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Research Article

Forecasting spread of invasive fish over a largescale network of lakes using local expert knowledge

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Abstract

Understanding spatial distribution patterns is essential to management of invasive species. Aquatic invasive species can be notably challenging to detect due to the substantial effort required to locate them underwater. This limitation has resulted in a lack of timely distribution maps, particularly over vast regions, and hindered efforts to understand, forecast, and manage the proliferation of invasive bigheaded carps (*Hypophthalmichthys* spp.). Much of the Mississippi River basin, particularly the Lower Mississippi Alluvial Valley, provides access to a massive network of interconnected floodplain lakes. In the absence of lake-specific monitoring data on carp occurrence status, we used local expert knowledge, provided by fish managers interviewed virtually, in conjunction with Maximum Entropy (MaxEnt) modeling, to predict bigheaded carps distribution in relation to lake physical characteristics. We predicted widespread carp invasion in more than 60% of over one thousand floodplain lakes, with lake size, inundation, and proximity to rivers closely related to carp presence. The resultant distribution map may be imprecise given the swift proliferation of bigheaded carps and sparse monitoring data, but it offers a baseline upon which presence data and range can be compared. This assessment method is also a resource for identifying priority management and conservation areas and can serve as a first step in conservation planning.

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Key words: Bighead carp, floodplain lakes, MaxEnt, silver carp, species distribution model

Introduction

Invasive organisms can be a major threat to ecosystems by disrupting biodiversity and ecosystem functions (Sala et al. 2000). Competition for vital resources, such as food, water, and habitat, can be exacerbated when invasive species are present (Zwerschke et al. 2018). Human activities have enabled the spread of invasive species, both directly through intentional and unintentional translocations, and indirectly through habitat alterations (Ricciardi 2012). This is especially apparent in aquatic environments where artificial alterations in connectivity and flood regimes facilitate the dissemination and proliferation of invasive aquatic species and complicate the prediction of their spread pathways and distributions (Strayer 2010; Havel et al. 2015; Gallardo et al. 2016).

Understanding the geographical patterns of species distributions is key for the successful management of invasive species (Arim et al. 2006; Elith 2017). In aquatic systems, invaders can be rare, elusive, and nearly impossible to detect early during invasions as their low abundance makes monitoring colonization difficult (Jeliazkov et al. 2022). River fish are particularly difficult to sample due to high effort requirements (Dunn and Paukert 2020). In some cases, this is compounded by the lack of available methods for monitoring rare aquatic taxa (Lucas and Baras 2000; Wei et al. 2023). For example, physical surveillance may be impossible in remote riverine systems, and surveilling invasive species with molecular approaches (e.g., environmental DNA) is impractical over vast areas. This shortcoming could lead to an absence of timely distribution maps, which can hinder efforts to understand, predict, and control the spread of invasive aquatic species (Srivastava et al. 2019). Innovative new approaches are needed that are cost-effective and reliable, especially for species expected to expand swiftly and to have highly detrimental impacts to ecosystem integrity and services.

Bighead carp, *Hypophthalmichthys nobilis* (Richardson, 1845), and silver carp, *H. molitrix* (Valenciennes, 1884), collectively known as bigheaded carps, are invasive fish species in North America. They originated from East Asia and were moved to the Mississippi River basin in the 1970s for biocontrol in aquaculture operations. Likely due to flooding events, by the 1990s they had escaped captivity and began dispersing and reproducing across the Mississippi River basin (Kelly et al. 2011). It was not until 2007 that the first carp management plan was created (Conover et al. 2007; Brown et al. 2025). One goal of the management plan was to control the expansion of carp populations, mainly through monitoring coupled with rapid response programs. However, detecting invasive species such as carp when their abundance is low (i.e., at the invasion front) is difficult (Britton et al. 2011). The slow response and inadequate control methods have allowed bigheaded carps to rapidly expand in range and increase in abundance. Their expansion has elicited significant controversy and has prompted the natural resource conservation sector to allocate hundreds of millions of dollars to mitigate the observed and anticipated harm (Miranda 2023). Bigheaded carps are planktivorous filter feeders that consume substantial quantities of zooplankton and phytoplankton, potentially competing for food resources, directly or indirectly, with several native fish species at earlier life stages (Irons et al. 2007; Sampson et al. 2009; Minder and Pyron 2018; Harris et al. 2022). The significant disturbance they can cause to ecosystem processes has direct effects on native fish assemblages (DeBoer et al. 2018), altering fish assemblage composition and possibly biodiversity. The widespread success of bigheaded carps has been attributed to their extremely fast growth, early maturation, short generation time, highly adaptive nature, and access to eutrophic environments similar to those available in their native range (Miranda 2025).

Much of the Mississippi River basin, particularly the Lower Mississippi Alluvial Valley (LMAV), provides access to massive networks of interconnected floodplain lakes. Floodplain lakes are identified as the primary natural habitat for the development of juvenile bigheaded carps and for rapid growth to adulthood (Kolar et al. 2007; Chapman et al. 2016). At least 1,350 permanent floodplain lakes have been documented in the Lower Mississippi Alluvial Valley, in addition to many more ephemeral sloughs and swamplands (Baker et al. 1991; Miranda et al. 2021). These lakes vary in their level of connectivity to adjacent streams

(Ahmad et al. 2024) and provide hypereutrophic environments that facilitate rapid growth of bigheaded carps (Killgore et al. 2024). Additionally, these lakes offer seasonal access to flowing water, which is important for bigheaded carp reproduction and dispersal. Furthermore, floodplain lakes in the LMAV provide important recreational, economic, and ecological value such as ecosystem services, fishing, hunting, and water supply for agriculture (Jenkins et al. 2010). Agricultural development has severely impacted these floodplain lakes, resulting in increased connections through the creation of drainage canals, redirected connections caused by levee systems development, reduced water quality, and elevated nutrients and turbidity (Miranda et al. 2014).

A key challenge in managing rapidly expanding invasive bigheaded carps in this extensive aquatic network is having information on their spatial distribution. Mapping the known and predicted locations of bigheaded carps is central to guiding effective management and assessing the effect of management actions (Gallien et al. 2010; Elith 2017). For example, predicting which lakes are suitable for carp to inhabit could allow biologists to prioritize early detection and monitoring efforts in vulnerable lakes. A predictive map could also offer a benchmark for comparing the spread of carp.

Conventional lake monitoring used for fish populations can be effective at relatively small scales but becomes expensive at scales as large as the hundreds of lakes scattered throughout the LMAV. One low-cost option for gathering information on carp distribution could be by collecting local expert knowledge, which is accumulated through personal observations by people working in a region. This type of information has been used for documenting species occurrences in previous studies (Anadón et al. 2009) and such data can be collected over large spatial scales with personal interviews, mail surveys, telephone surveys, and internet surveys at a relatively low cost (Meijaard et al. 2011; Barela et al. 2021). This option allows for the synthesis of data across many small-scale efforts to gain insight across large areas, at no additional cost to the small-scale programs. This approach has been successfully used to gather data about invasive species effects and distribution (Azzurro et al. 2019) and estimating species densities (Van der Hoeven et al. 2004). However, local expert knowledge has not, to our knowledge, been used to forecast the potential distribution of invasive fish. Therefore, we set out to use the local knowledge of fish managers to learn about the distribution patterns of bigheaded carps in floodplain lakes of the vast LMAV. Specific objectives included 1) use local expert knowledge and species distribution models to identify lakes that are suitable for bigheaded carps; 2) contrast the physical characteristics of lakes predicted to be suitable and unsuitable for carp; and 3) identify spatial patterns in predicted carp invasion.

Methods

Study region

The LMAV is a large area in the United States that stretches from Cape Girardeau, Missouri until its terminus south of New Orleans, Louisiana. The region is roughly 1,000 km long and up to 150 km wide, spanning an area approximately 100,000 km^2 (Saucier 1994). This region is the Mississippi River's original floodplain, sculpted by thousands of years of fluvial processes such as changing river courses, erosion, and sedimentation (Smith 1996), leaving the valley with an array of unique characteristics that support aquatic biodiversity (Baker et al. 1991).

The LMAV was essentially covered with bottomland hardwood forests before the European arrival (Schoenholtz et al. 2001). About half of the natural bottomland forests were removed between the early 1800s and 1935 to facilitate agriculture (Stanturf 2009). The valley is currently made up of croplands on roughly 75% of its total surface, with water, wetlands, and widely scattered residual forests making up the remaining portion (King and Keeland 1999; Oswalt 2013). Construction of levees and several other types of flood-control projects to safeguard croplands have influenced connectivity between streams and floodplain lakes (Ahmad et al. 2024).

Determining bigheaded carp occurrences with local expert knowledge

To gather bigheaded carp presence data, we relied on the local knowledge available from agency fish biologists. The LMAV includes seven states, and each of these states is organized into multiple contiguous and non-overlapping geographic management areas. Depending on the state, these areas have various names (e.g., management districts, service areas, management regions), but we hereafter refer to these areas as fish management districts. Thus, the LMAV was geographically stratified into the existing fish management districts, and each of the 1,350 permanent lakes in the LMAV identified by Miranda et al. (2021) was matched to its corresponding fish management district. If a lake spanned two districts, such as when divided by a state boundary, it was allocated to the fish management district responsible for its oversight. If multiple districts were accountable for oversight, the lake was assigned to the district with the highest number of access areas. Lakes in each management district were sorted by their distance from a major river (i.e., distance to the nearest river with mean annual flow >170 m^2 s^{-1}; Miranda et al. 2021), and a 20% sample was drawn from the ordered list using systematic random sampling to ensure that the LMAV's connectivity spectrum was represented.

Fish biologists from each fish management district were identified and contacted to schedule interviews regarding bigheaded carp occurrence. Interviews were conducted virtually from January to July of 2023. Interviews began by reciting a script that provided a brief overview of the project and interview procedure (Appendix 1). After this brief introduction, a questionnaire (Appendix 2) was administered for each randomly selected lake. The questionnaire focused on carp occurrence while also inquiring about public perceptions about bigheaded carps and existing carp management strategies used in the lake; however, the latter information is not included here. Google Maps was used throughout the interview to provide images of each lake and their geographic location to avoid any misinterpretation concerning the lake in question. No follow-up questions were asked during the interview to prevent bias resulting from the sequence of the questions (Newing 2011). When the interviewee was unfamiliar with the lake in question, the lake was skipped, and the questionnaire was administered for the next randomly selected lake in the district. Interviewees were considered unfamiliar with carp status if they had never seen the lake firsthand, or if they stated that they did not know about the lake or carp presence in the lake. After completing the questionnaire for each lake, the interviewee was asked if they had information about any lakes immediately adjacent to the focal lake. If so, the questionnaire was administered for those lakes (i.e., similar to adaptive cluster sampling; Thompson 1990). At the end of each interview, biologists were asked to provide datasets or reports that contained information about carp populations or management in their districts. We scoured these data and reports and recorded any additional carp presence for lakes documented.

Forecasting bigheaded carp distribution in lakes of the LMAV

We used Maximum Entropy (MaxEnt) presence-only modeling to predict the distribution of bigheaded carps because absence data were deemed unreliable. In place of absences, MaxEnt uses background points sampled from the study area for which presence is unknown, i.e., pseudoabsences (Elith et al. 2006; Merow et al. 2013). Environmental variables at pseudoabsences are compared to environmental variables where a species occurs to estimate suitable species site conditions (VanDerWal et al. 2009; Papeş et al. 2016). MaxEnt then assigns predicted habitat suitability values across sites, where values closer to 0 indicate less suitable habitat and a lower probability and values closer to 1 indicate a higher suitability and higher probability of species presence. The predicted suitability reflects the realized distribution of already invaded lakes along with forecasts of lakes that are likely to be invaded in the future. Numerous environmental variables can affect fish occurrence in vast floodplains such as the LMAV, although a select few are typically investigated as they serve as indicators of many others (Table 1). Variables such as lake size and lake morphology have been shown to influence fish species distributions (Górski et al. 2013), and landcover surrounding water has been shown to influence water quality and fish assemblage composition (Dembkowski and Miranda 2014). Additionally, lake connectivity can influence inundation (Trigg et al. 2013; Wu and Lane 2017) and transport of materials and fishes (Borselli et al. 2008; Liu et al. 2020), potentially influencing carp distribution. Therefore, we gathered environmental variables from two existing datasets that provided morphometry, landcover, and connectivity of each LMAV lake. The morphometry and landcover datasets were obtained from Miranda et al. (2021), who used remote sensing to characterize lake morphometry and surrounding landcover. The connectivity dataset was obtained from Ahmad et al. (2025), who used Geographic Information Systems analyses to describe connectivity of lakes throughout the LMAV.

Highly correlated environmental variables can affect model performance (De Marco and Nobrega 2018). To mitigate correlations before using predictors in our species distribution model, we used logistic regression with a Least Absolute Shrinkage and Selection Operator (LASSO) to select variables, avoid multicollinearity, and reduce dimensionality of a model via a penalized likelihood approach (Tibshirani 1996; Jiang et al. 2016). LASSO identifies which variables may best predict an outcome by minimizing the residual sum of squares with a penalty (i.e., lambda) to the model coefficients which in turn shrinks coefficients of unimportant covariates to 0 (Tibshirani and Friedman 2020). We used a lambda value that resulted in minimum error and retained covariates with coefficients greater than 0 to be used in the species distribution model. The LASSO model was conducted using the *glmnet* R package (Friedman et al. 2010) in program R v. 4.3.3 (R Core Team 2023).

The MaxEnt model was applied to 1,086 lakes in the LMAV that had complete environmental variable data available. We used presence records obtained from the interviews, and we randomly created 10,000 pseudoabsences from lakes that had no known presence records (Barbet-Massin et al. 2012). For each carp presence and pseudoabsence location, we extracted values associated with predictor variables and used this information in the MaxEnt model (*dismo* R package, Hijmans et al. 2011; *rJava* R package, Urbanek 2023), which was run using default settings and no interactions between predictors. We calibrated models using 5-fold cross validation and used the resulting models to predict habitat suitability among all lakes.

To assess model performance, we used the *ROCR* R package (Sing et al. 2005) to calculate area under the receiver operating curve (AUC-ROC) and true skill statistic (TSS), and the *ecospat* R package (Broennimann et al. 2023) to calculate the Boyce index. The AUC-ROC value is a threshold-independent measure of overall model performance that compares the true positive rate to the false positive rate, or the probability that the model correctly predicts presence/absence (Hernandez et al. 2006). A higher AUC-ROC value indicated that the model's predicted habitat suitability was consistently higher at known presence locations than at pseudoabsences, with values ranging from 0 to 1. AUC-ROC values greater than 0.75 were considered indicative of a well performing model (Elith 2002), and values around 0.50 indicated random predictions (McGarvey et al. 2018). The TSS used both false absences and false presences to evaluate model performance and was calculated as the sum of sensitivity and specificity, minus 1. TSS values range from -1 to 1 and values greater than 0.60 were considered adequate (Coetzee et al. 2009). The Boyce index splits the study area into several bins, then calculates the ratio of presences to background area (Hirzel et al. 2006). A well performing model, which should predict higher habitat suitability in areas or bins with more recorded presences, will have a Boyce index value closer to -1 or 1. Boyce index values near zero indicate a model that produced random predictions.

Addressing objectives 1–3

To identify lakes potentially suitable for bigheaded carps (objective 1), we transformed the continuous MaxEnt output into a binary map of predicted suitable/unsuitable lakes using a maximum model sensitivity plus specificity threshold (Liu et al. 2013). While various thresholds are available and can alter the proportion of lakes predicted to be suitable for carp, we used this threshold as it is commonly used in ecology for species presence-pseudoabsence problems and aims to maximize the number of correctly predicted presences and absences (Liu et al. 2013). We avoided other thresholds, for example a maximum sensitivity threshold, which would increase the proportion of lakes predicted to be suitable for carp, but would come with the tradeoff of increased false positives. We used a permutation analysis of variance (PERMANOVA) to test if the lake characteristics selected by the MaxEnt model differed between lakes that were predicted to be suitable or unsuitable for bigheaded carps (objective 2). Primary drivers were identified as the three variables with the highest percent contribution to the model and permutation importance of environmental variables. Percent contribution refers to the contribution of each environmental variable to the overall fit of the model and is influenced by the order of variables used. Percent contribution is calculated by determining how much the model fit improves with the addition of each variable. Permutation importance is a measure of what variables are most important in making predictions, and it is not influenced by the order of variables. Permutation importance is determined by shuffling the values of one variable and determining if that results in changes to model accuracy (i.e., if the shuffling of a variable leads to a decreased AUC, that variable is deemed important). Drivers were log transformed to reduce dispersion and then normalized (mean = 0 and SD = 1) to achieve a common scale. The PERMANOVA was then applied to a similarity matrix constructed with Euclidean coefficients and implemented using *vegan* R package (Oksanen et al. 2022). If the PERMANOVA identified significant differences between the two groups of lakes, mean plots were used to visualize differences in environmental drivers. Lastly, we applied the Global Moran's I in ArcGIS Pro to test whether predicted carp presence was spatially random within the LMAV (objective 3). This index indicates the level of spatial autocorrelation in carp presence, signifying whether values tend to cluster together (positive spatial autocorrelation) or are dispersed (negative spatial autocorrelation) spatially across the LMAV, essentially showing how similar neighboring locations are to each other in terms of carp presence; a value close to zero indicates a random distribution.

Results

A total of 26 interviews were completed with agency fish biologists from 13 fish management districts throughout the LMAV. We administered the questionnaire for 131 of the 1,086 lakes and recorded 64 carp presences (48.9% of sampled lakes) from lakes within the study area (Fig. 1; Suppl. material 1: table S1). Interviews lasted 15 min to 2 h, depending on how many lakes were in each fish management district. The systematic random selection of lakes resulted in about half of the lakes chosen being in private lands, and therefore outside of fish management district jurisdiction. In most cases, respondents lacked specific information regarding carp presence in lakes within privately owned land, but respondents were often able to provide information about carp presence in adjacent public lakes. Additionally, twenty-four of these presence records came from supplementary information provided by agency biologists (i.e., datasets, reports).

The LASSO model implemented with logistic regression identified nine environmental variables suitable for inclusion as covariates in the MaxEnt model. These variables included lake area, lake length, probability depth, inundation index, agriculture cover, batture, disconnectedness, distance to river, and nearest neighbor (Table 1). Pearson's product moment correlations among these covariates were generally low (i.e., $r < 0.60$; Suppl. material 2: fig. S1). The MaxEnt model had AUC-ROC values ranging from 0.78 to 0.88, TSS values ranging from 0.60 to 0.70, and Boyce index values ranging from -0.71 to 0.87 across each fold from the 5-fold cross validation. The AUC-ROC value was 0.87, TSS was 0.62, and Boyce

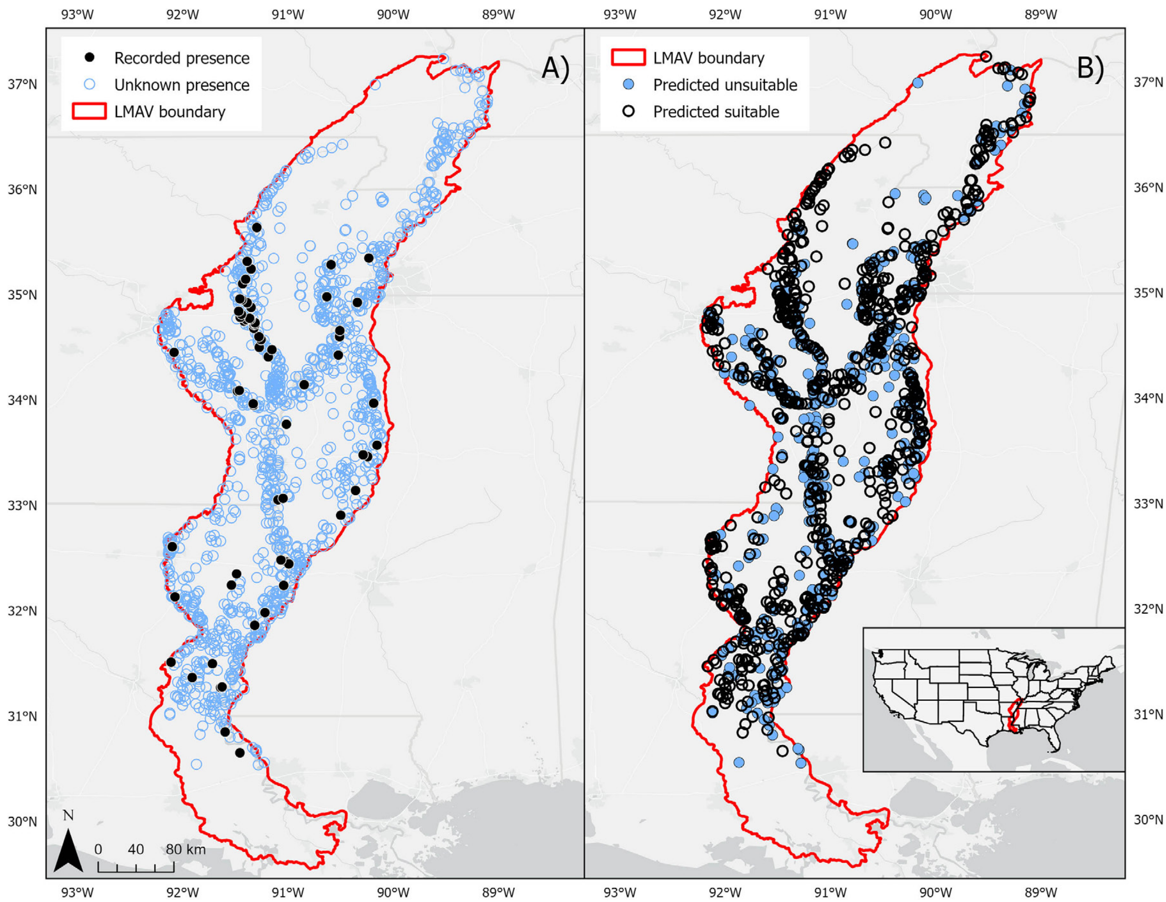

Figure 1. (**A**) bigheaded carp (*Hypophthalmichthys* spp.) presences recorded during interviews with biologists and (**B**) lakes predicted suitable and unsuitable for carp presence in floodplain lakes of the Lower Mississippi Alluvial Valley.

Table 1. Hypothesized lake characteristics that could be important in determining bigheaded carp (*Hypophthalmichthys* spp.) distribution in lakes of the Lower Mississippi Alluvial Valley (LMAV). CV = coefficient of variation; * = retained by Lasso procedure. Sources: Miranda et al. (2021), Ahmad et al. (2024).

Variable	Definition	Mean	CV	Rationale
Area*	Surface area of lake polygon feature (ha).	76	362	Surface area are correlated to fish assemblages in the LMAV (Dembkowski and Miranda 2014).
Mean width	Mean of several width measurements taken approximately every 100 m along the length of the lake (m).	172	117	Lake size and shape can influence fish species distributions (Górski et al. 2013).
Length*	The length of a line drawn through the center of the lake along its longest axis (km).	3.0	138	Elongated lakes tend to have strong interactions with the terrestrial ecosystem, allowing more nutrient input and possibly access corridors (Miranda et al. 2014).
Length-width ratio	Length divided by mean width.	27	158	Lake shape can influence fish species distributions (Górski et al. 2013).
Perimeter	Length of shoreline surrounding a lake (km).	7.7	165	Lake size and shape can influence fish species distributions (Górski et al. 2013).
Inundation index*	Relative frequency of lake inundation from 1983 to 2011, with 100 indicating the entire lake is always fully covered by water and values closer to 0 indicating that the area covered by water is reduced to nearly nil.	42	45	Flooding is strongly linked to presence of young-of-year bigheaded carp. Inundation can also increase connectivity and provide corridors for carp movement (DeGrandchamp et al. 2008; Gibson-Reinemer et al. 2017).
Shoreline development index	Ratio of lake shore length to the circumference of a circle with lake area.	3.0	54	Lake size and shape can influence fish species distributions (Górski et al. 2013).
Agriculture cover*	The percent of area within a 1-km buffer around the lake polygon that is comprised of agricultural cover (%).	43	70	Eutrophication due to excessive agricultural runoff can lead to anoxia and fish death (Pathak and Pathak (2012).
Forest and wetland cover	The percent of area within a 1-km buffer around the lake polygon that is comprised of forest or wetland cover (%).	41	70	Wetlands may provide a corridor between rivers and lakes, and reduce excess nutrient concentrations of through flowing water, influencing water quality and possibly carp distribution (Verhoeven et al. 2006). Lakes with disturbed riparian zones are vulnerable to excessive sedimentation, reduction in depth, and shifts in fish assemblage, possibly providing carp with the opportunity to invade (Dembkowski and Miranda 2014).
Batture*	Whether or not the lake is protected from major floods by a levee or floodwall, designated by a 0 if protected and a 1 if not protected.	0.53	94	Lakes regularly exposed to floods, like those between levees and the Mississippi River (batture) are more likely to be connected to waterways (DeGrandchamp et al. 2008; Gibson-Reinemer et al. 2017).
Disconnectedness*	Maximum number of consecutive months that a lake remained disconnected from a river during 2000–2022.	156	59	Carp cannot complete their lifecycle in lakes and must travel from lake to river to spawn. Greater disconnection may make it more difficult and less likely for invasion to occur in lakes that are disconnected (DeGrandchamp et al. 2008).
Longitude	The east-west position of a lake.	-91.04	0.01	Geographic location can influence water quality (Liu et al. 2010), and resource distribution and access, possibly influence carp presence in lakes.
Latitude	The north-south position of a lake.	33.79	4	Geographic location has been shown to influence water quality (Liu et al. 2010), and resource distribution and access, possibly influence carp presence in lakes.
Nearest neighbor*	Straight line distance to the nearest lake (km).	3.0	97	Lakes located close to other lakes that have been invaded may be more likely to be invaded (Shaker et al. 2017)
Distance to river*	Shortest network distance between a lake and a river with mean annual flow of at least 170 $m^2 s^{-1}$ (km).	26	129	Bigheaded carps have been documented in rivers throughout the Lower Mississippi Alluvial Valley (Chapman 2003), so lakes closer to those rivers may be more likely to have carp present.
Probability depth*	Probability of the lake maximum depth being > 2 m.	0.63	29	Shallow depth and backwaters have been associated with higher bigheaded carp density (MacNamara et al. 2018; Glubzinski et al. 2021).

index was 0.83 when the model was run using all data. Lake area, inundation index, and distance to river had the highest percent contribution to the model, and lake area, inundation index, and lake length had the highest permutation importance (Table 2). Smaller lakes that had high inundation potential and were closer to rivers were more likely to have carp present (Fig. 2).

Table 2. Percent contribution and permutation importance of covariates when the final MaxEnt model was run to predict bigheaded carp (*Hypophthalmichthys* spp.) presence throughout the Lower Mississippi Alluvial Valley floodplain (LMAV) lakes. Variables are as defined in Table 1. Percent contribution refers to contribution of each covariate to overall model fit, whereas permutation importance is calculated by shuffling values of one covariate and observing the change in area under the receiver operating curve. We interpret lake area, inundation index, and distance to river as the three covariates representing main drivers of bigheaded carp distribution in lakes of the LMAV based on inflection points in percent contribution and permutation importance.

Variables	Percent contribution	Permutation importance
Area	36.0	54.80
Inundation index	19.3	16.60
Distance to river	18.4	3.50
Nearest neighbor	9.7	6.70
Agriculture cover	7.0	5.30
Length	5.6	8.60
Probability depth	2.6	1.00
Disconnectedness	1.3	3.60
Batture	0.1	0.00

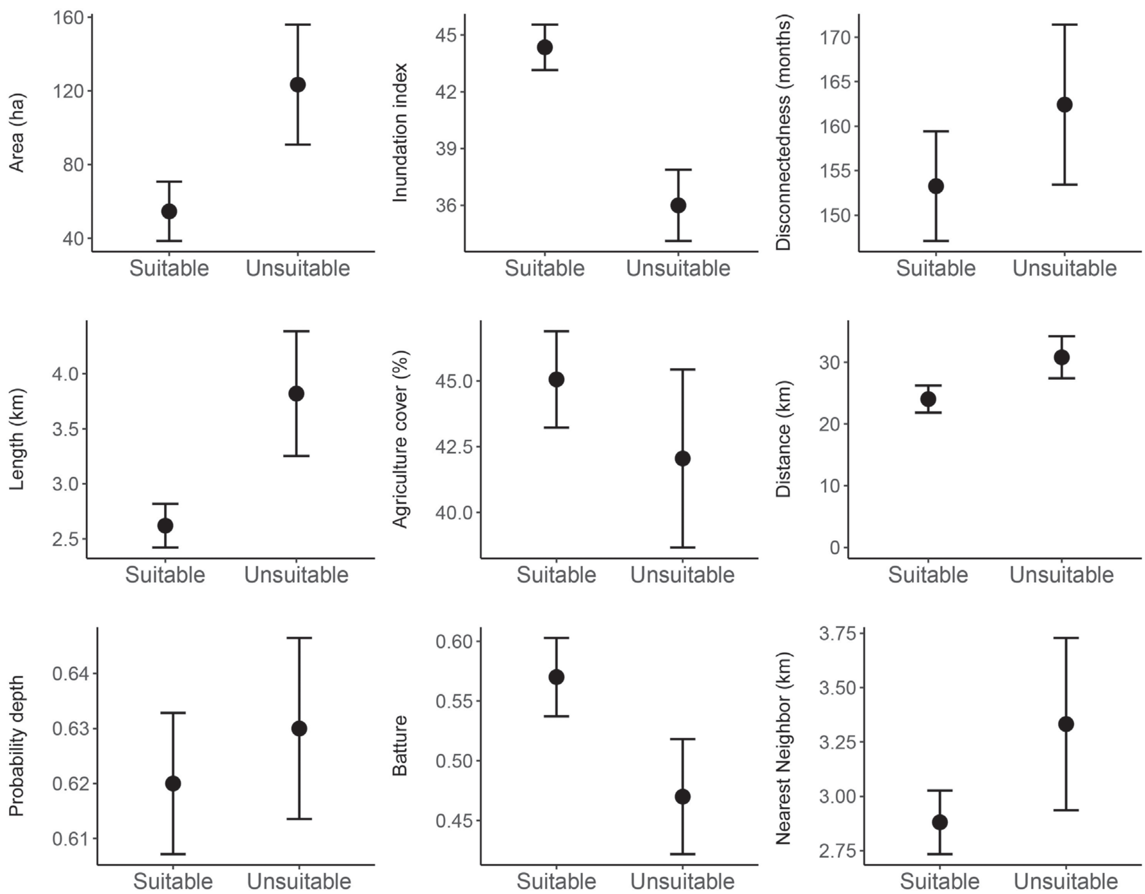

Figure 2. Mean ± 95% confidence intervals lake attributes in relation to predicted bigheaded carp (*Hypophthalmichthys* spp.) status in 1,089 lakes of the Lower Mississippi Alluvial Valley, as of 2023.

Adding the maximum model sensitivity to the model specificity threshold resulted in a threshold of 0.24, which was used to transform continuous habitat suitability values to binary predicted presences (>0.24) and absences (<0.24). This transformation forecasted that roughly 62% of the lakes in the LMAV supported bigheaded carps (Fig. 1b). The environmental characteristics were different between the lakes likely to support carp and lakes not likely to support carp (PERMANOVA Pseudo-F = 21.3, P = 0.001). Each of the nine environmental factors varied in lakes that were predicted to be suitable for carp and those that were not. The most pronounced disparities reflected the MaxEnt model, which included lake area, lake length, inundation index, and distance from lake to major river, except that batture also emerged as a disparity (Fig. 2). Smaller lakes with high inundation potential that were closer to rivers were more likely to have characteristics suitable to carp invasion (Suppl. material 3: fig. S2).

We observed a geographic pattern in predicted carp habitat suitability across the LMAV. The Moran's I index value was 0.12, revealing a positive and significant (P < 0.001) spatial autocorrelation, indicating that lakes that may support carp tend to cluster. In addition, nearest neighbor was moderately important in predicting suitability in the MaxEnt model. Clustering predominantly occurred along major rivers (Fig. 1). At the vast scale of the LMAV, no other clustering was evident.

Discussion

Bigheaded carps are widespread and continue to expand their distribution in the Mississippi River basin, creating significant risks to the sustainability of native freshwater ecosystems (DeBoer et al. 2018; Miranda 2023). Our study has produced the first published map that documents the potential spread of bigheaded carp across the vast alluvial valley of the Lower Mississippi River. Although by definition pseudoabsences may or may not represent true absences, we are confident that our pseudoabsences are reasonably accurate because 1) carp invaded decades ago, allowing biologists and the public ample opportunities to detect the fish, and 2) bigheaded carps are large and conspicuous, especially silver carp, which frequently leap out of the water. Additionally, our model was developed using several methods recommended to generate more accurate predictions of suitability (Yackulic et al. 2013). These methods included collecting presence data using standardized sampling, considering how carp detection varies with environmental variables such as lake area, and providing all necessary information to evaluate results (e.g., response curves).

We acknowledge that while the map may be imprecise given the swift proliferation of bigheaded carps and sparse monitoring data, the map is still an informative management tool. Its value lies in revealing broad patterns, core areas, prioritizing surveillance and monitoring, guiding interventions, and supporting communication and planning. The map shows that this expansion can occur throughout this extensive floodplain given the lake characteristics available to support occurrence of carps in this region. Considering that these lakes offer bigheaded carp preferred habitats and that carps have access to a diversity of river systems to facilitate reproduction and dispersal, we anticipate that dispersal throughout the Mississippi basin is likely, barring obstacles (e.g., dams) or infrequent connections (Ahmad et al. 2024). Stafford (2024) observed several long-range dispersal events by silver carp in the LMAV, including a single fish traveling 1,210 km in less than 1 year. Ahmad et al. (2024) reported that most lakes in the LMAV became disconnected, with some disconnections lasting up to 20 consecutive years. This should be sufficient to allow local extinction, as carp are short-lived (i.e., 8–10 years, Killgore et al. 2024) and unable to reproduce in lentic systems. Barriers in the discharge channels of these lakes may impede future repopulation, and harvesting programs may accelerate extinction. Deployment of monitoring and management activities can be informed by the resulting distribution map.

In the absence of lake-specific monitoring data on carp occurrence status, we used local expert knowledge in conjunction with MaxEnt to predict bigheaded carp potential occurrences based on lake physical characteristics. We predicted widespread carp invasion throughout LMAV lakes with lake size, inundation potential, and proximity to rivers closely related to carp distribution in the LMAV. Most lakes likely to have carps were < 25 ha in size and were <5 km from a river. We suspect that these small lakes may have a higher likelihood of carp occurrence because their river proximity exacerbates the chance of recurring flooding that allows for carp dispersal and occupancy. A potential bias is that carp may be more visible in smaller lakes because these waters are easier to scan and have a higher proportion of littoral area, which is their preferred environment (Besson et al. 2024). Additionally, because many of the small lakes were predominantly positioned along the White River in Arkansas, a region targeted for carp removal, enhanced surveillance may have resulted in increased local awareness in this northwestern region of the LMAV.

The relationships between inundation index, distance to rivers, and predicted habitat suitability are intuitive. Inundation index is a measure of long-term fluctuation in lake volume. Predicted habitat suitability was generally positive, where lakes with higher inundation index were predicted to be more likely to be suitable for bigheaded carp. A high inundation index means it is more likely that a lake remains close to full volume over time. Bigheaded carps are tolerant of poor water-quality (Kolar et al. 2007), so they can persist in floodplain lakes as long as lakes do not go dry, thus potentially explaining the importance of inundation. The relationship between distance to river and predicted habitat suitability was negative, where lakes with shorter distances to rivers were predicted more likely to have habitat suitable for carp. Lakes that are closer to rivers have a higher probability of initial invasion simply because the carp have more opportunities to reach them. However, given bigheaded carp cannot reproduce within lentic waterbodies (Kolar et al. 2007), hydrologic connections likely enable carp to exit lakes, spawn in adjacent rivers, and re-invade either through the direct channel connections or connections made by over-bank flooding.

We determined a significant geographic pattern existed in predicted carp occurrence across the LMAV, with nearly two thirds of lakes predicted to be suitable for carp often clustering in the northwest LMAV along the White River. Similarly, nearest neighbor was moderately important in predicting lake suitability. Because bigheaded carp were first released near this region, they have had a longer period to invade. Moreover, fish scientists in this region may have developed more programs and competence for surveillance of bigheaded carp populations. Spatial clustering of predicted carp occurrences within the river system of initial introduction could foreshadow that bigheaded carps will eventually invade higher densities of lakes throughout the LMAV.

Using local expert knowledge to gather invasive fish presence data was cost-effective and relatively low effort, but there were challenges. First, local expert knowledge is based on personal observations, which can be influenced by individuals' capacity to recall information and by the time elapsed since the waterbody was last visited. Moreover, respondents likely had varying tenures in their position, which also could have affected their knowledge of presence. We did not attempt to account for any tenure effects, as the relationship between tenure and knowledge, although presumably positive, was not documented. Second, because lakes were randomly selected, fish biologists were unable to provide information for roughly half of the lakes selected because they were on private land or otherwise not managed by their agency. While we could have obtained a larger sample size by collecting information only for lakes that biologists had knowledge about, it was important to select lakes at random to ensure that the sample of study lakes was representative of the breadth of lakes in the LMAV, reducing bias associated with agency management foci, and increasing the reliability of our results. Future studies may incorporate private landowners to obtain presence data for inaccessible lakes. Another drawback of using local expert knowledge is that it does not allow for the collection of absence data. Presence-absence data have been shown to be more reliable than presence-only data because presence-only runs the risk of not detecting fish that are actually present, such as where invasive species occur at low densities (Elith et al. 2020). Despite these challenges, its cost-effectiveness could make this method an excellent choice for large-scale work. The method can also be used to create new or to update distribution maps in other parts of the Mississippi basin, or to explore other elements of distribution, like size structure or temporal distribution.

The potential for widespread carp distribution identified in the LMAV highlights the need for rapid and aggressive management action. The map we produced offers a baseline for which data collection on presences and range expansion can be compared, and a resource for identifying priority management and conservation areas. Our results could be applied in many ways, but we see them used primarily as a first step in conservation planning. For instance, agencies may sample lakes predicted to not support carp to confirm their absence. They may then develop preventative measures against invasion such as barriers or other exclusionary constructions. Alternatively, agencies may target lakes predicted to support carp to confirm presence and then decide what management action would be most beneficial to minimize their effects.

Regardless of carp predicted status, continued monitoring through on-site surveys or local expert knowledge surveys such as ours are necessary to validate and update our estimates before and after conservation strategies are implemented. Modeling bigheaded carp distribution in the hundreds of LMAV oxbow lakes was an important step that can facilitate early detection and can guide on-site monitoring. This study offered a framework for an economical instrument that facilitates an initial assessment of large-scale invasive species monitoring.

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Author contribution

MP contributed to the research conceptualization, sample design and methodology, carried out data collection, performed data analysis and interpretation, ethics approval, and writing both the original draft and reviews and editing. LEM contributed to the research conceptualization, sample design and methodology, data collection, interpretation, ethics approval, funding provision and writing both the original draft and reviews and editing. MRB contributed to data analysis and interpretation, ethics approval, and review and editing. CGD contributed to sample design and methodology, data analysis and interpretation, ethics approval, and review and editing. LMB contributed to sample design and methodology, ethics approval, and review and editing. DR contributed to sample design and methodology, ethics approval, and review and editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary material.

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Appendix 1

Interview introduction script.

I am a graduate student at Mississippi State University. My thesis project is on bigheaded carp distribution patterns in the Lower Mississippi Alluvial Valley. Through a short survey I am gathering data on carp presence and lake characteristics that influence carp distribution. I will recommend management strategies based on the results.

The questions I ask you will be mostly closed ended. For each lake, I will read out the questions and record your responses. I will share a map of the lake to be sure we are talking about the same place. After each round of questions, I will ask if there are any adjacent lakes within a certain area, shown on the map, that you have information about. I will then administer the questionnaire for those lakes as well. You may ask for clarification at any time. I will repeat the questionnaire for as many lakes as we can within our allotted interview time. Do you have any questions before we begin?

Appendix 2

Interview questionnaire.

Lake ID:
State and management district:

Effort/Detectability

1. What is the name of this lake?

2. How long has your agency been responsible for monitoring this lake?
   - <1 year
   - 1–5 years
   - >5 years

3. How many times per year is this lake visited by a fisheries professional from your district?

   - >2 per week
   - 1 per week
   - 1–3 per month

- 2–10 per year
- 1 per year
- 1+ in 5 years

Carp Presence

4. Have you seen silver or bighead carps or signs of them in this lake? If so, how often?

- never
- rarely (1–2 times)
- commonly (2+ times)

5. Have there ever been reports of silver or bighead carp in this lake from other citizens, anglers, landowners, or other fisheries professionals?

- yes
- no

6. If yes to 4 or 5, how long have the silver or bighead carp been in this lake?

- <2 years
- 2–5 years
- >5 years

7. In the last 5 years, have you noticed any changes in the fishery or fish community that you attribute to bigheaded carp?

- yes
- no

8. Are there any water control structures on the lake?

- yes
- no

9. If yes, where are the water control structure(s) on the lake located?

Current Management Efforts (to be asked at the end of the interview)

10. Are there currently any invasive carp management strategies being implemented in your district? If so, what strategies?

11. What percent of oxbow lakes have carp control strategies in place?

12. Have there been any complaints about Silver Carp or Bighead Carp from the public that use lakes in your district?

Supplementary material 1

Geo-referenced bigheaded carp presence in lakes throughout the Lower Mississippi Alluvial Valley recorded during interviews with fish biologists

Authors: Michaela Palmieri, Leandro E. Miranda, Melanie R. Boudreau, Corey G. Dunn, Leslie M. Burger, Dennis Riecke

Data type: docx

Link: https://doi.org/10.3391/ai.2026.21.2.190069.suppl1

Supplementary material 2

Pearson's product-moment correlation coefficients between environmental covariates considered for evaluating bigheaded carp presence in lakes throughout the Lower Mississippi Alluvial Valley

Authors: Michaela Palmieri, Leandro E. Miranda, Melanie R. Boudreau, Corey G. Dunn, Leslie M. Burger, Dennis Riecke

Data type: docx

Link: https://doi.org/10.3391/ai.2026.21.2.190069.suppl2

Supplementary material 3

Relationships between MaxEnt habitat suitability values (y axis) and covariates (x axis; Table 2.1) included in the species distribution model of bigheaded carp presence in lakes throughout the Lower Mississippi Alluvial Valley

Authors: Michaela Palmieri, Leandro E. Miranda, Melanie R. Boudreau, Corey G. Dunn, Leslie M. Burger, Dennis Riecke

Data type: docx

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