SPECIAL SECTION

Avoiding a Macabre Future for Macrhybopsis—Improving Management and Conservation of Chubs

Conservation at the nexus of niches: Multidimensional niche modeling to improve management of Prairie Chub

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Abstract

Objective: A central challenge in applied ecology is understanding how organisms are spatially and temporally distributed and how management might be tailored to maintain or restore species distributions. The niche concept is central to understanding species distributions, but the diversity of niche definitions requires that multiple dimensions be considered. For example, the Grinnellian niche concept focuses on environmental conditions that allow species to persist, the Eltonian niche concept stresses the influence of biotic interactions, and the fundamental niche concept considers both abiotic and biotic environmental features to define spaces that organisms could occupy.

Methods: We combined abiotic (A), biotic (B), and movement (M) information (collectively, BAM model) to map the multidimensional niche of Prairie Chub Macrhybopsis australis, a regionally endemic freshwater fish currently under review for listing under the Endangered Species Act. We estimated A using remotely sensed environmental riverscape variables, B using the spatial distribution of a hybridization zone between Prairie Chub and Shoal Chub M. hyostoma, and M using data from a mark–recapture study.

Result: The BAM model estimated the spatial extent of multiple niches, including the Grinnellian (A; extent = 944 km of river), Eltonian (B; 2974 km), and fundamental niche (overlap of A + B; 645 km) niches. When A, B, and M components were combined, the estimated extent of the Prairie Chub niche was 645 km.

Conclusion: Our work shows that the realized, multidimensional niche of Prairie Chub includes medium to large rivers with high habitat connectivity in the upper-middle Red River basin upstream of the distribution of Shoal Chub. The current Prairie Chub distribution could be maintained by preventing further habitat fragmentation and maintaining the environmental gradient separating Prairie Chub from Shoal Chub. Expansion of the species distribution may be possible through restoration of longitudinal fluvial connectivity.

KEYWORDS
distribution, in-stream flow, riparian and stream ecology, threatened and endangered species
INTRODUCTION

A central challenge in ecology is developing predictions for how organisms are distributed across space and time. Ecological niche concepts provide a useful framework for understanding and predicting species distributions (Godsall 2010; Pocheville 2015). For example, the Grinnellian niche identifies the range of abiotic characteristics with positive population growth (Grinnell 1917), the Eltonian niche emphasizes biological interactions, such as predator–prey dynamics (Elton 1927), and the fundamental niche considers multiple abiotic and biotic dimensions (Hutchinson 1957). Niches are further distinguished via the fundamental versus realized niche. The Grinnellian fundamental niche reflects all of the abiotic factors that are positively correlated with positive intrinsic growth and can be measured using coarse-scale environmental data that are useful for understanding species distributions (Soberón 2007). The realized niche is the overlap between abiotic and biotic factors that provide positive intrinsic growth. Niche definition is further confounded by differences in source versus sink dynamics. Source habitats are locations where populations experience positive intrinsic growth (i.e., birth rates > death rates), whereas sink habitats result in negative population growth rate and are maintained only by dispersal from source habitats (Pulliam 1988). Consequently, although Grinnellian niches are density independent and rely on coarse-scale environmental factors that regulate species distributions (Holmes et al. 2005), understanding movement by organisms among patches is critical for understanding species distributions (Soberón 2007).

Environmental or ecological niche models (ENMs) are useful methods for defining species distributions. An ENM predicts how organisms may respond to environmental change, which is useful for creating conservation plans and developing population viability analyses (Franklin 2010). A typical ENM is an empirical model based on occurrence and environmental data that, together, enable predictions regarding occupied habitats (Guisan and Thuiller 2005). Organism occurrences may be predicted across space and time using historical, contemporary, and projected future environmental conditions (Elith and Leathwick 2009; Domisch et al. 2015). Incorporating species movement into ENMs remains a challenge for improving predictions of species distributions (Holloway et al. 2016). Soberón and Peterson (2005) developed a conceptual framework for identifying coarse-scale source and sink habitats based on inclusion of biotic (B), abiotic (A), and movement (M) parameters (collectively, the BAM model) in ENMs. The B component is the geographic area where the biotic conditions are suitable for the species to have positive population growth; the A component is the geographic area in which the abiotic components are suitable for the species to have positive intrinsic growth, such as an ENM; and the M component is the geographic area where the species can disperse (Soberón 2007). A benefit of Soberón and Peterson’s (2005) approach is that the foundations for investigating source versus sink locations are established and adding in movement data is increasingly useful information for conservation biology (Heinrichs et al. 2019).

Dispersal and related source–sink dynamics may make it difficult to determine if individuals occupy a source or sink patch or use both (Pulliam 1988). Dispersal encompasses three stages: emigration, transfer, and immigration (Clobert et al. 2012). The emigration stage is defined as leaving the natal or parental habitat, the transfer stage is a transient or wandering phase, and the immigration stage occurs when entering a new habitat (Clobert et al. 2012). These three stages may be affected by environmental, spatial, or intrinsic factors, including changes in movement behavior (e.g., Fraser et al. 2001) or environmental constraints (Vasudev et al. 2015). Species dispersal ability plays a role in determining habitat accessibility. For example, fishes are good model organisms for studying naturally versus human constrained dispersal because they are confined to the water in all stages of life (with few exceptions; see Furness 2016). Furthermore, fish access to upstream or downstream environments may be hindered due to barriers that are physical (e.g., dams and waterfalls) or biological (e.g., interspecific competition and hybridization; Rahel and McLaughlin 2018; Sotola et al. 2019). These factors can fragment dispersal-mediated links between source and sink habitats, ultimately altering species distributions (Fagan et al. 2002; Perkin and Gido 2012). Consequently, it is necessary to develop spatially and temporally explicit predictors for source and sink habitats so that mechanisms regulating fish species distributions can be uncovered (Schlosser 1991).

Improving the conservation of fishes requires greater understanding of how natural riverscape features and habitat connectivity interact to determine distributions (Fullerton et al. 2010). Among riverine fishes, those inhabiting the Great Plains of North America have truncated distributions due to habitat alterations (Hoagstrom et al. 2011). Widespread dam construction, groundwater...
PRAIRIE CHUB NICHE NEXUS

The purpose of this study was to help define the spatial distribution of Prairie Chub using a BAM modeling approach. The range of Prairie Chub is affected by interactions with Shoal Chub in the form of a large hybridization and introgression zone in the lower portions of Prairie Chub range (Sotola et al. 2019). The truncated range of Prairie Chub is hypothesized to be related to factors such as habitat alteration and fragmentation (Winston et al. 1991; Perkin and Gido 2011). Finally, Prairie Chub dispersal is greater than expected under the prevailing models used to predict stream fish movement and this high level of dispersal has unknown consequences for the distribution (Steffensmeier et al. 2022). Despite previous studies on Prairie Chub distribution (e.g., Mollenhauer et al. 2021), there is no information regarding integration of BAM components to delineate the range of the species. The degrees to which the BAM components of Prairie Chub distribution overlap might be used to delineate source versus sink habitats across the riverscape and ultimately identify conservation areas for the species (Figure 1). We hypothesized that inclusion of information pertaining to hybridization would result in a better model fit compared with assessment of habitat alone (i.e., biological interactions; Wisz et al. 2013). Further, we hypothesized that inclusion of dispersal information would result in better model performance compared with assessment of habitat and biological information alone. This hypothesis was based on the notion that dispersal can increase realized niches compared with fundamental niches because of source–sink dynamics and species movement across the riverscape (Soberón 2007).

METHODS

Study area

The upper Red River basin is located along the border of Oklahoma and Texas upstream of the Lake Texoma Reservoir in the United States (Figure 2). This region has an average of 82 cm of precipitation annually, a mean annual air temperature of 18.0°C, and a mean annual water temperature of 19.3°C (Benke and Cushing 2005). Rangeland and cropland cover 80–90% of the basin (Benke and Cushing 2005). The basin is characterized by a gently sloping floodplain with sandy riverbeds and unpredictable seasonal flow variability, especially prior to dam and reservoir construction (Benke and Cushing 2005). Dams and reservoirs in the study area include Lake Altus, Lake Kemp, Lake Santa Rosa, and Lake Texoma, all of which are considered impassable for Prairie Chub (e.g., Winston et al. 1991). Prairie Chub range does not extend downstream of Lake Texoma, and Shoal Chub inhabits areas downstream and immediately upstream of Lake Texoma (Miller and Robison 2004; Sotola et al. 2019). Upstream of...
Lake Texoma, a hybridization zone exists in which Shoal Chub genes introgress into the genome of Prairie Chub (Sotola et al. 2019).

**Occurrence data collection**

We obtained existing occurrence data for Prairie Chub throughout the Red River basin upstream of Lake Texoma. Fish sampling was conducted via seining during the summers of 2013, 2015, 2016, 2019, 2020, and 2021 (Table 1). Occurrence data (1 = presence, 0 = absence) were compiled across all survey sites. Absence was defined as lack of collection of the species, but we did not model imperfect detection because temporal replication of collections was insufficient for fitting models at the scale of interconfluence stream segments (but see Mollenhauer et al. 2021 for coarse-scale occupancy modeling) and because our focus was on traditional methods for fitting ENMs without consideration of detection. Occurrence data were georeferenced and assigned to stream segments from the medium-resolution National Hydrography Dataset (NHD; McKay et al. 2012). We divided the database of collections into a training subset (n = 93 collections) and a testing subset (n = 45 collections). The training data set was selected based on samples being collected on both sides of the Oklahoma–Texas border within each study included in the data set, while the testing data set was selected based on comprehensive sampling on the Oklahoma (Starks et al. 2018) or Texas (Ruppel et al. 2020) sides of the border only within each study included in the data set (Table 1; see Random Forest Modeling section below).

**Biotic dimension**

The biological component of the BAM framework is the area where species interactions affect occurrence of Prairie Chub. Within the Red River basin, there is a large hybridization zone in which Shoal Chub and Prairie Chub...
interbreed. This zone was described by Sotola et al. (2019), who showed that Shoal Chub was introgressing with Prairie Chub. We identified NHD stream segments within this zone and coded them separately from other segments (hybridization zone = 0, nonhybridization zone = 1). This resulted in hybridization zone segments receiving a probability of Prairie Chub occurrence of zero for the \( B \) component. If Prairie Chub probability of occurrence based on the \( A \) dimension was low (see next section), then there would be little change in Prairie Chub distribution when biological interactions were considered. We recognize that other forms of biological interactions are possible, namely predator–prey dynamics. However, spatial data on these forms of biological interactions are not currently available, so we focused on hybridization and introgression. Prior to modeling, we adjusted the training and testing data sets to code Prairie Chub as absent immediately upstream of Lake Texoma because Sotola et al. (2019) detected only Shoal Chub in this region. We felt this adjustment was necessary because most community collection databases within the training and testing data sets did not use molecular techniques to identify specimens; therefore, Shoal Chub was likely identified as Prairie Chub for the downstreammost locations (i.e., within 45 km of Lake Texoma).
TABLE 2 Environmental variable codes, descriptions, and sources used to model distribution of Prairie Chub using an ecological niche model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>StreamOrder</td>
<td>Stream order (Strahler 1957)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>L_SLOPE</td>
<td>Local stream channel slope (m/m)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>TM2D</td>
<td>Total main-stem distance between upstream and downstream dams (km)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>UDOR</td>
<td>Percent of estimated annual discharge stored in upstream reservoirs (%)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>DMD</td>
<td>Density of downstream main-stem dams (number/100km)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>UM2D</td>
<td>Distance to upstream main-stem dam (km)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>UMO</td>
<td>Percent of open upstream main stem (%)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>UNDR</td>
<td>Upstream network dam density per stream network length (number/100km)</td>
<td>Cooper et al. (2017)</td>
</tr>
<tr>
<td>N_CROP</td>
<td>Percent crop land use in network catchment (%)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>L_CROP</td>
<td>Percent crop land use in local catchment (%)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>N_PASTURE</td>
<td>Percent pasture land use in network catchment (%)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>L_URBANL</td>
<td>Percent low-intensity urban land use in local catchment (%)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>L_URBANH</td>
<td>Percent high-intensity urban land use in local catchment (%)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>L_POPDENS</td>
<td>Human population density in local catchment (people/km)</td>
<td>Daniel et al. (2019)</td>
</tr>
<tr>
<td>cumu_hci</td>
<td>Averaged anthropogenic disturbance index (1 = highest risk of habitat degradation)</td>
<td>Daniel et al. (2019)</td>
</tr>
</tbody>
</table>

Abiotic dimension

We compiled aquatic landscape data, including land use, land cover, hydrologic, climatic, and habitat disturbance data, at both local and network scales (Table 2). The local scale is the area of land draining immediately into an interconfluence stream segment, excluding all upstream segments, whereas the network scale includes the focal segment plus all upstream segments (Hill et al. 2017). These two scales have been used in ENMs for freshwater fishes in other studies (Perkin et al. 2019a) based on the medium-resolution NHD stream identification code (i.e., COMID), which allows for precise mapping of species distributions. Land use and land cover data included attributes such as agriculture, urbanization, and forested land covers, as well as cumulative habitat disturbance assigned to NHD stream segments by Daniel et al. (2019). Hydrologic and climatic variables include attributes such as stream slope, average annual discharge, average annual precipitation, and average annual air temperature assigned to NHD stream segments by McKay et al. (2012). Habitat connectivity attributes were based on the suite of connectivity indices assigned to NHD stream segments by Cooper et al. (2017). Among fragmentation metrics, when the distance to the upstream main-stem dam (environmental variable code UM2D) was coded as −99 to represent a lack of an upstream dam, we recoded these values to the maximum value for the riverscape to allow for inclusion of this metric in the model, which emphasizes shorter fragments that are correlated with extirpation (Winston et al. 1991). All geospatial data were linked to NHD stream segments in ArcGIS 10.8.1 (ESRI, Redlands, California) using table joins based on COMID. We tested for multicollinearity among variables using the “cor” function from the “corrplot” package in R and retained 16 abiotic variables (Table 2) that were not correlated to each other based on $r < 0.70$ (Parker et al. 2021; Figure A.1 in the Appendix).

Movement dimension

We used dispersal information to assess the $M$ component of Prairie Chub ecology. For this assessment, we estimated Prairie Chub probability density kernels based on mark–recapture observations from Steffensmeier et al. (2022). In their study, Steffensmeier et al. (2022) compared movement distances and rates of Prairie Chub with those obtained from the “fishmove” package in R (Radinger and Wolter 2014) and found that Prairie Chub moved distances more than an order of magnitude greater compared with the typical stream fish of their size (Steffensmeier et al. 2022). Specifically, instead of moving the distance expected by a fish ≈58 mm TL, Prairie Chub moved a distance equivalent to a fish 800 mm TL. We estimated...
movement using the “fishmove” function from R and parameterized the predictive movement model using TL = 800, time = 730 days (equivalent to the 2-year lifespan of Prairie Chub; Ruppel et al. 2020), caudal fin aspect ratio = 1.09 (height of the caudal fin squared, divided by the surface area; Pauly 1989), and spatially defined stream order (Strahler 1957) values from all locations within the upper Red River basin where Prairie Chub were predicted to occur. This approach resulted in stream-order-specific estimates for lifetime (2 years) dispersal of the stationary and mobile components of the population (Table 3). Because our interest was in evaluating how movement relates to species distribution, we focused on movement by the mobile component from the peripheries of continuous portions of Prairie Chub distribution as predicted from the A + B dimensions described above.

Random forest modeling

We used random forest modeling (Cutler et al. 2007) to develop an ENM to predict the probability of occurrence of Prairie Chub for stream segments in the upper Red River basin. This allowed us to use the Grinnellian niche concept to predict the realized niche of Prairie Chub across broad spatial extents based on BAM parameters (Soberón 2007). Prior to modeling, we addressed class imbalance among presence and absence using the synthetic minority over-sampling technique (SMOTE) described by Chawla et al. (2002). Briefly, this method involves the creation of synthetic observations in the minority class to achieve a more equal sample size between classes and improve model performance (Chawla et al. 2002). We used the “SMOTE” function from the “DMwR” package (Torgo 2010) in R to resample our data from 93 observations (0 = 63, 1 = 30) to 120 observations (0 = 60, 1 = 60) by doubling the minority class and subsampling the majority class. Next, we tuned the model using the function “tuneRF” from the “randomForest” package to determine the number of variables to try at each split in the model. We fit the model using the “randomForest” package in R to estimate the probability of occurrence (0–1) for each stream segment (Breiman 2001) using 1000 trees and four variables at each split. We tested whether the model predictions were significantly more accurate compared with random chance using the “rf.significance” function from the “rfUtilities” package (Evans and Murphy 2018). We assessed model performance using sensitivity (observed occurrence correctly predicted by the model), specificity (observed absences correctly predicted by the model), and Kappa (ratio of expected versus observed accuracy of the model) as suggested by Leroy et al. (2018). We assessed relative variable importance using the mean decrease in Gini (i.e., change in node purity when each variable was excluded from a subset of trees) to identify which variables were most important for generating accurate predictions of occurrence. We also used the “rf.partial.prob” function from the “rfUtilities” package to produce partial dependence plots that showed the individual effects of the top six most important variables, while holding all other variables at their mean (Evans and Murphy 2018). These partial dependence plots included locally weighted regression lines to show the smoothed effect of each variable on the probability of occurrence of Prairie Chub. We used the independent data set for model validation, which is an important component of the ENM to test the application of the model and reduce bias. We used the “confusionMatrix” function from the “caret” package in R to assess model performance using the independent data set and reported the same sensitivity, specificity, and Kappa assessment parameters. Finally, we used the “predict.randomForest” function from the “randomForest” package to estimate the predicted probability of occurrence for all NHD stream segments in the study area (Figure 2), including a continuous probability of occurrence ranging from 0.00 to 1.00, as well as a binary presence (1) or absence (0) prediction (Liaw and Wiener 2002).

Geographic information systems analysis

We used GIS to map multiple niche dimensions for Prairie Chub using the BAM framework. For each panel within our overlapping BAM conceptual diagram (Figure 1), we measured longitudinal distance in kilometers of river to quantify the results. This process began with the random forest model fit to the A component (see Figure A.2). We used the predicted probability of occurrence of Prairie Chub from the random forest model to estimate the species distribution based only on abiotic features. This extent is consistent with the Grinnellian niche concept because it considers only environmental variables. We

### TABLE 3 Prairie Chub movement predictions across a gradient of stream size (stream order; Strahler 1957) based on data from Steffensmeier et al. (2022). Movement distances (in meters; 95% CI in parentheses) are given for stationary (σ stationary) and mobile (σ mobile) components of the population as defined by Radinger and Wolter (2014).

<table>
<thead>
<tr>
<th>Stream order</th>
<th>σ Stationary (m)</th>
<th>σ Mobile (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Second</td>
<td>366 (119–1125)</td>
<td>5490 (2297–13,127)</td>
</tr>
<tr>
<td>Third</td>
<td>528 (195–1428)</td>
<td>8758 (4056–18,914)</td>
</tr>
<tr>
<td>Fourth</td>
<td>717 (285–1801)</td>
<td>13,074 (6417–26,638)</td>
</tr>
<tr>
<td>Fifth</td>
<td>938 (388–2271)</td>
<td>18,671 (9424–36,996)</td>
</tr>
<tr>
<td>Sixth</td>
<td>1193 (496–7871)</td>
<td>25,487 (12,902–50,352)</td>
</tr>
<tr>
<td>Seventh</td>
<td>1499 (610–3679)</td>
<td>34,407 (17,187–68,887)</td>
</tr>
</tbody>
</table>
then calculated the extent of the study area in which Prairie Chub and Shoal Chub did and did not overlap to represent the Eltonian niche influenced by biological interactions. Next, we combined the A and B dimensions of Prairie Chub niche by multiplying the probability of occurrence from the A component and B component. This yielded an estimate of the fundamental niche for Prairie Chub in which abiotic and biotic dimensions were combined. If the hybridization zone was on the fringe of the Prairie Chub Grinnellian niche, then there would be little change in the basinwide distribution of the species. Alternatively, if the hybridization zone was within the predicted geographic distribution of Prairie Chub based on the A dimension alone, then the realized niche (i.e., components A+B) of Prairie Chub would be smaller than inferred from the A dimension. Next, we adjusted segment-specific probability of occurrence from the A+B dimensions by adding the dispersal-based probability of occurrence from the “fishmove” output. In the full BAM model (A+B+M), if sink habitats exist, then they would be characterized by a greater probability of colonization from dispersal compared with probability of occurrence based on abiotic and biotic variables alone. If Prairie Chub distribution was maintained by movement from source to sink patches, then the basinwide distribution of Prairie Chub would increase compared with the previous iteration B+A form of the BAM model.

Hypothesis testing

We tested two hypotheses regarding shifts in Prairie Chub occurrence under B, B+A, and B+A+M scenarios by assessing performance of the fitted model on the independent testing data set. We first assessed performance of the fitted model with only the A component and quantified sensitivity, specificity, Kappa, Jaccard similarity index, and Sørensen similarity index (Leroy et al. 2018; Parker et al. 2021). Jaccard’s similarity index and Sørensen’s similarity index are calculated based on the confusion matrix of correctly classified occurrences (i.e., true positives), correctly classified absences (i.e., true negatives), incorrectly classified occurrences (i.e., false positive), and incorrectly classified absences (i.e., false negatives; Leroy et al. 2018; Parker et al. 2021). We followed the methods from Parker et al. (2021) to calculate Jaccard’s similarity index and Sørensen’s similarity index, which ranged in values from 0.00 to 1.00, with values closer to 1.00 showing better agreement between observed versus predicted occurrences. Next, we adjusted model predictions to be zero within the hybridization and introgression zone (i.e., generating the B+A scenario) and again assessed performance on the independent data set. Improvement in the model performance metrics from the A-only to B+A scenario would support our hypothesis that inclusion of the biotic component of Prairie Chub niche improves the model fit. We then adjusted model predictions after incorporating movement as described above (i.e., generating the B+A+M scenario) and again assessed performance on the independent data set. Improvement in the model performance metrics from the A-only and B+A scenarios would support our hypothesis that inclusion of movement information further improves the definition of the distribution of the species.

RESULTS

Random forest model

The random forest model representing the A dimension of Prairie Chub niche produced predictions that were

<table>
<thead>
<tr>
<th>Performance metric</th>
<th>Training data</th>
<th>Cross validation</th>
<th>A independent validation</th>
<th>B+A independent validation</th>
<th>B+A+M independent validation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sensitivity</td>
<td>0.95</td>
<td>0.88</td>
<td>0.72</td>
<td>0.64</td>
<td>0.88</td>
</tr>
<tr>
<td>Specificity</td>
<td>0.94</td>
<td>0.92</td>
<td>0.94</td>
<td>0.94</td>
<td>0.88</td>
</tr>
<tr>
<td>Kappa</td>
<td>0.82</td>
<td>0.84</td>
<td>0.63</td>
<td>0.52</td>
<td>0.76</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
<td>0.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Jaccard</td>
<td>0.83</td>
<td>0.82</td>
<td>0.69</td>
<td>0.62</td>
<td>0.81</td>
</tr>
<tr>
<td>Sørensen</td>
<td>0.90</td>
<td>0.90</td>
<td>0.82</td>
<td>0.77</td>
<td>0.90</td>
</tr>
</tbody>
</table>
significantly ($p < 0.005$) more accurate than random chance. The model training data set had high sensitivity (0.95), specificity (0.94), Kappa (0.82), Jaccard similarity index (0.83), and Sørensen’s similarity index (0.90) values. The sensitivity (0.88), specificity (0.92), Kappa (0.84), Jaccard similarity index (0.82), and Sørensen’s similarity index (0.90) also remained high under five-fold cross validation of the training data set (Table 4). When assessed using the independent testing data set, the model remained significant ($p < 0.005$) with high specificity (0.94), but sensitivity (0.72), Kappa (0.63), Jaccard similarity index (0.69), and Sørensen’s similarity index (0.82) declined. The six most important variables (based on our variable importance plot; Figure 3) for predicting Prairie Chub occurrence were distance to upstream main-stem dam (UM2D), stream order, density of downstream main-stem dams (DMD), upstream network dam density per stream network length (UNDR), total main-stem distance between upstream and downstream dams (TM2D), and percent of open upstream main stem (UMO). Partial dependence plots showed that Prairie Chub probability of occurrence was most likely where distance to upstream dam was $>200$ km (Figure 4A), stream order was $>5$ (Figure 4B), density of downstream main-stem dams was 0.3–0.4 (Figure 4C), upstream dam density was <2 (Figure 4D), distance between reservoirs was $>600$ km (Figure 4E), and open upstream main stem was $>40\%$ (Figure 4F). Partial dependence plots for remaining variables, shown in Figure 3, are given in Figure A.3 and illustrate lower probability of occurrence in highly altered watersheds. The model projected to the entire riverscape upstream of Lake Texoma showed strong agreement with the independent data set and revealed spatial hotspots of high probability of occurrence for Prairie Chub in the lower North Fork Wichita River upstream of Lake Kemp, lower Pease River, lower Prairie Dog Town Fork Red River, lower North Fork Red River, and main-stem Red River upstream of the confluence with the Wichita River (Figure 5).

**Framework for BAM model**

Inclusion of BAM components improved prediction of Prairie Chub distribution. The model predictions based on $B + A$ were significantly more accurate than random chance ($p = 0.04$) with high specificity (0.94), but sensitivity declined from 0.72 to 0.64, Kappa declined from 0.63 to 0.52, Jaccard similarity index declined from 0.69 to 0.62, and Sørensen’s similarity index declined from 0.82 to 0.77 relative to the $A$-only model (Table 4). Inclusion of $B + A + M$ components resulted in significant predictive ability ($p < 0.001$) and improved sensitivity (0.88 vs. 0.64), Kappa (0.76 vs. 0.52), Jaccard similarity index (0.81 vs. 0.69), and Sørensen’s similarity index (0.90 vs. 0.82) relative to the $A$-only model, whereas specificity declined slightly (0.88 vs. 0.94). Based on these results, there was no support for our first hypothesis that inclusion of $B$ along

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**Figure 3** Variable importance plot illustrating mean decrease in Gini (i.e., change in node purity when each variable was excluded from a subset of trees), where the largest value is the most important variable (i.e., how important a variable is for estimating the value of the target variable across all trees). See Table 2 for definitions of variable codes.
with \( A \) would improve prediction of Prairie Chub distribution. However, there was support for the hypothesis that inclusion of \( M \) information would improve model performance. The full BAM model estimated the realized niche of Prairie Chub to be 645 km, the geographic extent of hybridization sink was 34 km, and the geographic extent of habitat sink was 212 km (Table A.1 in the Appendix). Habitat sinks were in tributary streams west and north of the realized niche of Prairie Chub, whereas the hybridization sink was in the downstream extent of the main-stem Red River within the hybridization zone (Figure 6).

**DISCUSSION**

Including Prairie Chub movement in ecological niche modeling improved the accuracy of predictions. In fact, the locations identified as movement sinks in this study are the same locations in which the detection of Prairie Chub varied among wet and dry periods as documented by Mollenhauer et al. (2021). Thus, our work provides support that the inclusion of movement data can improve the accuracy of species distribution models (Holloway et al. 2016). The distribution of Prairie Chub has received increased attention during the past three decades. Winston et al. (1991) documented the extirpation of Speckled Chub *M. aestivalis* (now Prairie Chub) upstream of Altus Reservoir on the North Fork Red River. Eisenhour (2004) reviewed the distribution of Prairie Chub and noted apparent extirpation from the upper Washita River of Oklahoma, where the species was last collected in 1926. Perkin and Gido (2011) reviewed occurrence of Prairie Chub within broadscale stream fragments in the upper Red River basin and considered the population in the Wichita River upstream of Lake Kemp to be declining, while the population in the main-stem Red River and connected tributaries was considered stable. Most recently, Mollenhauer et al. (2021) assessed temporal dynamics in the detection of Prairie Chub and found that the species was detected further upstream within major tributaries during wet years compared to dry years. In that study, the spatial distribution of the species depended on
FIGURE 5  Validation map illustrating predicted suitability from the ecological niche model (i.e., abiotic data only; A scenario) as a heat map (warmer colors = high probability of occurrence for interconfluence stream segment) and points from the independent testing data set overlaid and coded as presence (solid circles) or absence (gray boxes) of Prairie Chub.

FIGURE 6  (A) Map showing the biotic, abiotic, and movement results in the Red River basin, with (B) a diagram showing the total kilometers of river for each component of the BAM model for Prairie Chub. Letters A, D, E, and G together represent the Grinnellian niche, letters B, D, F, and G together represent the Eltonian niche, and letters D and G together represent the fundamental niche. Letter G represents the realized nexus of niches for Prairie Chub and the length of stream that might be considered source populations. See Table A.1 for letter definitions (A–H).
the sampling time because the species was missing from some locations that are prone to cessation of flow during dry periods (Mollenhauer et al. 2021). An apparent mechanism for the dynamic nature of Prairie Chub occurrence was suggested by Ruppel et al. (2020), who hypothesized that movement was primarily linked to refuge-seeking behavior. Our work advances these findings by revealing that inclusion of Prairie Chub dispersal (Steffensmeier et al. 2022) is likely to be critical for understanding the distribution of the species, a challenge facing many organisms in need of conservation (Heinrichs et al. 2019).

Prairie Chub distribution correlated strongly with abiotic variables associated with fluvial habitat connectivity. Prairie streams are connected across four riverscape dimensions—vertical between groundwater and surface water, lateral between stream channels and floodplains, longitudinal from upstream to downstream, and temporal with respect to hydrology and its effects on channel geomorphology (Ward 1989). Great Plains streams are now highly fragmented by groundwater extraction (Perkin et al. 2017a), narrowing of channels and isolation of floodplains (Friedman et al. 1998), channel fragmentation by structures used to divert and store surface water (Perkin et al. 2015a), and highly altered flow regimes (Costigan and Daniels 2012). Prairie Chub has been affected by fragmentation on all four dimensions. Eisenhour (2004) noted that groundwater declines threatened Prairie Chub because loss of vertical hydrologic connectivity increases the likelihood of stream drying, a contributor to summertime local extirpations. That is, populations at locations prone to drying are maintained through recolonization (Eisenhour 2004), which is not possible when dams block movement (Winston et al. 1991; Perkin and Gido 2011). Reduced water availability also increases salinity concentrations in these Great Plains streams. While salinity tolerance is higher in Prairie Chub than most freshwater fishes, increases to the already relatively high salt concentrations surpass the upper threshold of physiological tolerance for the species. Consequently, long-term changes in fish community composition are greatest at locations with increased water extractions, and Prairie Chub is among the declining species (Taylor 2010). Mollenhauer et al. (2021) modeled the distribution of Prairie Chub using hierarchical occupancy modeling and found that the species was most likely to occupy hydrologic response units that had <1.5 upstream dams per 100 km (UNDR; Cooper et al. 2017). Similarly, Perkin and Gido (2011) estimated that Prairie Chub required a minimum of 128 km between main-stem reservoirs for persistence. Our work confirms these previous findings. We found that occurrence of Prairie Chub was greatest among stream fragments with upstream network dam density <2 dams/100 km (Figure 4D) and at locations with >150 km in length between main-stem barriers (Figure 4E). We also found that Prairie Chub suitability was low within 150 km downstream of reservoirs (Figure 4D). This finding is consistent with extirpation of the regionally endemic Burrhead Chub in the Guadalupe River basin (Edwards 1978; Perkin et al. 2013) and the decline of Shoal Chub throughout 250 km of the Sabine River downstream of the Toledo Bend Reservoir (Perkin et al. 2017b). Finally, our results revealed that the highest suitability of Prairie Chub was among large stream fragments with high densities of downstream dams (DMD; Cooper et al. 2017). This pattern is consistent with the federally listed Spotfin Chub Erimonax monachus that is essentially isolated upstream of large reservoirs (Perkin et al. 2019a) and highlights the lack of downstream connectivity that has already contributed to the decline and extirpation of Prairie Chub (Winston et al. 1991).

Biological interactions are contributing, at least in part, to the current distribution of Prairie Chub. Although the effects of environmental filtering generally outweigh the effects of biotic interactions within Great Plains prairie streams (Nguyen et al. 2023, this special section), strong species interactions can affect stream fish distributions (Giam and Olden 2016). In some prairie streams, the introduction of nonnative species has contributed to rapid replacement of native species through competition (Hoagstrom et al. 2010) or hybridization and introgression (Wilde and Echelle 1992). For Prairie Chub, hybridization with Shoal Chub is a well-documented form of biological interaction. When describing the species that composed the Speckled Chub clade west of the Mississippi River, Eisenhour (2004) suggested that there was limited evidence for hybridization and introgression among Prairie Chub and Shoal Chub in the “middle” Red River. However, using new technology in the form of single nucleotide polymorphisms, Sotola et al. (2019) discovered a large hybridization and introgression zone in the area just upstream of Lake Texoma, and this zone was the focus of biological interactions in the current study. The most recent hypothesized phylogenetic relationships among Macrhybopsis fishes posits that Prairie Chub and Shoal Chub evolved allopatrically and that the hybridization and introgression range in the upper Red River is the consequence of secondary contact (Hoagstrom and Echelle 2022). However, Sotola et al. (2019) found evidence that isolation between Prairie Chub and Shoal Chub was supported by ecological responses to salinity gradients in the upper Red River, with Prairie Chub being relatively more tolerant of higher salinities (though an upper tolerance threshold likely exists; Ruppel et al. 2020). This hypothesis suggests that biological interactions alone do not contribute to the small area of overlap between the two species. Our inclusion of biological interactions within the hybridization zone did not improve performance of
the ENM on the independent data set, perhaps because hybridization is not the chief factor contributing to the downstream extent of Prairie Chub distribution. Future ENM research focused on developing segment-level estimates of water salinity to test whether, and to what extent, spatial gradients in salinity correlate with the downstream extent of Prairie Chub occurrence just upstream of Lake Texoma would be beneficial. This will be challenging given the high volatility of salinity concentrations and limited locations where it is monitored (e.g., Ruppel et al. 2020), but recent advances in modeling might pave the way to such research (Olson 2019). Future studies might also consider additional biotic interactions, such as interspecific competition between other fishes and Prairie Chub. For example, Winston et al. (1991) found strong negative co-occurrence relationships between Red River Shiner Notropis Bairdi and Sand Shiner N. Stramineus and suggested competition as a mechanism. Future research may also focus only on abiotic and movement factors; our study suggests that adding in biotic interactions decreases model performance compared to the abiotic-only model. Until such research is conducted, our findings support the assertion that environmental filtering exudes a stronger effect on species distributions than biological interactions (Giam and Olden 2016; Nguyen et al. 2023).

Our results suggest that the distribution of Prairie Chub is strongly tied to movement ecology. Traditionally, ENMs have ignored movement or included only simple estimates of movement (e.g., no movement or unconstrained movement) when delineating species distributions (Miller and Holloway 2015). Recognition of the limitations imposed by ignoring movement led to modeling frameworks capable of integrating movement, including the BAM framework we employed here (Barve et al. 2011). We found that including spatially explicit estimates of movement (i.e., B + a + M) explained more variation in the independent testing data set compared with models that excluded movement data (i.e., A, B + A). This finding is likely related to the fact that Prairie Chub is capable of long-distance movements over short time periods. For example, Steffensmeier et al. (2022) showed that Prairie Chub population(s) in the main-stem Red River, lower Salt Fork Red River, and lower Pease River exhibited leptokurtic summer movement distributions, a signal of heterogeneous populations composed of both stationary and mobile individuals (Skalski and Gilliam 2000; Radinger and Wolter 2014). The distances moved by both stationary and mobile components of the Prairie Chub population were orders of magnitude greater than those of stream fishes of similar size, meaning the population can maintain broadscale functional connectivity (Steffensmeier et al. 2022). For example, Prairie Chub maintained no isolation by distance in molecular structure over 600 km of the Red River and its tributaries studied by Ruppel et al. (2020). However, the lack of structure upstream and downstream of the dams that separate the upper Wichita River from the main-stem Red River (Kemp and Diversion dams) despite the dams being in place since the 1920s suggests either continued connection (unlikely; Ruppel et al. 2020) or large and well-connected population sizes prior to fragmentation combined with maintenance of genetic variation in the isolated fragments. Osborne et al. (2014) investigated the relationship between fragmentation and genetic structure for multiple Great Plains fishes and found no relationship, leading the authors to suggest that demographic changes that contribute to population extirpations outpace genetic bottlenecks and other signals of isolation.

We hypothesize that historical movements by Prairie Chub throughout the upper Red River basin were sufficient to link tributaries and main stems prior to fragmentation. This hypothesis is supported by at least three lines of evidence. First, Steffensmeier et al. (2022) recaptured a Prairie Chub that moved from the main-stem Red River into the lower Salt Fork Red River (12 km). Second, Ruppel et al. (2020) suggested that Prairie Chub were capable of long-distance movements to recolonize the upper Pease River, where time series surveys documented occurrence, absence, and then occurrence again. Third, Mollenhauer et al. (2021) reported the occurrence of a single Prairie Chub far upstream in the Prairie Dog Town Fork of the Red River well beyond the locations of other detections in the data set but within the distance the species was estimated to be able to move from the edge of its realized niche as defined here. Members of the pelagic-broadcast-spawning reproductive guild (Worthington et al. 2018; Ruppel et al. 2020), far upstream habitats may be important in maintaining downstream populations due to ichthyoplankton drift or downstream drying (Moore 1944; Bottrell et al. 1964; Platania and Altenbach 1998). This might be due to increasing retention of ova and larvae at upstream reaches or mitigation of downstream displacement via drift (Platania and Altenbach 1998; Albers and Wildhaber 2017). Thus, our findings further support previous calls for maintenance of broadscale habitat connectivity to benefit Prairie Chub by providing dispersal corridors (Winston et al. 1991; Eisenhour 2004; Perkin and Gido 2011; Mollenhauer et al. 2021; Steffensmeier et al. 2022).

Management and conservation implications

Our findings suggest that Prairie Chub distribution is affected by longitudinal habitat fragmentation and altered land cover and land use but perhaps minimally by
hybridization and introgression with Shoal Chub. Each of these threats could be mitigated with a suite of management actions. Multiple methods have uncovered consistent relationships between habitat fragmentation and Prairie Chub decline, including a review of historical ichthyology collections (Winston et al. 1991), parsimonious measures of connectivity (Perkin and Gido 2011), hierarchical modeling of hydrologic response units and multivariate measurements of connectivity (Mollenhauer et al. 2021), and multidimensional niche modeling (this study). Existing longitudinal connectivity could be maintained to prevent further declines based on the strong relationship between Prairie Chub occurrence and measurements of habitat fragmentation. This management approach allows for treating Prairie Chub distribution as temporally fluctuating, including greater upstream occurrence when conditions are appropriate (Mollenhauer et al. 2021). We also found that local land use and agricultural activities correlated with Prairie Chub distribution but to a lesser degree than habitat connectivity. Land use change has been shown to affect Great Plains fish distributions (Gido et al. 2010), and we found that Prairie Chub occurrence was greatest where network-scale row-crop agriculture and local-scale low-intensity urbanization were least. Riparian and stream corridor buffers might represent a management strategy for mitigating the effects of land cover conversion on Prairie Chub distribution (Dosskey 1998). Greater investigation into the hybridization and introgression zone is needed to understand if the zone is stationary or temporally fluctuates in size and extent (Sotola et al. 2019). For other fishes threatened by the combined effects of habitat loss and introgression, these threats each operate from upstream and downstream directions to squeeze out threatened species (e.g., Parker et al. 2021). The hybridization and introgression zone for Prairie Chub and Shoal Chub is considered natural (Hoagstrom and Echelle 2022), but it is possible that the zone is maintained by environmental gradients that prevent the upstream expansion of Shoal Chub. Sotola et al. (2019) found evidence that a water salinity gradient might be contributing to minimal overlap between the two species. It is possible that desalination of water in the upper Red River basin might alter the current salinity gradient and negatively affect Prairie Chub distribution by allowing the upstream expansion of Shoal Chub (Eisenhour 2004).

Managing Prairie Chub to address listing under the Endangered Species Act requires consideration of representation, resiliency, and redundancy. Representation addresses whether the full range of ecological settings within the historical range of the species are occupied, resiliency addresses population attributes that allow for long-term persistence in the face of disturbance, and redundancy requires the establishment of multiple populations to spread extinction risk across geographic space (Wolf et al. 2015). Prairie Chub has lost representation in the North Fork Red River upstream of Lake Altus and in the Washita River of Oklahoma. Our work suggests that restoring representation within the North Fork Red River is only likely to be successful through improved recolonization of the area via barrier mitigation or other forms of assisted recolonization. Our implementation of the BAM framework illustrated that the area upstream of the Altus Dam is within a distance that Prairie Chub could disperse (i.e., $M$ component) from its range downstream of the dam, but the area upstream of the dam is likely a sink based on environmental covariates we used (i.e., $A$ component). Consequently, reintroduction of Prairie Chub in the North Fork Red River upstream of Lake Altus is unlikely to be successful unless future research reveals that habitats are appropriate for persistence of the species. Prairie Chub has shown resiliency in tributary streams that are prone to drying, and the species was not extirpated upstream of Kemp Reservoir during the extreme drought of 2011 and 2012 when similarly isolated populations of other Macrhybopsis spp. were extirpated elsewhere in the Great Plains (e.g., Perkin et al. 2015b, 2019b). Ruppel et al. (2020) demonstrated seasonal absence of Prairie Chub in the upper Pease River, followed by apparent recolonization when higher flows returned. This resiliency was likely driven, at least in part, by recolonization from the lower Pease River or main-stem Red River, and maintaining connectivity among these locations is likely a critical aspect to maintaining Prairie Chub resiliency (Ruppel et al. 2020; Steffensmeier et al. 2022). Available genetic data (Sotola et al. 2019; Ruppel et al. 2020) and movement estimates (Steffensmeier et al. 2022) suggest that Prairie Chub redundancy is limited to two populations, including (1) the main-stem Red River and lower portions of connected tributaries and (2) the Wichita River and its forks upstream of Lake Kemp and Lake Diversion. Opportunities to create additional redundancy are limited within the upper Red River basin based on our findings. The species does not occur downstream of Lake Texoma, and the abiotic settings upstream of Lake Altus and Lake Santa Rosa are not conducive to persistence of the species based on our modeling. The only remaining historical range of Prairie Chub is the upper Washita River, where the species has not been collected in nearly a century (Eisenhour 2004); although this location was outside the scope of our study, it may be a location of interest and warrant future research. In summary, our work suggests that long-term persistence of Prairie Chub populations would benefit from maintenance of existing fluvial connectivity. Hydrological regimes and their effects on fluvial geomorphology and environmental conditions required for spawning and recruitment also are critical for the pelagic broadcast spawner, an aspect
that was not investigated here. Opportunities to improve connectivity and mitigate urban and agricultural land use should be sought if the conservation goal is to increase the spatial distribution of this imperiled fish.

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CONFLICT OF INTEREST STATEMENT
The authors state there is no conflict of interest in this article.

DATA AVAILABILITY STATEMENT
At the time of publication, data were not publicly available from the Oklahoma Department of Wildlife Conservation (questions about data availability, jim.burroughs@odwc.ok.gov).

ETHICS STATEMENT
This study was performed under the guidance of the ETHICS STATEMENT

CONFLICT OF INTEREST STATEMENT
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REFERENCES


**SUPPORTING INFORMATION**

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

**Appendix: Additional Data**

**TABLE A.1** Prairie Chub niche dimensions corresponding with the BAM model shown in Figure 6. Letter codes represent 1-, 2-, and 3-dimension niches that include (1) or exclude (0) biotic, abiotic, and movement niche components. The total length of kilometers of river included in each niche dimension is listed, along with classification of niche dimensions as the source (i.e., alignment of all niche components) or various sinks linked to hybridization (hyb), dispersal (dis), or habitat (hab). Letters A, D, E, and G together represent the Grinnellian niche, letters B, D, F, and G together represent the Eltonian niche, and letters D and G together represent the fundamental niche.

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<th>Movement niche</th>
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<th>Definition</th>
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<td>0</td>
<td>2117</td>
<td>Sink–hab–dis</td>
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<tr>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>Sink–hyb–hab</td>
</tr>
<tr>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>Sink–dis</td>
</tr>
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<td>1</td>
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**FIGURE A.1** Correlation matrix of each abiotic variable used in the analysis. We tested for multicollinearity of two variables (i.e., $r < |0.70|)$, and if they were correlated, then one variable was retained and one variable was dropped. This was done multiple times until we ended with 15 variables leftover. See Table 2 for variable definitions.

**FIGURE A.2** Flow chart of methods used to identify source–sink habitats for Prairie Chub in the Red River basin, including abiotic (yellow), biotic (blue), and movement (red) niche components. Boxes within the central arrow illustrate statistical methods, with input data identified using solid arrows. The dashed arrow from random forest modeling shows that the output from the random forest modeling is used in the integration of movement information into the model. Spatial overlap among abiotic, biotic, and movement niche dimensions illustrate source habitats as illustrated by the Venn diagram from Figure 1.
Figure A.3  Partial dependence plots with locally weighted regression curves (dashed line) and 95% confidence intervals (shaded area) for the other nine variables included (excluding the top six; Figure 4) in the ecological niche model fit to Prairie Chub occurrence. Variables are defined in Table 2 and include (A) percent of estimated discharge stored in upstream reservoirs (UDOR), (B) percent crop land use in network catchment (N_CROP), (C) local stream channel slope (L_SLOPE), (D) low-intensity urban land use in local catchment (L_URBANL), (E) anthropogenic disturbance index (cumu_hci), (F) human population density in local catchment (L_POPDENS), (G) crop land use in local catchment (L_CROP), (H) high-intensity urban land use in local catchment (L_URBANH), and (I) pasture land use in network catchment (N_PASTURE).