake}^i is the lake-specific conditional occupancy rate; $\beta_{0,i}$ is the intercept; $\beta_{k,i}$ is a vector of coefficients corresponding to the effect of lake-level predictors; \mathbf{X}_{lake} is a matrix of lake-level predictors; k indexes each predictor variable; i indexes each conditional occupancy rate; and $lake$ indexes each lake surveyed.

Accounting for imperfect detection.—Detection of gar species by conventional gears is imperfect and subject to

model coefficients. Models were initialized with 25,000 burn-in iterations and 75,000 total iterations for three independent chains. Predictors were centered to 0 by subtracting the mean and were scaled by dividing by the SD of the predictor values. Model convergence was assessed by visual inspection of trace plots of monitored parameters and based on whether the Brooks and Gelman diagnostic (\hat{R}) was less than 1.01 (Brooks and Gelman 1998). Inference of predictors on gar-specific occupancy and detection probability was conducted on the model with the highest posterior model weight. No inferences were made when the intercept-only model performed best, as intercept-only models only provided evidence for candidate predictors other than those parameterized. Models with the highest posterior model weight were used in subsequent analyses evaluating and predicting species co-occurrence.

Quantifying species co-occurrence.—We used estimated gar occurrence rates (ψ) to calculate an SIF and associated uncertainty in our analysis. First, unconditional occupancy rates were calculated from the probability of each gar assemblage (Table 2). Species interaction factors were calculated to describe the co-occurrence of species pairs from the unconditional occupancy rates (MacKenzie et al. 2004; Richmond et al. 2010; Waddle et al. 2010). Specifically, the SIF between each species pair was calculated as

$$\text{SIF} = \frac{\Psi_{\text{Species1,Species2}}}{\Psi_{\text{Species1}} \cdot \Psi_{\text{Species2}}}, \quad (5)$$

where $\Psi_{\text{Species1,Species2}}$ is the probability of both species occurring; Ψ_{Species1} is the occurrence probability for species 1; and Ψ_{Species2} is the occurrence probability for species 2. These values were derived from the posterior distributions of conditional occurrence probabilities and were used to estimate pairwise SIF values and 95% Bayesian credible intervals (BCIs). If species co-occur randomly, then the SIF is equal to 1. If species occur together more frequently than expected, then the SIF value is greater than 1; if species co-occur less frequently than expected, then the SIF is less than 1. Model-weighted SIFs and associated 95% BCIs were used for inference of co-occurrence patterns. We also used a similar approach to evaluate three-way species co-occurrence patterns, calculated as

$$\text{SIF} = \frac{\Psi_{\text{Species1,Species2,Species3}}}{\Psi_{\text{Species1}} \cdot \Psi_{\text{Species2}} \cdot \Psi_{\text{Species3}}}, \quad (6)$$

where $\Psi_{\text{Species1,Species2,Species3}}$ is the probability of all three species occurring together; and Ψ_{Species1} , Ψ_{Species2} , and Ψ_{Species3} are the respective unconditional occupancy probabilities for each species.

Application to species monitoring and management.—Sampling and monitoring of species are important for the development of species distribution models that provide decision-relevant information and predictions. We used estimated detection probabilities for each species to calculate the cumulative detection probabilities and describe the number of transects necessary to achieve prescribed detection probabilities. Cumulative detection was calculated as $1 - (1 - P)^n$, where P is the detection probability for a single transect and n is the number of sampled transects.

Information from SIFs was included in co-occurrence models and should reduce uncertainty in lake-specific occupancy rates. To evaluate this potential benefit, we compared lake-level estimates of ψ for Longnose Gar that were fitted using the co-occurrence model described above. We limited this analysis to Longnose Gar because we assumed that model performance would improve substantially for the least common species when including species co-occurrence. We also fitted single-species occupancy models assuming that gar species co-occur randomly (i.e., occupancy models that did not account for species co-occurrence patterns) by using the variable selection described above. We visually compared the lake-specific estimates of ψ to evaluate the potential effect of accounting for the SIF between Longnose Gar and Shortnose Gar. We also calculated the width of the 95% BCI for estimates and compared the two approaches visually. Specifically, if one approach increases or decreases uncertainty in lake-specific estimates of ψ , then the 95% BCI width will fall above or below the line when plotted against a 1:1 line.

RESULTS

Detection and Occurrence Patterns of Gar Species

Gar species occur frequently in floodplain habitats associated with the Mississippi River and its larger tributaries (Table 3). A representative of the family taxonomic groups was captured in over 95% of the floodplain lakes sampled. Spotted Gar were the most abundant ($n = 2,296$) and frequently encountered species, occurring in approximately 78% of samples (Table 3). Shortnose Gar ($n = 194$) and Longnose Gar ($n = 167$) were uncommon and encountered in about 27% and 12% of the electrofishing transects, respectively (Table 3).

Selection of Environmental Covariates of Detection

Covariates retained in the detection model with the highest posterior probability varied among gar species, but all retained covariates in the species-specific detection models were interpretable (i.e., the 95% BCIs did not include 0). The detection model with the highest posterior probability for Spotted Gar included a positive effect of

TABLE 3. Species-specific model posterior probabilities and retained environmental covariates for top-performing candidate models used to estimate detection (BCI = Bayesian credible interval). Top-performing models were used to estimate occupancy of each possible gar assemblage by using retained lake-level environmental covariates in addition to the intercept term. An uppercase letter denotes that the species is present, and a lowercase letter denotes that it is absent (*A*, *a* = Spotted Gar; *B*, *b* = Shortnose Gar; *C*, *c* = Longnose Gar).

Parameter	Posterior models	Model posterior probability	Retained model parameters	Parameter estimates (95% BCI)
Species-specific detection probabilities (<i>P</i>)				
Spotted Gar	56	0.45	Intercept	
			Turbidity (NTU)	0.57 (0.28, 0.88)
Shortnose Gar	57	0.27	Intercept	
			Maximum depth (m)	0.34 (0.08, 0.60)
			Turbidity (NTU)	0.45 (0.24, 0.67)
			Electrofishing effort	0.64 (0.11, 1.54)
Longnose Gar	63	0.20	Intercept	
			Maximum depth (m)	0.36 (0.11, 0.61)
			Turbidity (NTU)	-0.34 (-0.65, -0.06)
			Length : width ratio	-1.38 (-2.24, -0.56)
			Lake surface area (km ²)	2.13 (1.07, 3.24)
Conditional occupancy probabilities (ψ)				
ψ^A	128	0.36	Intercept	3.761 (2.436, 5.518)
ψ^{AB}	128	0.41	Intercept	0.305 (-0.246, 0.885)
ψ^{aB}	128	0.22	Intercept	-0.072 (-3.286, 3.184)
ψ^{ABC}	128	0.18	Intercept	1.227 (0.073, 2.631)
			Distance to river (km)	-1.720 (-3.250, -0.349)
			River : lake elevation change (m)	-2.002 (-3.656, -0.589)
ψ^{AbC}	127	0.20	Intercept	-2.347 (-4.132, -0.871)
			Latitude	2.085 (-3.200, 3.754)
ψ^{aBC}	128	0.22	Intercept	-0.033 (-0.04, 3.202)
ψ^{abc}	128	0.22	Intercept	-0.035 (-3.248, 3.193)

lake turbidity (Figure 3; Table 3). The detection model with the highest posterior probability for Shortnose Gar included positive effects of maximum depth, lake turbidity, and electrofishing effort (Figure 3; Table 3). The detection model with the highest posterior probability for Longnose Gar included positive effects of maximum depth and lake surface area and negative effects of turbidity and length : width ratio (Figure 3; Table 3). An additional 55, 56, and 62 models were retained in the posterior distribution of models for Spotted Gar, Shortnose Gar, and Longnose Gar, respectively (Table 3).

Influence of Environmental Covariates on Conditional Occupancy Probabilities

Posterior models varied among conditional occupancy probabilities (Figure 3). No covariates were retained in the model selection process (i.e., the intercept-only model had the highest posterior model weight) for ψ^a , ψ^{AB} , ψ^{aB} , ψ^{aBC} , and ψ^{abc} . In these cases, the intercept was used to estimate the probabilities (Figure 3; Table 3). This result is attributed to the high occupancy rates of Spotted Gar in the study lakes. The probability that Longnose Gar were

present given the presence of Spotted Gar and Shortnose Gar (ψ^{ABC}) was a function of distance to the nearest river and the river : lake elevation change (Figure 4). Lakes further separated from the river channel either by distance (β coefficient = -1.72; 95% BCI = -3.25, -0.35) or elevation change (β coefficient = -2.00; 95% BCI = -3.66, -0.59) were less likely to contain Longnose Gar given that Spotted Gar and Shortnose Gar were present (Figure 4). The probability of Longnose Gar occupancy given the presence of Spotted Gar and the absence of Shortnose Gar (ψ^{AbC}) increased with latitude (Figure 4). Floodplain lakes further north in the study region (β coefficient = 2.08; 95% BCI = 0.62-3.75) were much more likely to have Longnose Gar and Spotted Gar, without Shortnose Gar (Figure 4).

Unconditional Occupancy Probabilities and Species Interaction Factors

Gar assemblage probabilities varied between naïve (i.e., not accounting for imperfect detection) and unconditional (i.e., SIFs and imperfect detection) owing to our accounting for species co-occurrence patterns and imperfect detection (Table 4). The probability of all gar species being

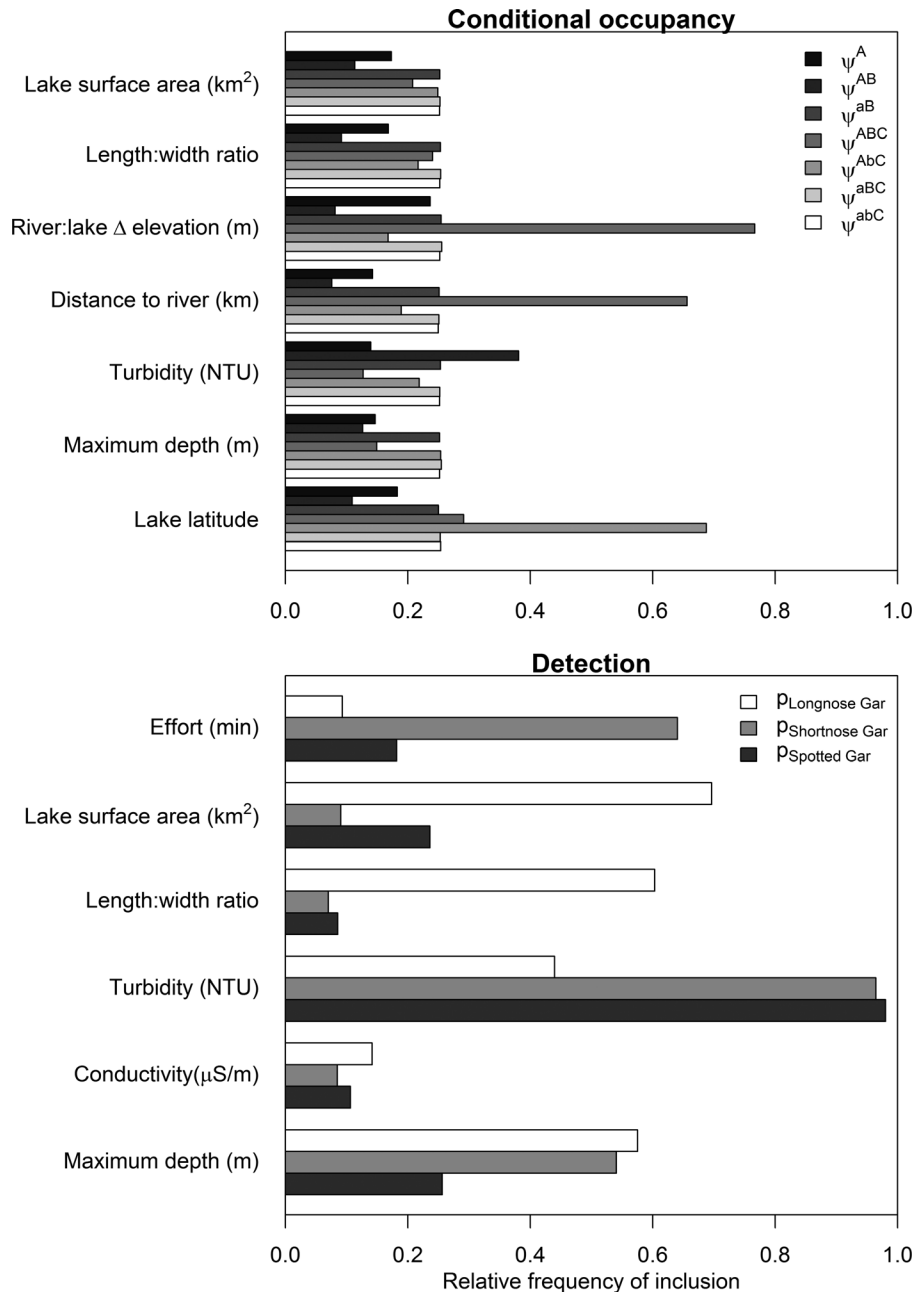


FIGURE 3. Relative frequency of covariate inclusion in posterior model samples for conditional occupancy rates (ψ ; top panel) and detection probabilities (P ; bottom panel). The relative importance of each predictor variable increases as the value approaches 1, but only beta (β) estimates with 95% Bayesian credible intervals that do not include zero are interpreted.

absent from a floodplain lake was very low ($P[000] < 0.01$; Table 4). Occupancy estimates for Shortnose Gar and Longnose Gar occurring in isolation were also low ($P[010] < 0.01$; $P[001] < 0.01$), while the probability of Spotted Gar occurring in isolation was relatively high ($P[100] = 0.37$; Table 4). Model evidence indicates that Spotted Gar occurrence patterns were independent of the other two gar species because 95% BCI values for SIFs

overlapped 1 (Figure 5). There was evidence of a positive SIF between Shortnose Gar and Longnose Gar ($\text{SIF} = 1.58$; 95% BCI = 1.27–2.00) and that these species co-occurred more often than expected in floodplain lakes (Figure 5). However, these species were rarely captured in the same electrofishing transects (~3% of transects). The SIF changed little when the influence of Spotted Gar was added in a three-way analysis of co-occurrence ($\text{SIF} =$

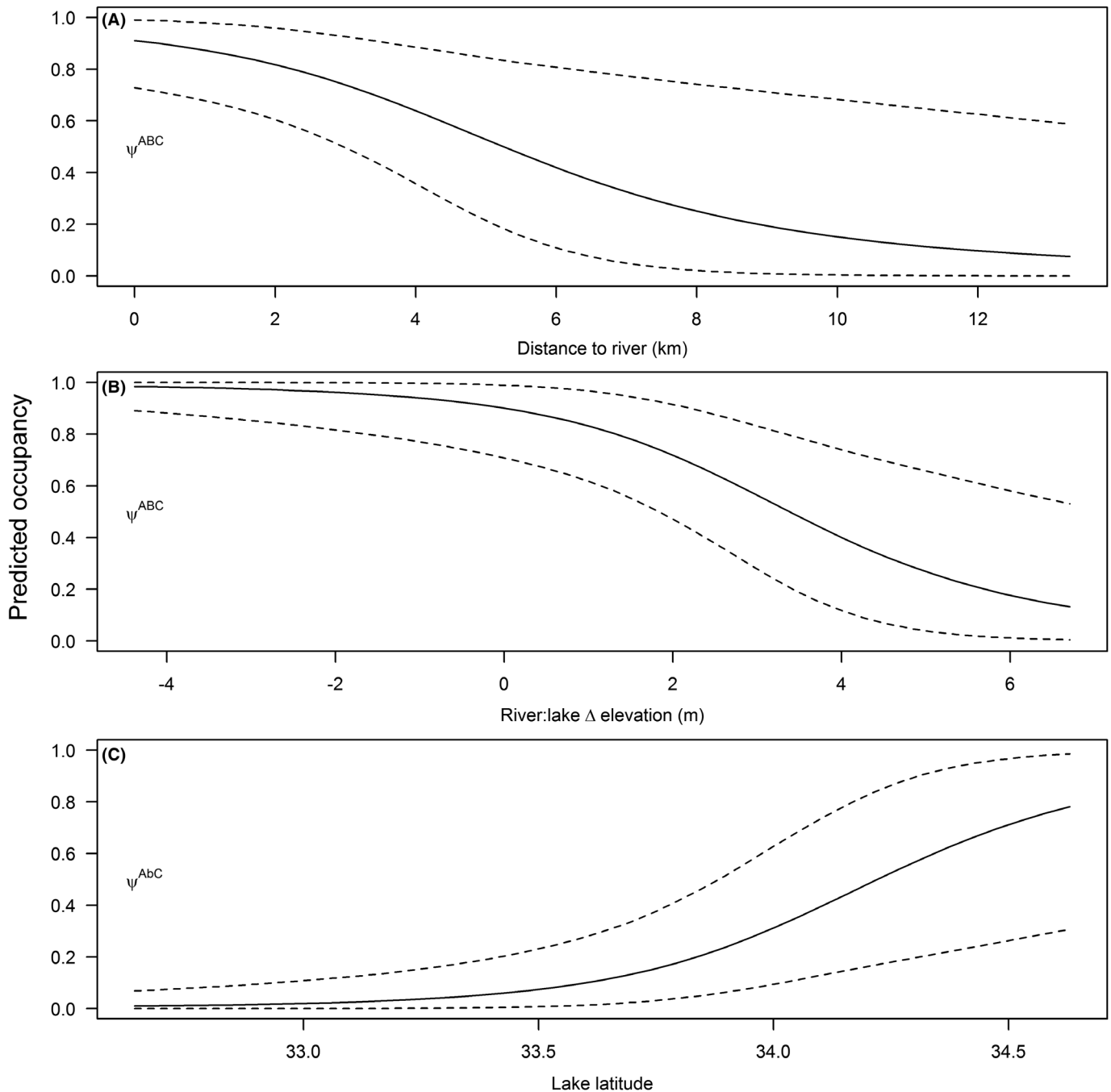


FIGURE 4. Influence of the three retained environmental covariates: the distance to the nearest large river system (km), river:lake elevation change (m), and lake latitude on conditional occupancy probabilities ψ^{ABC} and ψ^{AbC} in the sampled floodplain lakes ($N=62$). An uppercase letter denotes that the species is present, and a lowercase letter denotes that it is absent (A , a =Spotted Gar; B , b =Shortnose Gar; C , c =Longnose Gar). Dotted lines denote 95% Bayesian credible intervals.

1.60; 95% BCI=1.28–2.02), further indicating that this ubiquitous species has little influence on the distributions of Shortnose Gar and Longnose Gar (Table 4). Co-occurrence of Shortnose Gar and Longnose Gar was influenced by the proximity of a floodplain lake to a river (i.e., river:

lake elevation change and linear distance) and by lake latitude (Figure 6). Thus, future attempts to describe the distributions of these species, particularly the Longnose Gar, will benefit from integrating both local abiotic conditions and the SIF (Figure 6).

TABLE 4. Naïve occupancy estimates, unconditional occurrence probabilities (with 95% Bayesian credible intervals [BCIs]), and species interaction factors (SIFs; with 95% BCIs) for each possible gar species assemblage (1 = species present; 0 = species absent) under average conditions in floodplain lakes associated with the lower Mississippi River and its larger tributaries in Mississippi and Arkansas.

Gar assemblage			Occupancy		
Spotted Gar	Shortnose Gar	Longnose Gar	Naïve	Unconditional	SIF
1	1	1	0.31	0.42 (0.27–0.57)	1.60 (1.28–2.02)
1	1	0	0.21	0.14 (0.04–0.28)	1.00 (0.97–1.05)
1	0	1	0.08	0.04 (0.01–0.12)	0.99 (0.96–1.04)
0	1	1	0.00	0.007 (<0.001–0.03)	1.58 (1.27–2.00)
1	0	0	0.29	0.37 (0.24–0.50)	
0	1	0	0.00	0.007 (<0.001–0.03)	
0	0	1	0.00	0.007 (<0.001–0.03)	
0	0	0	0.02	0.008 (<0.001–0.04)	

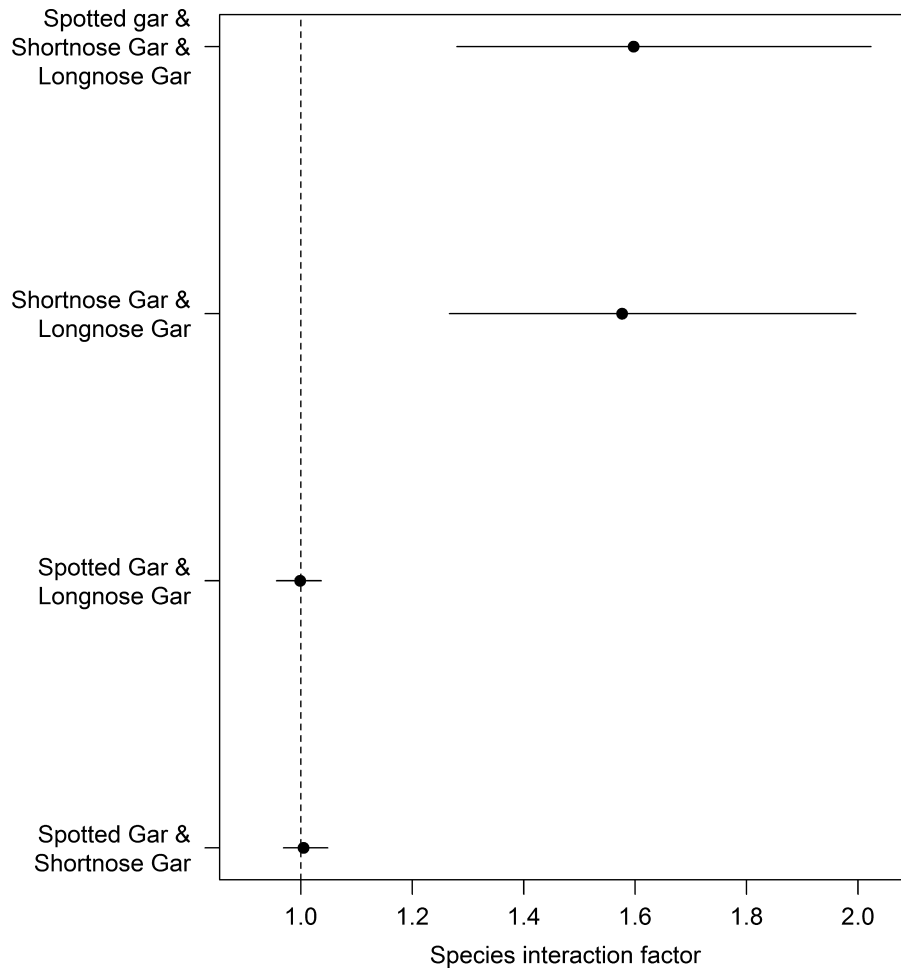


FIGURE 5. Species interaction factors (SIFs; with 95% Bayesian credible intervals), representing the level of co-occurrence between gar species in floodplain lakes associated with the major tributaries of the lower Mississippi River. An SIF value exceeding 1.0 indicates that the species co-occur more often than expected, a value less than 1 indicates that the species co-occur less often than expected, and a value of 1 (vertical dashed line) indicates that the species are co-occurring randomly.

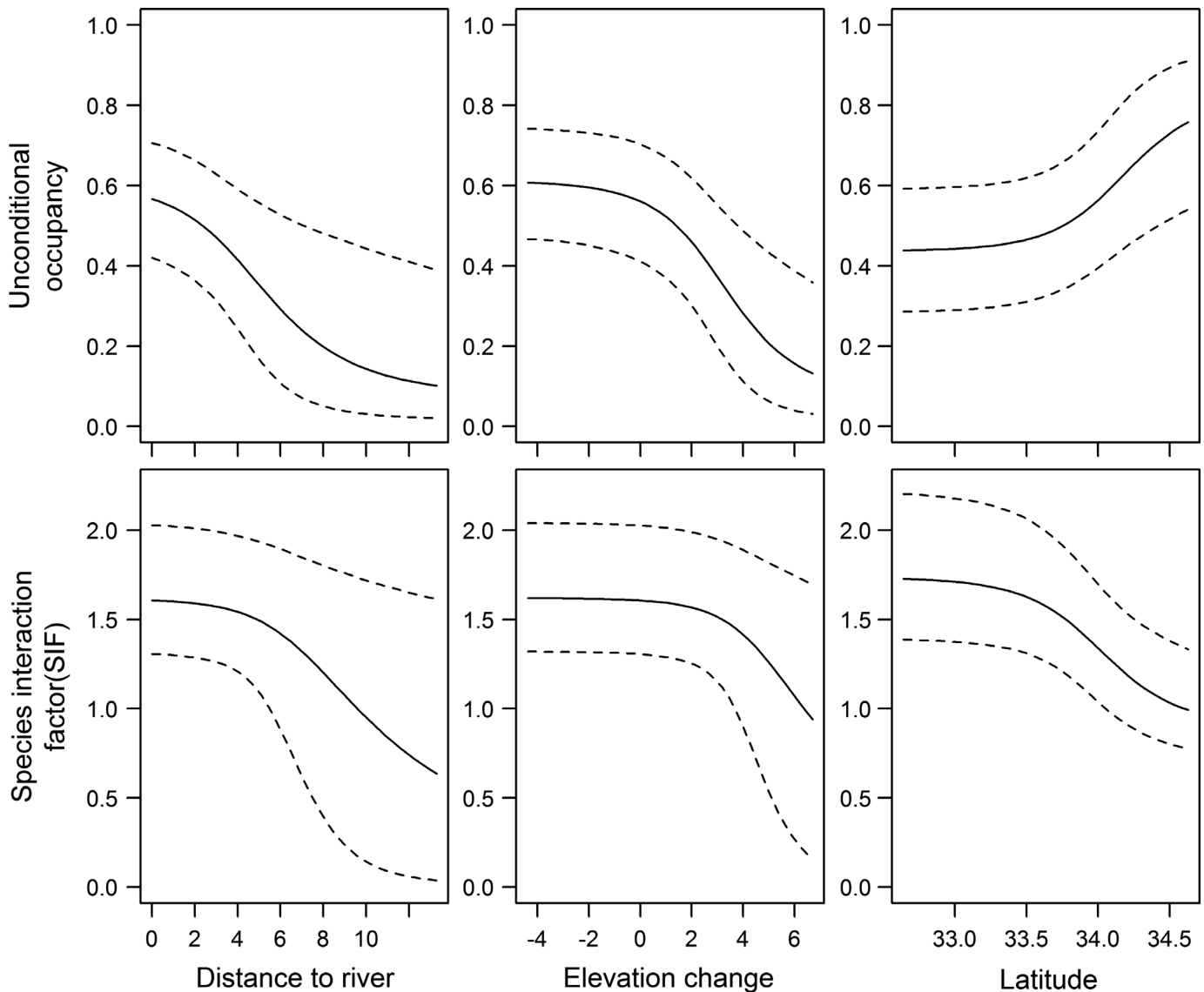


FIGURE 6. Relationship between the unconditional occupancy probability for Longnose Gar occurrence or the species interaction factor (SIF) for co-occurrence of Shortnose Gar and Longnose Gar and covariates retained by the variable selection (distance to river, km; elevation change, m; and latitude) in floodplain lakes associated with the major tributaries of the lower Mississippi River.

Applications to Species Monitoring

Monitoring of gar species could be improved by sufficiently sampling systems and leveraging species co-occurrence patterns to improve occupancy estimates. Specifically, given average conditions the number of 15-min electrofishing transects needed to detect all three gar species 80% of the time was approximately six (Figure 7). By accounting for the co-occurrence of Shortnose Gar and Longnose Gar, the occupancy probabilities at low values were improved over the single-species Longnose Gar occupancy model (Figure 8). Additionally, high lake-specific Longnose Gar occupancy rates predicted from the single-species occupancy model were reduced (Figure 8). The differences in estimated occupancy probability for Longnose

Gar between the co-occurrence model and the single-species occupancy model are due to the inclusion of Shortnose Gar data (e.g., occupancy probability was higher if Shortnose Gar were present and detected). The positive relationship we identified between Shortnose Gar and Longnose Gar occurrence resulted in the reduction of uncertainty in our lake-specific occupancy rates relative to occupancy probabilities predicted from single-species occupancy models (Figure 8).

DISCUSSION

We provide an unprecedented understanding of the co-occurrence patterns of several species belonging to an

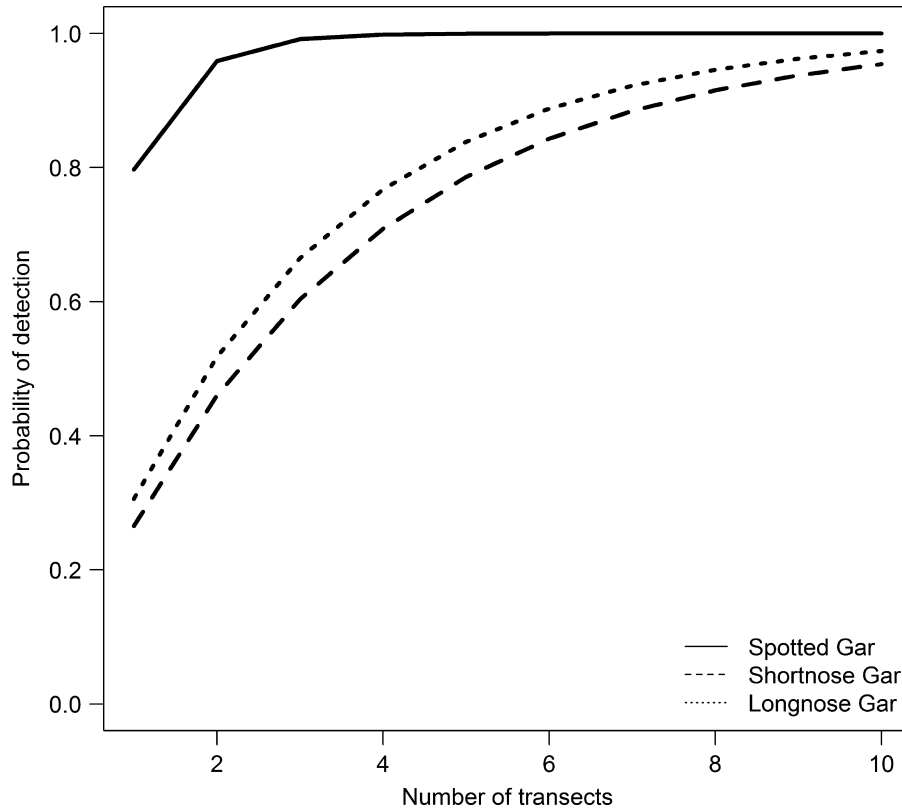


FIGURE 7. Cumulative detection probabilities for Spotted Gar, Shortnose Gar, and Longnose Gar in relation to an increasing number of 15-min electrofishing transects under average conditions in floodplain lakes associated with major tributaries to the lower Mississippi River.

understudied taxonomic guild of fishes, which can be leveraged to reduce uncertainty associated with occupancy estimates and to better inform future species distributional models. By extending the two-species co-occurrence model developed by Richmond et al. (2010) to facilitate inclusion of additional species, we were able to identify the relative importance of specific macrohabitat features for structuring three-species gar assemblages in diverse floodplain lakes. Ultimately, we provided new insight into gar co-occurrence patterns and developed a tool to identify the potential for biotic interactions among multiple fish species.

Gars are abundant in river-floodplain fish communities; however, relatively little is known about how prey and habitats are partitioned among the species of this lineage (Robertson et al. 2008; Walker et al. 2013). It has been suggested that gars segregate among available habitats in southeastern riverscapes, with specific species becoming more abundant near river ecosystems (i.e., Longnose Gar and Alligator Gar) and the other species being dominant in more distant floodplain habitats (Robertson et al. 2008). However, in other regions similar habitat preferences have been reported for all species (Holloway 1954; Goodyear 1967; Snedden et al. 1999) and instead, diets were

partitioned (Walker et al. 2013). We provide additional evidence that coexistence of gar species occurs non-randomly throughout the riverscape.

Relatively strong co-occurrence patterns were identified between Shortnose Gar and Longnose Gar. The degree of separation of floodplain lakes from nearby tributaries (i.e., linear distance to the river and the elevation change between the lake and river) and lake latitude seem to establish the abiotic context in which the occurrence of these two gar species is mediated (Hoeinghaus et al. 2007; Englund et al. 2009; Hein et al. 2013; Peoples and Frimpong 2016b). The occurrence of assemblages with Longnose Gar was more likely in floodplain lakes neighboring river ecosystems. Similar associations of riverine species with more frequently inundated floodplain habitats have been well documented (Miranda and Lucas 2004; Miranda 2005; Zeug et al. 2005; Zeug and Winemiller 2008) and have been previously described for Longnose Gar (Netsch and Witt 1962; Johnson and Noltie 1996; Robertson et al. 2008). Shortnose Gar and Longnose Gar were frequently encountered within the same ecosystems, but areas where Shortnose Gar were captured without Longnose Gar were characteristically more stable environments (i.e., flooded less frequently) located further from the river channel,

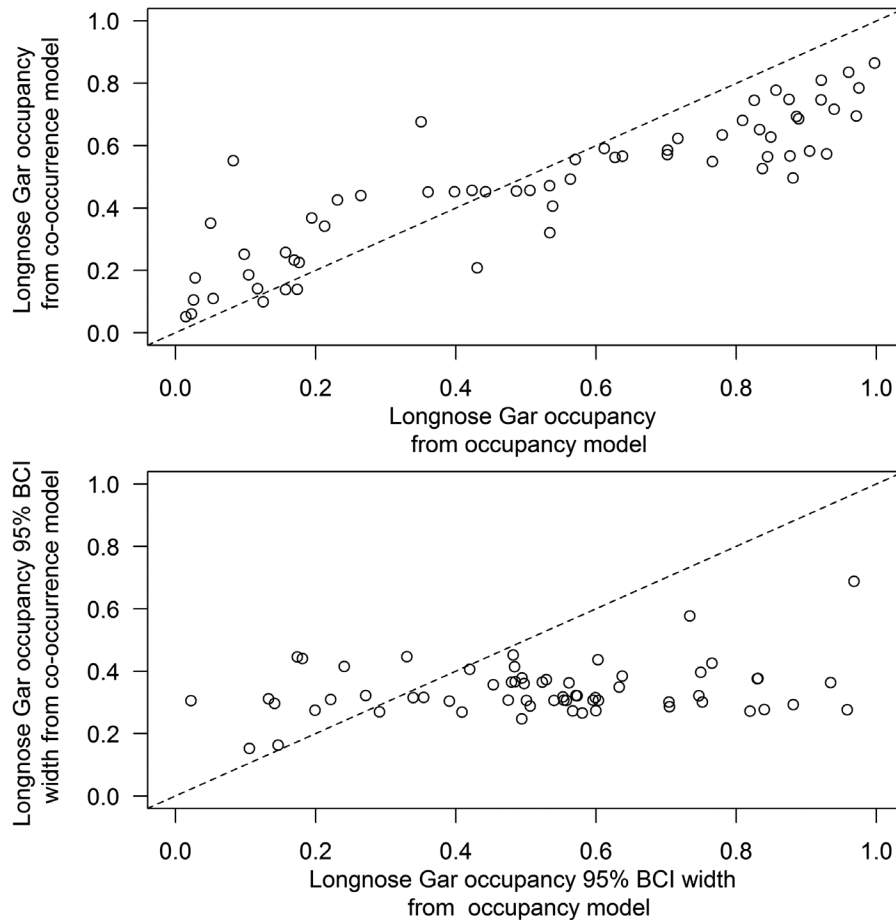


FIGURE 8. Comparison of lake-specific Longnose Gar occupancy estimates (upper panel) and 95% Bayesian credible intervals (BCIs; lower panel) from co-occurrence occupancy models (y -axis) and single-species models (x -axis). Each point represents a sampled floodplain lake.

particularly those in more northerly latitudes. These closely related species likely utilize similar lake-level macrohabitats, but rare evidence of co-occurrence within electrofishing transects (<3% of transects) suggests that the observed co-occurrence patterns were scale dependent. Shortnose Gar and Longnose Gar are functionally similar congeners that seemingly partition habitats at relatively small spatial scales that were undetected by the current analysis (Robertson et al. 2008; Walker et al. 2013). Although we detected evidence of positive co-occurrence patterns, the mechanism by which interactions between these two species influence assemblage structures remains unclear (i.e., facilitation versus shared habitat preferences).

Model evidence suggested that the occurrence of Spotted Gar was independent of the other two gar species, arising from the common use of habitats by both Shortnose Gar and Longnose Gar (Snedden et al. 1999; Robertson et al. 2008; Walker et al. 2013). Weaker SIFs involving Spotted Gar suggest that the ubiquitous nature of this species in the sampling area was the result of the

widespread availability of suitable habitats and was not influenced by the occurrence patterns of other gars. This insight into the context dependency of gar species co-occurrence could help to predict the responses of these species to the continued disconnection of floodplain lakes and river ecosystems in the region (Sparks 1995; Remo et al. 2008; Chamberlain et al. 2014).

We have demonstrated the effectiveness of a novel technique for leveraging interaction factors to inform descriptions of the distribution of a taxonomic guild of fishes across a gradient of floodplain ecosystems. By utilizing this three-way parameterization of the co-occurrence model, researchers and managers can identify habitat features and species relationships that may influence the occupancy of numerous other rare, endangered, and/or elusive species. The presented model structure is more parsimonious than similar tools that are often applied to multiple species pairs, as fewer parameters are estimated, consequently decreasing the likelihood of erroneously identifying strong relationships. Specifically, there is no

need to assume that detection probabilities are conditional on the presence of co-occurring species, an important distinction given the lack of evidence to support that assumption. By leveraging negative (i.e., avoidance or competitive exclusion) or positive (i.e., shared habitat preferences or facilitation) co-occurrence patterns, conservation planners can reduce the uncertainty associated with species distribution models and improve inference.

Multispecies (i.e., three or more species) co-occurrence modeling provides a robust tool for describing co-occurrence and patterns of assemblage structure (Gotelli 2000; Richmond et al. 2010; Rota et al. 2016; Lamothe et al. 2019). Using this new model parameterization, we identified a positive co-occurrence pattern between Longnose Gar and Shortnose Gar, which was largely unaffected by the presence of Spotted Gar. Strong co-occurrence patterns between these two species can be used to improve the confidence in species distribution models for the subordinate species, the Longnose Gar. Further inquiry into the possible biotic interactions between Longnose Gar and Shortnose Gar via small-scale experimentation or alternative model structures is necessary to describe the mechanism(s) by which co-occurrence is mediated (i.e., facilitation or shared habitats). We have, however, demonstrated how the occurrence patterns of Shortnose Gar can be used to better predict the distribution of the less common Longnose Gar in floodplain lakes. Additionally, if Spotted Gar had not been so commonly encountered, then the novelty of the three-species SIF would have been better realized. This method of occupancy modeling demonstrates how species distribution models can be improved by utilizing abiotic and biotic features of the target ecosystems.

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