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Agricultural conservation may not help Midwestern US freshwater biodiversity in a changing climate



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Best management practices (BMPs) for agricultural conservation have been promoted in the US
- BMPs target at future environmental resilience but still lacking rigorous biological evaluation
- We projected agricultural conservation to benefit non-point source pollution control, not future freshwater biodiversity
- Future agricultural conservation should more restore natural patterns of temperature and flow for freshwater biodiversity
- Future agricultural conservation on biodiversity should also consider keeping local stakeholders engaged

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ABSTRACT

Global climate change and agricultural disturbance often drive freshwater biodiversity changes at the regional level, particularly in the Midwestern US. Agricultural conservation practices have been implemented to reduce sediment and nutrient loading (e.g., crop rotation, cover crops, reduced tillage, and modified fertilizer application) for longterm economic sustainability and environmental resilience. However, the effectiveness of these efforts on freshwater biodiversity is not conclusive. In this study, we used the Kaskaskia River Watershed, Illinois as an example to evaluate how agricultural conservation practices affects both taxonomic and functional diversity under climate changes. The measures of trait-based functional diversity provide mechanistic explanations of biological changes. In specific, we model and predict 1) species richness (SR), 2) functional dispersion (FDis), and 3) functional evenness (FEve). FDis and FEve were based on ecology (life history, habitat preference, and trophic level) and physiology (thermal preference, swimming preference, etc.). The best random-forest regression models showed that flow, temperature, nitrate, and the watershed area were among the top predictors of the three biodiversity measures. We then used the models to predict the changes of SR and FDis under RCP8.5 climate change scenarios. SR and FDis were predicted to decrease in most sites, up to 20 % and 4 % by 2099, respectively. When agricultural conservation practices were considered together with climate changes, the decreasing trends of SR and FDis remained, suggesting climate change outweighed potential agriculture conservation efforts. Thus, climate-change effects on temperature and flow regimes need to be incorporated into the design of agricultural practices for freshwater biodiversity conservation.

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1. Introduction

Global climate change is driving ecosystem reorganization (Antão et al., 2020; Comte et al., 2021). Freshwater ecosystems are among the most threatened in the world as they are relatively isolated, fragmented, and oftentimes heavily exploited (Woodward et al., 2010). Freshwater fish have the highest extinction rates among vertebrates (Grooten and Almond, 2018). In rivers, thermal and flow regimes are top factors altered by climate change (Jones, 2011; Webb, 1996) that are driving ecosystem changes, including displacement of sensitive fishes with more tolerant species (Comte et al., 2021). In global temperate regions, the US Mississippi River Basin is a hotspot of freshwater fish diversity, supporting recreational and commercial fisheries and various ecosystem services (Allan et al., 1997; Pracheil et al., 2013). Climate change projections on freshwater fish in the Mississippi River basin can be exemplary for other river basins globally.

Regional land-use can interact with climate change to strongly affect freshwater biodiversity. This interaction can exert additive, synergistic, or antagonistic impacts on riverine ecosystems (Radinger et al., 2016). Agriculture is the greatest driver among all land-use changes, encompassing over 40 % world's land surface, including the majority of the Mississippi River basin (Raven and Wagner, 2021). In agricultural landscapes, the impacts of climate change on temperature and flow can be intensified due to 1) increased solar radiation following the reduction of riparian cover (Caissie, 2006), 2) altered flow patterns from subsurface drain tiles and surface ditches (Blann et al., 2009), and 3) decreased groundwater recharge after water extraction for irrigation (Loheide and Gorelick, 2006). Moreover, nutrient input from fertilizers and toxicants from pesticides can further stress the fragile riverine communities (Op de Beeck et al., 2017; Wang et al., 2020).

To improve water quality in agricultural watersheds in a changing climate, best management practices (BMPs) have been promoted in the US, which mainly aim to reduce non-point source pollution, including sediment and nutrient loading, to ensure long-term economic sustainability and environmental resilience (Bekele et al., 2012). Within agricultural landscapes, excessive nutrient input through runoff, siltation from soil loss, and more extreme temperature changes from loss of the riparian zone all could negatively impact stream fish communities locally, thus BMPs potentially could help with both water quality and freshwater biodiversity (Dala-Corte et al., 2016; Mantyka-Pringle et al., 2016; Larentis et al., 2022). However, the effectiveness of such conservation efforts on local aquatic biodiversity has yet to be rigorously evaluated and confirmed, especially in a changing climate (Allan, 2004; South et al., 2019). In theory, agricultural conservation using BMPs, by the name itself, should create a balance between agricultural production and ecosystem equilibrium. In the Midwestern US, Fraker et al. (2020) projected the effects of scheduled BMPs such as erosion control and nutrient management in the Western Basin of Lake Erie. With BMPs simulated during the years 2020-2065, they found large-bodied, coolwater species would suffer more, while small-bodied warmwater species would benefit more under climate change, despite the fact that BMPs would effectively improve overall water quality. Together, results from climate modeling projections of Fraker et al. (2020) suggest negative impacts of BMPs on freshwater communities when coolwater species play an important role in local communities. However, what if BMPs are applied in a watershed that mostly consists of warmwater species, such as the Mississippi River Basin? Will BMPs be able to benefit both water quality and freshwater biodiversity?

To evaluate the effectiveness of conservation efforts on riverine ecosystems under climate change, taxonomic diversity indices based on presence and abundance data have been important tools (Oberdorff et al., 2011). Unfortunately, these biodiversity measures cannot identify the mechanism (s) responsible for changes to the community behind the numbers, such as the replacement of sensitive species by tolerant ones, or the invasion of nuisance species (Murdoch et al., 2020). In the last two decades, traitbased community ecology has gained greater attention when modeling biodiversity responses under climate change. Because it can incorporate both taxonomic diversity, and the physiological, morphological, or life-history characteristics of each species (Mcgill et al., 2006; Poff, 1997; Zakharova et al., 2019). Such an approach offers the potential to reveal mechanistic explanations for community changes, which can be generalized across different ecosystems (Frimpong and Angermeier, 2010; Olden et al., 2006). Functional diversity indices, developed from the quantification of functional traits (Petchey and Gaston, 2006), can elucidate species' roles in ecosystem functioning, thus offering better explanatory power of how climate and land-use drive ecosystem changes (Cadotte et al., 2011). When it comes to conservation and restoration, functional diversity could be a better choice for decision-making processes (Malaterre et al., 2019).

To assess how climate and agriculture can affect riverine biodiversity, we used the Kaskaskia River Watershed in Illinois, within the Mississippi River Basin in the Midwestern US as an example, due to its over 50 years' standardized fish sampling program, extensive monitoring on water quality, heavily altered riverine environment by agriculture, and existing species abundance and occupancy modeling (Cao et al., 2016; Acero Triana et al., 2021) for the foundation of this trait-level and community-level modeling. As such, we sought to quantify 1) the current spatial distribution of biodiversity (i.e., functional and taxonomic diversity) for fish communities, 2) the key environmental drivers on fish biodiversity, 3) the potential changes in fish biodiversity under future climate, and most importantly, 4) whether agricultural conservation practices could help with fish biodiversity conservation under climate change.

2. Materials and methods

2.1. Study area

The Kaskaskia River Watershed is a major tributary of the Mississippi River, located in central and southwestern Illinois, US (Fig. 1). It drains 14,880 km², 10.2 % of Illinois (USACE, 2017). Prior to European settlement in the 1700s, the watershed was mainly covered by prairies and forests. Today, the land cover has been altered to predominately croplands (63 %), mostly corn and soybeans. Forest and grasslands have decreased to 16 % and 9 %, respectively, while urban or impervious surface has increased to 9 % (USDA, 2016). Besides land cover, many meandering streams and rivers have also been channelized and dredged, with drain tiles installed in most farmland (Blann et al., 2009). Two large reservoirs, Lake Shelbyville and Carlyle Lake, were constructed on the main channel during 1960–1970s (Shasteen et al., 2013). Changes in land cover and flow regime accelerated the fragmentation and degradation of aquatic ecosystems in the Kaskaskia River Watershed (Acero Triana et al., 2021; Larimore and Bayley, 1996).

2.2. Data source

2.2.1. Fish sampling data

Fish data were combined from two datasets: 1) the Intensive Basin Survey monitored by Illinois Department of Natural Resource (IDNR) and Illinois Environmental Protection Agency (IEPA); 2) Monitoring and Assessment of Aquatic Life Program from Illinois Natural History Survey (INHS). Sampling sites were determined by fisheries biologists, based on geology, biodiversity, pollution, and historical sampling records (Cao et al., 2016). Fish sampling followed standard IDNR protocols (IDNR, 2010) using an electric seine or backpack electrofishing, as well as boat electrofishing, during May-October from 1952 to 2015 (Cao et al., 2016). To avoid sampling inconsistency and represent the latest fish community composition across the Kaskaskia River Watershed, we only included the latest year records per sampling site after 1995. Due to the productive and speciose nature of Midwestern streams and rivers (Smith et al., 2010), we further excluded fish samples with <20 individuals per site and <5 species per site to avoid any bias from improper field operations (Cao et al., 2015). These criteria resulted in 91 fish sites in 1st-4th order streams and rivers distributed evenly across the entire watershed.



Fig. 1. Land cover of the Kaskaskia River Watershed.

2.2.2. Environmental data

We grouped environmental data into two categories: 1) variables affected by climate and agricultural practices, including those describing water quality, water temperature, and flow, referred to as climate-related variables hereafter, and 2) non-climate variables that were not expected to change over the period from 1995 to 2100. Water quality here was included as a climate-related variable because flow regime or precipitation changes from climate change can strongly affect mobilization of nutrients from fields to stream channels (Michalak, 2016).

For climate-related data, we utilized a hydrologic model previously generated for the entire Kaskaskia River Watershed (Acero Triana et al., 2021). This hydrologic model was based on the Soil and Water Assessment Tool (SWAT), using topography, soil, land cover, meteorology, and agricultural conservation practices as inputs. The climate-related outputs of the model included streamflow, suspended sediment, nitrate, and dissolved oxygen. Besides these, water temperature was estimated by regression between air and water temperature records at two gauges in the watershed where water temperature measurements are available. All five variables were calculated with mean, minimum, maximum, and standard deviation annually based on daily values from 1990 to 2015 for the baseline model (current) and from 2019 to 2100 for the projection. The spatial resolution of these variables was at the subbasin level (n = 175), where a subbasin was defined as the drainage area of one stream or river segment. Future environmental projections were built upon the baseline model, using future climate conditions and scenario-based agricultural conservation practices.

Future climate projections were based on 32 different temperature and precipitation projections from the Atmosphere-Ocean Global Climate Models (AOGCM) under the highest representative concentration pathway (RCP8.5). RCP8.5 could upper-bound the worst scenarios of future climate for the Kaskaskia River Watershed, by simulating the highest greenhouse gas emissions without mitigation policies (Riahi et al., 2011). As part of these projections, minimum, mean, and maximum annual air temperature were projected to increase by 0.92, 0.61, and 0.79 °C per decade, with a total increase of 8.82, 5.62, and 7.56 °C by 2100, respectively. Mean annual precipitation was projected to increase slightly, with minimum, mean, and maximum precipitation amounts close to 750, 1000, and 1500 mm, by 2100, respectively.

The scenario-based agricultural conservation practices considered in the model were, 1) crop rotation, 2) cover crops, 3) reduced tillage, and 4) reduced or split fertilizer application. These four practices were prioritized by landowners in the Kaskaskia River Watershed, and believed to help improve the sustainability and resilience of the watershed, based on a previous survey (Shipley et al., 2020) and state conservation reports (IDNR, 2017; IEPA, 2019). Twelve agricultural conservation scenarios were generated that incorporated these four conservation practices, with different magnitudes (Acero Triana et al., 2021). These agricultural conservation practices were predicted to be very effective for nutrient and sediment input reduction into streams, with local nitrate predicted to decrease up to 40 % and 30 % during 2020-2029 and 2030-2039, respectively, and suspended sediment predicted to decrease up to 40 % and 40 % during the same period. For future projections, we first averaged 32 climate scenarios for changes in air temperature and precipitation, then applied the 12 different agricultural conservation scenarios above climate change.

For non-climate environmental data, we referred to previous species distribution models across streams in Illinois, US (Cao et al., 2016). Based on the rankings of how non-climate environmental variables influenced fish species abundance, we selected 15 variables: soil permeability, land cover (% forest cover and % agricultural cover), channel gradient, watershed slope (total-watershed and local-watershed slope), bedrock depth (<15 m and <30 m below), dam (having upstream dam, distance to upstream dam, having downstream dam, and distance to downstream dam), stream order, sinuosity, and watershed area. These 15 variables were selected among >300 candidate environmental variables compiled from the Great Lakes Regional Aquatic Gap Analysis Project (Brenden et al., 2008; Cao et al., 2016; McKenna et al., 2013; Steen et al., 2008). The resolution was at the reach level, where the reach was defined as a stream section between the confluences of an upstream tributary.

2.3. Data analysis

2.3.1. Functional traits

Compared to taxonomy-based models, trait-based models have the potential to provide a mechanistic understanding about fish distribution and community changes (Frimpong and Angermeier, 2010). Among all fish traits, ecological traits involving life history, trophic level, and habitat preference are well studied, widely available, and have been proven to effectively predict species distributions under environmental change (Blanck et al., 2007; Mao et al., 2021; Olden et al., 2006; Parker et al., 2018). Besides these, physiological tolerance is directly related to habitat selection for fish, making physiological traits ideal to model future species distribution when evolutionary potentials of a species is excluded (Giacomini et al., 2013; Lange et al., 2016). We thus used both ecological and physiological trait groups (Table 1) for each species.

2.3.2. Functional diversity indices

Out of many functional diversity indices, we focused on two: functional dispersion (FDis) and functional evenness (FEve) as 1) they represent different aspects of functional diversity; 2) they are not sensitive to species richness, and 3) they can be used to test unlimited numbers of traits (Laliberté and Legendre, 2010; Mao et al., 2021; Parker et al., 2018). We did not test functional richness (FRic) because 1) it cannot account for the relative abundance of species (Laliberté and Legendre, 2010; Pla et al., 2011) and 2) it is always strongly correlated with species richness, thus unable to offer much extra information compared to traditional species richness (SR). We then used traditional species richness as an alternative to our two functional diversity indices.

FDis measures the variability of species traits in a local community by quantifying the spread of traits from the centroid in high-dimensional space for all species. It accounts for species abundance by shifting the centroid towards more abundant species. FDis has its lower boundary at zero and no upper boundary. The fewer traits that abundant species share, the higher the FDis value will be (Laliberté and Legendre, 2010; Pla et al., 2011).

FEve measures the regularity of species traits. It is calculated by minimum spanning tree method, which connects all trait points in a highdimensional space, using the lowest total tree branch length. FEve has a boundary between zero and one. The fewer common traits that species share, or the less evenly distributed species abundance is, the higher FEve value will be (Gaëlle and Jean-Claude, 2018).

To evaluate how different trait types were associated with all environmental variables described earlier, we calculated FDis and FEve based on 1) ecological traits (FDis_E and FEve_E), 2) physiological traits (FDis_P, FEve_P), and 3) both ecological and physiological traits (FDis, FEve) for all 91 sampling sites. These indices were weighted with abundance, which was square-root transformed to reduce sampling bias, especially from the weight of abundant, but small species (e.g., American gizzard shad *Dorosoma cepedianum*). We also calculated SR at each site for comparisons. All functional indices were generated using the package "FD" (Cutler et al., 2007; Laliberté et al., 2014) in R 4.0.2 (R Core Team, 2020). The cailliez correction was implemented for the species-by-species distance matrix because traits involve both quantitative and qualitative variables (Laliberté et al., 2014). As a result, seven diversity indices (FDis_E, FEve_E, FDis_P, FEve_P, FDis, FEve, and SR) were calculated and modeled.

2.3.3. Random forest modeling

We used random forest (RF) regression (Breiman, 2001) to assess how climate-related and non-climate environmental variables influence biodiversity. We selected RF to model current and future biodiversity changes because 1) it does not require assumptions of data distributions and variable independences; 2) it automatically accounts for interactions among environmental variables; and 3) it allows more predictors than observations in models (Cutler et al., 2007). To define the current relationship between

Table 1

Functional traits of fish used to calculate functional diversity indices in the Kaskaskia River Watershed, extracted from FishBase (http://www.fishbase.org/), Fishtraits Database (http://www.fishbraits.info/), BioNet (https://programs.iowadnr.gov/bionet/Fish/Species/List), Environment Protection Agency (https://archive.epa.gov/water/archive/web/html/app_c-1.html), and previous study (Whittier et al., 2007).

Trait	Туре	Description and (or) units
Habitat preference	Categorical	1) small substrate, 2) large substrate, 3) vegetation or debris, and 4) pelagic
Trophic level	Numeric	2-4.5 Based on food items
Lifespan	Numeric	Maximum age (years)
Mature age	Numeric	Mean age at maturation (years)
Fecundity	Numeric	No. of eggs or offspring per breeding season (log transformation)
Parental care Factor		With or without parental care
Water quality tolerance	Factor with levels	1) tolerant, 2) intermediate, and 3) intolerant
Thermal tolerance	Factor with levels	Summer maximum temperature: 1) cool: 18–25 °C and 2) warm \ge 25 °C
Swimming factor	Numeric	Ratio of minimum depth of the caudal peduncle to the maximum caudal fin depth
Flow preference	Factor with levels	1) slow, 2) moderate, and 3) fast
Maximum total length	Numeric	Maximum total body length (mm)
	Trait Habitat preference Trophic level Lifespan Mature age Fecundity Parental care Water quality tolerance Thermal tolerance Swimming factor Flow preference Maximum total length	TraitTypeHabitat preferenceCategoricalTrophic levelNumericLifespanNumericMature ageNumericFecundityNumericParental careFactorWater quality toleranceFactor with levelsThermal toleranceFactor with levelsSwimming factorNumericFlow preferenceFactor with levelsMaximum total lengthNumeric

biodiversity measures and environmental data for FDis, FEve, and SR at each sampling site, we used 1) five years' averaged climate-related variables and 2) five years' averaged climate-related variables together with additional non-climate variables as predictors in RF after comparing model R² from one year to up to five-years average. In all models, we also included year as an extra variable to check for temporal influences as fish samples were collected over 20 years. We trained all models with 500 trees to stabilize estimates of variable importance, then excluded all variables with negative contributions to the output. All RF models were built using package "ranger" (Wright et al., 2020), with relative importance per variable calculated using the "importance" function. The positive, negative, or multimodal relationships between environmental variables and biodiversity indices were evaluated using "partial-dependence" in the package "randomForest" (Liaw and Wiener, 2002). Based on model performance measured from pseudo- R^2 values, we selected the best fitting models for FDis, FEve, and SR, respectively. We then used the best models to predict future biodiversity changes every 10 years under climate change only or climate change with the 12 agriculture conservation scenarios described above (Fig. 2).

2.3.4. Site-specific projection comparisons

To identify what climate-related environmental variables were projected to have the largest difference between sites with highest and lowest predicted biodiversity, we selected 10 highest and 10 lowest FDis/SR sites projected in 2049 under different agricultural scenarios, then used *t*tests to compare climate-related environmental variables between high and low sites.

3. Results

3.1. Spatial patterns of the biodiversity measures

RF models were generated for 86 fish species recorded at 91 sites using environmental variables as independent variables and FDis, FEve, or SR as dependent variables (Fig. 3), with all 7 \times 2 combinations (columns \times rows in Table 2). Among FDis, FEve, and SR, FDis models had the best fits (R² = 0.26–0.44), followed by SR models ($R^2 = 0.25$ –0.29), with FEve models having the lowest performance ($R^2 = 0.02$ –0.10) (Table. 2). Models had better performance overall when considering both climate-related and non-climate explanatory variables than climate-related variables only, with R^2 increasing by up to 0.12. For functional indices, when including both ecological and physiological traits, models had better performance than either ecological or physiological traits alone.

For all models with $R^2 \ge 0.10$, partial-dependence plots helped explain how FDis, FEve, and SR can be driven by environmental variables (Table 3). When only climate-related variables were used as predictors in models, flow and temperature were dominant, including annual mean, min, max, and standard deviation: FDis E based on ecological traits was positively related to flow, which is responsible for up to 69 % of variance explained by the model. FEve E based on ecological traits was positively related to temperature, responsible for up to 39 % of variance explained by the model, while FDis P based on physiological traits and SR were negatively related to temperature, responsible for up to 54 % of the variance explained by the model. When both climate-related and non-climate variables were included in models, flow and temperature still showed high importance, up to 34 % and 44 % of variance explained by the model, respectively. However, non-climate variables, including watershed area, bedrock depth, and % agriculture land cover, also played an important role in these models. Among non-climate variables, watershed area was ranked high, up to 52 % and 40 % of variance explained for FDis and FDis_E, respectively.

3.2. Climate and agricultural conservation projections

Based on contemporary conditions, we selected FDis and SR to predict the influence of future climate and agricultural conservation practices on biodiversity in the Kaskaskia River Watershed (Fig. 4, Tables S1–S2). Without agricultural conservation scenarios, when including both climaterelated and non-climate variables, SR was generally expected to decrease, up to 6 % on average from 2019 to 2049. From 2049 to 2099, SR was expected to increase, from – 6 % back to – 4 % relative to 2019 levels. For site-specific predictions, the largest decrease was shown to be – 20 % in 2049 compared to 2019. When climate-related variables were considered



Fig. 2. Conceptual modeling framework for the projection of stream fish biodiversity under climate change (RCP8.5) and 12 different agricultural conservation scenarios by 2100.



Fig. 3. Functional dispersion (FDis) (a), functional evenness (FEve) (b), and species richness (SR) (c) at 91 sites over 1995–2015 in the Kaskaskia River Watershed, estimated based on six ecological and five physiological traits of 86 species.

alone, the trend of SR changes stayed the same, but average SR was predicted to be lower than SR in models with both climate-related and nonclimate variables. Compared to predictions of SR changes, FDis had similar trends, with up to -1.1 % from 2019 to 2049. After 2049, FDis showed a gradual increase, eventually back to -0.5 % in 2099 relative to 2019. The site-specific predictions of FDis had up to -4.0 % in 2049 compared to 2019, then a gradual increase, with -1.6 % in 2099 compared to 2019 in the best site. Similar to SR, when climate-related variables were considered alone, the trends of FDis stayed the same but were predicted to be lower on average.

All 12 agricultural conservation scenarios were not able to reverse the moderately decreasing trends of SR and FDis (Fig. 5, Tables S1–S2). No agricultural conservation scenarios would enhance average SR over 1 %. Sitespecific predictions (Figs. S1–S2) showed larger site differences when implementing agricultural conservation scenarios compared to no conservation, with the largest decrease in SR changing from – 20 % to – 22 % by 2049. Similar to SR, the overall decrease of FDis was not reversed with agricultural conservation scenarios, with the enhancement of overall FDis <0.2 %. Despite no significant reverse in SR and FDis under agricultural conservation on reduction of minimum, mean, and maximum nitrate and nitrate, no matter through reduction or split of nitrate use, crop rotation, cover crop, or no-tillage (Tables S3–S8).

Regardless of application or absence of agricultural conservation scenarios, higher FDis sites could still have higher flow and nitrate (Fig. S3). For SR, without agricultural conservation scenarios, higher SR sites could have higher nitrate while dissolved oxygen could be lower. After

Table 2

 R^2 values in random forest models for functional dispersion and evenness based on 1) ecological traits (FDis_E and FEve_E), 2) physiological traits (FDis_P, FEve_P), and 3) both ecological and physiological traits (FDis, FEve). Species richness (SR) is also calculated for comparisons.

Environmental variables	Ecology	7	Physiol	ogy	Ecology & Physiology		SR
	FDis_E	FEve_E	FDis_P	FEve_P	FDis	FEve	
SWAT	0.26	0.10	0.37	0.02	0.32	0.10	0.25
SWAT & non-climate	0.36	0.10	0.39	0.09	0.44	0.10	0.29
environment							

SWAT: Sol & Water Assessment Tool.

agricultural conservation scenarios, the difference of nitrate or dissolved oxygen between high and low SR sites reduced, partially replaced by flow variables as the top-ranking differences. (Fig. S3).

4. Discussion

We examined environmental drivers of stream fish biodiversity measures (SR, FDis, and FEve) in the Kaskaskia River Watershed, Illinois. We then extrapolated the potential changes in biodiversity in all sampling sites across the watershed to 2099. Our model predicts moderate impacts of climate changes on fish communities in the Kaskaskia River Watershed within the Mississippi River Basin, a heavily altered yet speciose river system. When global climate change and regional agricultural conservation practices acted together, our model predict that agricultural conservation practices, which mainly focus on reducing nutrient and sediment loss, did little to help reverse moderate declines in fish biodiversity under climate change.

4.1. Environmental drivers of functional diversity

High functional diversity implies efficient use of resource by the local biological community, oftentimes associated with heterogeneous habitats (Diaz and Cabido, 2001). Compared to taxonomic diversity, such as species richness, functional diversity helps us to infer the causation of community changes due to environmental disturbances (Mcgill et al., 2006). Because functional diversity is estimated based on species traits, whether selected traits are highly relevant to local environmental conditions will determine the performance of functional diversity in predicting environmental impacts on the local community (Wood et al., 2015).

In this study, we showed that functional indices based on both ecological and physiological traits were most strongly associated with the environment (i.e., higher R^2 in RF models). FDis measures the variability of species traits in a local community, however, physiological traits have been used much less than ecological traits. The physiological traits used in this study describe the tolerance of fishes to water quality, temperature, and flow, and they are particularly relevant for assessing the joint effects of climate changes and agricultural practices. FEve based on either ecological or physiological traits or both showed weak correlation with the environment (low R^2), in agreement with Parker et al. (2018). Thus, the FEve measure may not be useful for detecting the effects of climate change and agriculture conservation scenarios on fish communities, although further investigation is needed.

Table 3

Responses of biodiversity measures to the top-5 environmental predictors in random forest (RF) models. The order of numbers represents variable importance ranking in each model (measured with "importance" function in "ranger"). The symbol in parenthesis denotes the relationship between the variable and the response (+ positive, - negative, - multimodal) inferred through partial-dependence plots (measured with "partialPlot" function in "randomForest"). See Table 2 for definitions of the abbreviations of functional diversity and species richness. Climate-related variables include water temperature, flow, suspended sediment, nitrate, and dissolved oxygen. Mtry in Random Forest represents the number of variables randomly sampled as candidates at each split.

Environmental variables		Climate-related						Climate-related & non-climate					
Responses		FDis	FEve	FDis_E	FEve_E	FDis_P	SR	FDis	FEve	FDis_E	FEve_EW	FDis_P	SR
Temperature	Mean		3(+)		1(+)	3(-)	5(-)		3(+)		4(+)	3 (~)	
	Min		4(+)		5(+)	5 (~)			5 (~)				
	Max		2(+)		3(+)	1(-)	1(-)		2(+)		3(+)	1(-)	3(-)
	Std				4(+)	2(-)	3(-)					2(-)	
Flow	Mean	1(+)		1(+)			2(+)	2(+)		2(+)			
	Min	5(+)	1(+)	5(+)	2(+)		4(+)		1(+)	4(+)			
	Max	2(+)		3(+)				3(+)					
	Std	3(+)		2(+)				4(+)		3(+)			
Suspended sediment	Mean												
	Min												
	Max		5(-)										
	Std												
Nitrate	Mean												
	Min	4 (~)		5(+)				5 (~)					4 (~)
	Max					4(-)							
	Std												
Dissolved oxygen	Mean												
	Min												
	Max												
	Std												
Soil permeability													1(-)
Land cover	% Forest												
	% Agriculture								4(-)		2(-)		5(+)
Channel gradient													
Watershed slope	Total watershed												
	Local watershed											4 (~)	
Bedrock depth	<15 m										5(+)		
	<30 m										1(-)	5(+)	
Dam	Upstream												
	Distance to upstream												
	Downstream												
	Distance to downstream												
Stream order													
Sinuosity										5 (~)			
Watershed area								1(+)		1(+)			2(+)
mtry in RF		5	10	2	3	6	5	16	14	16	5	12	10

Among all environmental factors, flow and temperature were the two most important drivers of FDis and FEve. In FEve models, temperature factors contributed up to \sim 40 % among all independent variables and positively affected FEve. The Kaskaskia River Watershed already has high summer temperatures, thus may not provide ideal habitats for coolwater species. This was confirmed by the fact that only eight of the 86 fish species sampled classified as coolwater fish (Buisson et al., 2008; Hansen et al., 2017). Thus, warmer water in the Kaskaskia River Watershed under future climate scenarios may not significantly change fish community composition, but, in fact, may increase productivity to better support local warmwater fish species (Rathert et al., 1999; Wehrly et al., 2003), benefiting FEve. Minimum flow was also positively associated with FEve, likely because it influences both habitat size and connectivity (Jaeger et al., 2014). In FDis models containing ecological traits, flow was the top predictor, accounting for up to 70 % in relative importance among all variables, which was positively affecting FDis. This is understandable as flow increases connectivity between habitats (Falke and Fausch, 2010; Jaeger et al., 2014). Also, more flow means more habitats, thus offering more niche space for more species, especially larger predators (Angermeier and Schlosser, 1989; Petermann et al., 2015; Xenopoulos and Lodge, 2006).

When physiological traits were considered alone, temperature became the top predictor, and was negatively associated with FDis. This trend may have been driven by coolwater species, despite their rarity in the Kaskaskia River Watershed fish communities. Besides temperature and flow, a medium level of nitrate was also positively associated with FDis, implying appropriate level of primary production could contribute to functionally diversified fish communities. Non-climate variables also explained a significant portion of FDis and FEve distributions. Watershed area accounted for up to 52 % of variable importance for FDis among all non-climate variables, likely because larger watersheds yield more flow, thus providing more habitat space (Xenopoulos and Lodge, 2006). Dams were never a top predictor in any FDis or FEve models, suggesting limited impacts on fish communities in the Kaskaskia River Watershed. This is likely due to 1) a low percentage of potamodromous fish species in the Midwestern US and 2) such limited potamodromous fish species already distributed across the whole Kaskaskia River Watershed (Dean et al., 2022; Smith et al., 2010), making the impact of damming invisible at the community level. SR models also showed similar results with FDis, but with lower R², suggesting that trait-based functional dispersion could be more informative for predicting climate-change impacts on aquatic communities.

4.2. Climate change, agricultural conservation, and future biodiversity

When climate change was considered alone, we found a moderate downward trend of FDis and SR under RCP8.5 by 2099, with the most severe decrease expected during 2029 to 2049; after 2049, declines in FDis and SR were predicted to ease or stop. Under RCP8.5 global warming scenarios, we expect air temperature to increase 0.61 °C per decade in the Kaskaskia River Watershed, together with slight increases in precipitation (Acero Triana et al., 2021). Severe climate change may minimally threaten fish communities of the Kaskaskia River Watershed because only eight of 86 fish species currently present are coolwater fishes, and only 15 are



Fig. 4. Predicted changes of functional dispersion (FDis) (a) and species richness (SR) (b) in the Kaskaskia River Watershed under averaged RCP8.5 climate change scenarios, using six ecological and five physiological traits of 86 species for calculation. Climate-related variables includes water temperature, flow, suspended sediment, nitrate, and dissolved oxygen.

classified as sensitive to poor water quality. This is different from many other watersheds worldwide, such as in Europe (Buisson et al., 2013; Markovic et al., 2014) and the Verde River Basin of North America (Jaeger et al., 2014) where the majority of fish communities were threatened by climate change. For the majority of fish species in Midwestern agricultural watersheds like the Kaskaskia, climate change in the 21st century may benefit their fitness (Rountrey et al., 2014). However, caution should be made here as we could either overestimate or underestimate the impacts from climate change. For potential overestimation, we here used the most extreme scenario RCP8.5, it would always be better to model the same watershed under more different RCP scenarios and make comparisons. For potential underestimation, we did not include heatwaves, drought, and flooding simulations in the models, thus the impacts of climate change could be underestimated. Also, we did not have lab-derived data or longterm field monitoring information on how increased temperatures could alter physiological function, like metabolism (e.g., standard metabolic rate and aerobic scope) for warmwater species, thus altering their growth and reproduction, and eventually their fitness and distributions (Rummer et al., 2014; Stillman, 2019). Under elevated temperature, the oxygen demand of fish tissue can increase exponentially until a critical temperature, where oxygen demand for maintenance exceeds cardiorespiratory capacity, causing a loss of performance (Pörtner, 2010). Studies on metabolism during warming have gained attention, but mostly on cold- or coolwater species, not warmwater ones (Lennox et al., 2018; Oligny-Hébert et al., 2015).

We cannot avoid the impacts of climate change locally, but we do have the potential to reduce climate impacts through appropriate regional landuse management (Lawrence et al., 2014; Oliver and Morecroft, 2014). Through simulating 12 agricultural conservation scenarios targeted at the economic sustainability and environmental resilience of the watershed (Shipley et al., 2020), we expected positive responses in fish communities. However, none of these agricultural conservation scenarios improved either SR or FDis. This indicates that management for ecosystem services (i.e., minimizing nutrient and sediment input into rivers) will not have significant co-benefits to fish communities of the Kaskaskia River Watershed (Smith et al., 2015; Xiao et al., 2018). Our results generally agree with similar projections in the Western Lake Erie Basin in the Midwestern US, which also predicted that agricultural conservation practices will benefit water quality but not overall biodiversity (Fraker et al., 2020). This is understandable because the agricultural conservation practices we assessed were prioritized to reduce nutrient and sediment input, while such reduction in the Kaskaskia River Watershed may not benefit fish communities as high SR or FDis sites could have higher nitrate levels instead of lower. Under climate change, positive effects from nutrient and sediment control on nearby stream fish communities (i.e., SR or FDis) could be trivial or even offset by negative climate impacts. What really could improve SR or FDis is to improve the variability of temperature or flow under climate change, which were the strongest drivers in our models and largest differences between high and low SR or FDis projected sites. We therefore would expect biodiversity increases when conservation practices focus on mitigating temperature and flow impacts, such as building wooded riparian zones or recovering river sinuosity (Allen, 2005; Beechie et al., 2015; Bowler et al., 2012). Such improvements in land-use near streams could be critical for both taxonomic and functional biodiversity (Dala-Corte et al., 2016). Also, such land-use changes could have co-benefits on nutrient and sediment reduction from an agricultural conservation perspective, with the riparian zone functioning as the interface between aquatic community and terrestrial agricultural production (Lind et al., 2019). However, the economic benefits of such conservation efforts may not elicit the interests of farmers. Only if we find a way to make conservation practices benefit both biodiversity and agriculture production, and these economic benefits can be quantified (Chan et al., 2011; Hermoso et al., 2018), would we anticipate long-term collaboration between farming and conservation.

Taxonomic or functional diversity may not be prioritized when landowners consider conservation actions in the Kaskaskia River Watershed



Fig. 5. Predicted changes of functional dispersion (FDis) (a) and species richness (SR) (b) under different agricultural conservation scenarios with climate change in the Kaskaskia River Watershed. The baseline is model projection in 2019. 00 represents no agricultural conservation, 01 and 02 represent 10 % and 20 % reduction of nitrate application in corn field, 03 and 04 represent the different splits of nitrate application. 05–07 represent different crop rotations in corn and soybean fields. 08 and 09 represent the use of winter wheat as cover crops in corn and soybean fields. 10–12 represent the reduced till or no-till in corn and soybean fields. Models use both ecological and physiological traits of each species for FDis measurement, and both climate-related and non-climate variables for environmental information.

(Shipley et al., 2020). Instead, the focus of landowner interests may involve enhancing the abundance of sportfish species, such as walleye (Sander vitreus), muskellunge (Esox masquinongy), and smallmouth bass (Micropterus dolomieu) due to their importance in recreation or food. Because these species are also sensitive to temperature and nutrients, we can motivate the conservation interests of landowners through conserving sport fishes as 'umbrella species', which could further benefit broader fish communities (Roberge and Angelstam, 2004). Also, another practical way to enhance native biodiversity when collaborating with landowners is to first target at controlling nuisance or invasive species, especially sliver carp (Hypophthalmichthys molitrix) and bighead carp (Hypophthalmichthys nobilis) in the North America. Because such efforts of controlling invasive species could help restore natural flow and temperature regimes that promote the competitiveness of native species indirectly (Lawrence et al., 2014; Rahel et al., 2008). Overall, it may be difficult to stimulate public interests in conserving biodiversity alone, but if we can combine it with other benefits, we could gain more support from landowners for win-wins of ecosystem service actions for biodiversity. Determining how to mitigate temperature and flow impacts on "important" species is a realistic direction to begin designing such conservation plans.

4.3. Future conservation planning

In this study, we modeled the relationships between fish biodiversity and a range of environmental variables, then predicted fish biodiversity changes under climate change projections and agricultural conservation scenarios. The basin-wide averages of both taxonomic and functional diversity were predicted to decrease moderately. However, the magnitude of the decrease varied greatly across sites. We therefore recommend that future efforts prioritize the monitoring of sites predicted to have the biggest biodiversity changes when designing basin-wide conservation practices. With such prioritization, we can establish long-term monitoring programs on how key drivers (e.g., flow, temperature, and nitrate) shape local fish communities. Also, local riverine biodiversity relies on dispersal (Falke and Fausch, 2010). Improving connectivity among sites (e.g., barrier removals) while optimizing tradeoffs between conservation and ecosystem services provision should also be a priority (Erős et al., 2018). What is more, with moderate predicted deceases of biodiversity in watersheds, like the Kaskaskia in this study, conservation efforts of both governmental agencies and NGO may shift their focus to coolwater or sensitive species, instead of only the overall biodiversity.

During future conservations, we should better collaborate with local residents when designing conservation practices (Allen, 2005; Stubbs, 2014). To achieve this, while targeting the restoration of biodiversity, we recommend incorporating both key species enhancement and invasive species control into planning. With such an approach, residents can better appreciate the importance of freshwater diversity besides economic stability under climate change (Ban et al., 2013).

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CRediT authorship contribution statement

Qihong Dai: Conceptualization, Funding application, Methodology, Software, Data curation, Visualization, Writing - Original draft preparation and review. Yong Cao: Conceptualization, Writing – Review. Maria L. Chu, Conceptualization, Funding application, Writing – Review. Eric R. Larson: Conceptualization, Writing – Review. Cory D. Suski: Supervision, Conceptualization, Funding application, Writing – Review.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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