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# Hierarchy in Factors Affecting Fish Biodiversity in Floodplain Lakes of the Mississippi Alluvial Valley

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# Hierarchy in factors affecting fish biodiversity in floodplain lakes of the Mississippi Alluvial Valley

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**Abstract** River-floodplain ecosystems offer some of the most diverse and dynamic environments in the world. Accordingly, floodplain habitats harbor diverse fish assemblages. Fish biodiversity in floodplain lakes may be influenced by multiple variables operating on disparate scales, and these variables may exhibit a hierarchical organization depending on whether one variable governs another. In this study, we examined the interaction between primary variables descriptive of floodplain lake large-scale features, suites of secondary variables descriptive of water quality and primary productivity, and a set of tertiary variables descriptive of fish biodiversity across a range of floodplain lakes in the Mississippi Alluvial Valley of Mississippi and Arkansas (USA). Lakes varied considerably in their representation of primary, secondary, and tertiary variables. Multivariate direct gradient analyses indicated that lake maximum depth and the percentage of agricultural land surrounding a lake were the most important factors controlling variation in suites of secondary and tertiary variables, followed to a lesser extent by lake surface area. Fish biodiversity was generally greatest in large, deep lakes with lower proportions of watershed agricultural land. Our results may help foster a holistic approach to floodplain lake management and suggest the framework for a feedback model wherein primary variables can be manipulated for conservation and restoration purposes and secondary and tertiary variables can be used to monitor the success of such efforts.

**Keywords** Floodplain lake · Biodiversity · Mississippi Alluvial Valley · Environmental variables · Scale · Hierarchy

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## Introduction

Riverine floodplains are among the most biologically diverse ecosystems in the world (Tockner and Stanford 2002). Most of this biological diversity is supported by the dynamic nature and diverse environmental conditions inherent in river-floodplain ecosystems (Baker et al. 1991; Sabo and Kelso 1991). Environmental factors determine aquatic community organization by acting as filters that affect the capacity of species to occupy a given area (Tonn et al. 1990). Fish species distributions and community composition can be affected by environmental factors directly via limits on physiological tolerance or indirectly via constraints on biotic interactions (Miranda and Lucas 2004).

Environmental variables that determine fish community composition likely show a hierarchical organization. Thus, variables may be classified as primary, secondary, or tertiary depending on whether one variable governs another. Lake physical characteristics (primary variables) may influence lake water quality and primary productivity characteristics (secondary variables). Likewise, primary and secondary variables may influence the fish assemblage (tertiary variables). For example, vertical stratification of temperature and dissolved oxygen concentrations are largely controlled by depth (Dake and Harleman 1969), whereas the presence of a fish species may be controlled by temperature and oxygen as well as by the diversity of habitat afforded by depth (Miranda 2010). Similarly, lake acidity is influenced by the relative position of the lake within the landscape; lakes over carbonate-based sediments show less impact of acidification than lakes over granite-based sediments (Jackson et al. 2001), affecting species composition through water chemistry and through the location of the lake within the broader ecological environment.

Numerous studies have identified environmental variables as determinants of floodplain lake fish communities (e.g., Winemiller et al. 2000; Miranda and Lucas 2004; Penczak et al. 2004; Tales and Berrebi 2007). These studies sometimes confound primary and secondary variables in their analyses. As a result, a study might conclude that land use and chlorophyll-*a* are key variables, when in fact these variables represent disparate scales and chlorophyll-*a* (the secondary variable) may be governed by land use (the primary variable). Additional studies are needed because (1) relatively little information is available about how variables representing different scales interact in floodplain lakes; (2) understanding the hierarchy of variables can foster the development of a more holistic approach to floodplain ecosystem conservation and restoration; and (3) the hierarchy of variables should be considered in management with primary variables probably being the focus of conservation and restoration strategies because these are often variables that managers can actually manipulate; secondary and tertiary variables may instead be useful for monitoring the result of conservation and restoration efforts.

We examined the interaction between primary environmental variables descriptive of floodplain lake large-scale features, suites of secondary variables descriptive of water quality and primary productivity, and a set of tertiary variables descriptive of fish biodiversity across a range of floodplain lakes in the Mississippi Alluvial Valley of Mississippi and Arkansas. Lake depth, surface area, degree of connectivity with closest river, and land use around the lake were considered as primary variables. These variables have been identified by other authors as the driving forces for many processes in standing bodies of water (e.g., Lucas 1985; Junk et al. 1989; Magnuson et al. 1998; Tejerina-Garro et al. 1998). The specific objective of this study was to estimate the relative importance of each primary variable in controlling the variation in suites of secondary and tertiary variables, as well as the relation between suites of secondary and tertiary variables. We hypothesized that the suites of secondary variables would be more important in controlling the variation in the tertiary variables because fish biodiversity is likely affected on a more proximate level by water quality and primary productivity variables than by large-scale primary variables.

## Methods

### Study lakes

Fifty-four floodplain lakes were investigated from July 2006 to August 2010 (Fig. 1). Lakes were chosen from selected river basins in Mississippi and Arkansas. Forty-six lakes were sampled twice each and eight lakes were sampled once. Forty-one lakes were situated adjacent to the Yazoo River and its major tributaries (the Coldwater, Sunflower, Yalobusha, and Tallahatchie rivers) and 13 lakes were within the Arkansas, Ouachita, and White river basins. Eight lakes from the White River Basin were located within the White River National Wildlife Refuge, Arkansas. Three lakes from the Yazoo River Basin were located within the Delta National Forest, Mississippi. All lakes were channel remnants of varying lengths. Lakes were selected based on accessibility and diverse representation of physical and chemical habitat characteristics. In particular, efforts were made to select lakes along gradients of depth,

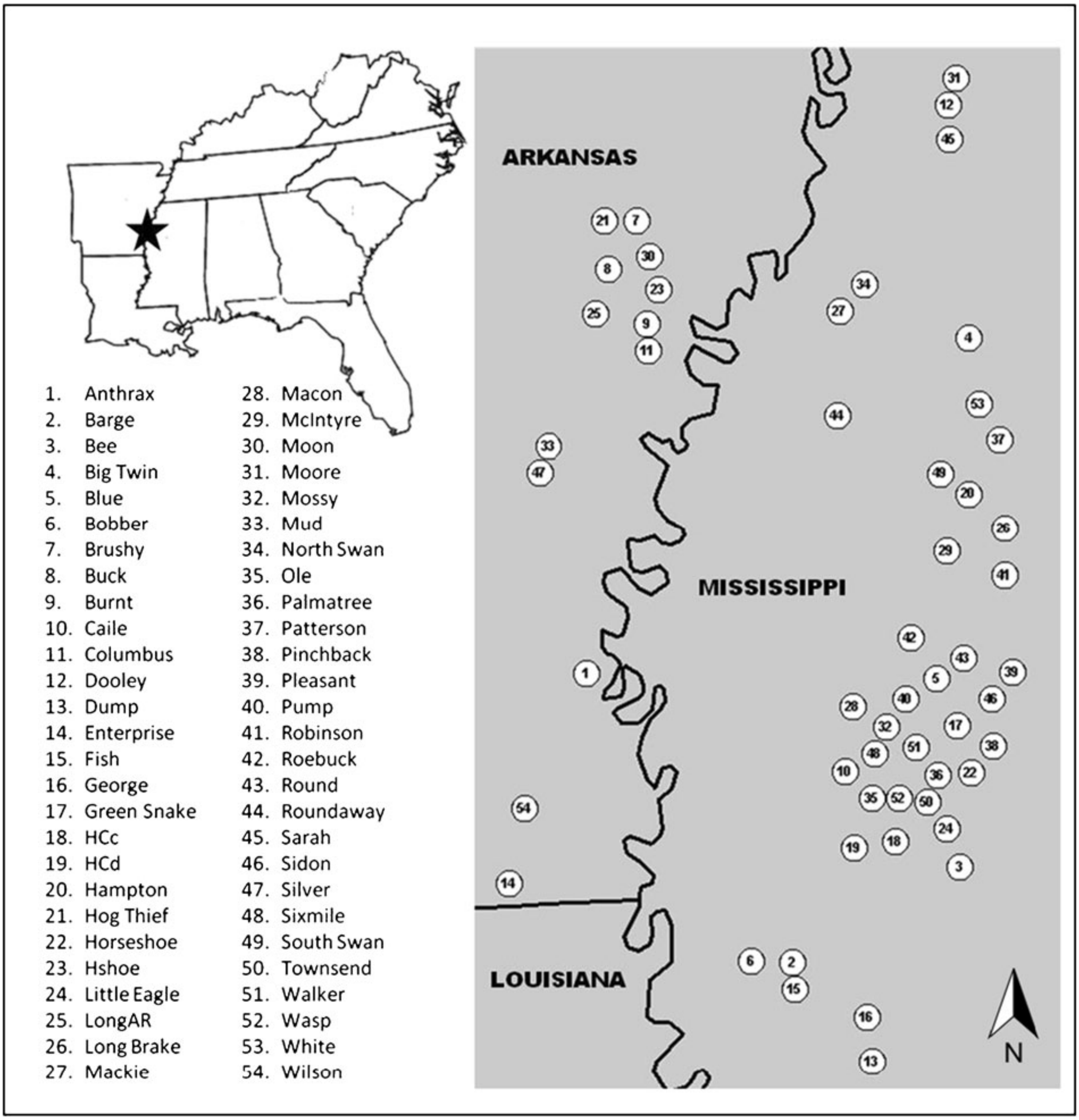


**Fig. 1** Map of the lower Mississippi Alluvial Valley region of Mississippi and Arkansas, with names and locations of 54 lakes sampled from 2006 to 2010. The inset identifies the location of the study region in the southeastern United States

surface area, degree of connectivity with closest rivers, and watershed composition.

## Primary variable selection and collection

Maximum depth, surface area, floodplain lake-river channel interconnectedness, and percentage of watershed agricultural land were selected a priori as primary environmental variables. They were selected on the basis that they seem to be the driving forces behind the variation in other lake water quality and primary productivity variables and because they are often identified as fundamental to many processes in floodplain dynamics (Junk et al. 1989; Baker et al. 1991; Miranda 2005; Lubinski et al. 2008). Thus, the primary environmental variables were selected based on the premise that they act independently and collectively to shape floodplain lake water quality, primary productivity, and fish biodiversity characteristics.

Maximum depth was defined as the deepest point detected by depth soundings taken with a handheld (DF2200PX, NorCross Marine,[1] Orlando, Florida) or boat-mounted (X126 DF Sonar, Lowrance Electronics, Tulsa, Oklahoma) depth finder in a zig-zag pattern along the former thalweg between the two ends of each lake. Maximum depth was selected as a primary variable as opposed to mean depth because it better characterizes the cross-sectional morphology of abandoned river channels than mean depth.

Surface area and land use composition surrounding each lake were calculated using spatial analyst tools in the Arc-GIS software package. Aerial photography and satellite images for lakes within Mississippi were available from the National Agricultural Imagery Program (NAIP) and were obtained from the Mississippi Automated Resource Information System (MARIS; MARIS 2003). Images of the 13 lakes in Arkansas were obtained from the United States Geological Survey (USGS) Southeast Gap Analysis Project (SEGAP) database. Lakes were treated as polygons, and those not already identified as water bodies in Arc-GIS were digitized as such.

Individual lake watersheds could not be defined due to the lack of sufficient topographic relief in the region (Baker et al. 1991). Instead, concentric bands (50, 500, 1000, and 5000 m) were drawn around each lake. Percentages of land use classifications available from the MARIS and SEGAP databases were calculated within each band. Percentage of row-crop agriculture was selected as a primary variable over other land use classifications because of the notable historical influences agricultural practices have had on the lower Mississippi Alluvial Valley ecoregion (Smith 1954; King and Keeland 1999). Preliminary analyses using pairwise comparisons of mean percent coverage indicated no statistically significant increases in percentage of row-crop agriculture beyond the 1000 m band; thus, percentage agriculture in the 1000 m band was used for all subsequent analyses.

[1] The use of trade, product, industry, or firm names or products or software is for informative purposes only and does not constitute an endorsement by the U.S. government or U.S. Geological Survey.

Interconnectedness between each floodplain lake and the closest river was measured using effective distance, defined as the stream channel distance between each lake and the nearest river. Other indices of lake-river interconnectedness include counts of inlets/outlets and area of neighboring water bodies (Miyazono et al. 2010), qualitative indices (Miranda 2005; Lubinski et al. 2008), and comparisons of direct field observations of flooding with river discharge levels (Zeug et al. 2005). The methods of Zeug et al. (2005) are possibly the most precise; however, direct field observation of flooding at all study lakes included in the present study was impractical. Differences in elevation between oxbow lakes and the nearest rivers are important in affecting connectivity; however, available elevation data were of relatively low resolution and agricultural practices have likely altered the landscape to the point where elevation data find use only in limited settings. Because of the limited utility of elevation data within the study region, effective distance was used as a proxy for other more involved measurements. Effective distance is easily measured and should suitably index connectivity in that lakes closer to the nearest rivers (i.e., have a shorter effective distance) are thought to be connected on a more frequent basis than lakes with farther effective distances.

## Secondary variable selection and collection

Turbidity (nephelometric turbidity units; NTU), pH, dissolved oxygen (DO; mg $L^{-1}$), DO saturation (%), temperature (°C), and water transparency (cm) were measured in the summer (June–August) from the epilimnion at a single point near the deepest point in each lake. Turbidity, pH, DO and DO saturation, and temperature were measured in situ with a Eureka Manta™ multiprobe (Eureka Environmental Engineering, Austin, Texas). Water transparency was measured using a Secchi disk (20 cm diameter). The aforementioned variables were combined into a multivariate matrix reflective of overall water quality characteristics.

Concentrations of chlorophyll-*a* and phycocyanin (fluorescence units; FU) and the chlorophyll-*a*:phycocyanin ratio were also measured in the summer (June–August) from the epilimnion at a single point near the deepest point in each lake using an *Aqua*fluor™ handheld fluorometer (Turner Designs, Sunnyvale, California). The chlorophyll-*a*:phycocyanin ratio was considered because it reportedly reflects the availability of nitrogen and phosphorous (nitrogen-limited lakes would tend to have higher ratios; Foy 1993). Chlorophyll-*a* fluorescence, phycocyanin fluorescence, and the chlorophyll-*a*:phycocyanin ratio were combined and treated as a separate secondary data matrix reflective of overall primary productivity.

## Fish collections

Fish were collected during daytime hours by a boat electrofisher equipped with a GPP 7.5 Smith-Root™ pulsator unit (Smith-Root, Inc., Vancouver, Washington). Pulsed DC electricity was cycled at 60 Hz with voltage output adjusted according to the specific conductance of each lake to maintain a constant output of 6–8 A. Individual samples consisted of 0.25 h of continuous electrofishing along indiscriminate shoreline areas. Sampling lasted 0.5–2.0 h depending on lake area. Fish were netted from the bow of the boat by two netters equipped with 2.7 m (handle length) dip nets with 0.4 cm bar mesh. Fish were identified to species and counted before release near the site of capture. Those species too difficult to identify in the field were preserved in a 10% formalin solution and transported to the lab for positive identification with taxonomic keys (Ross 2001).

## Fish biodiversity metrics

Fish assemblage descriptors were classified as tertiary variables on the basis that they are likely affected either directly or indirectly by primary and secondary variables. Species richness, diversity, dominance, and evenness metrics were calculated using diversity modules available in the PAST™ and PRIMER-E™ ecological software packages (Hammer et al. 2001; Clarke and Gorley 2006). Species richness metrics included raw species richness ($S_{raw}$), rarefied species richness ($S_{rare}$), Margalef's species richness ($S_{Margalef}$), and Menhinick's species richness ($S_{Menhinick}$). Diversity metrics included the Shannon diversity index (H′) and Fisher's α diversity index ($F_{\alpha}$). Dominance was measured with a variant of the Simpson's diversity index (D), hereafter referred to as Simpson's dominance (1-D) and the Berger-Parker index (d). Evenness was measured with Buzas and Gibson's evenness index (E) and Pielou's evenness index (J). Dominance and evenness metrics are inversely related but both index overall equitability of individuals among taxa (Hammer et al. 2001). Collections of threadfin shad (*Dorosoma petenense*) and gizzard shad (*Dorosoma cepedianum*) did not accurately reflect their true abundance in the study lakes due to their fleeing behavior in response to energized water. Hence, they were excluded from calculation of metrics sensitive to species abundance (i.e., diversity, dominance, and evenness metrics) but were included in metrics of species richness.

The aforementioned species richness, diversity, dominance, and evenness metrics have traditionally been used in a univariate sense, examining trends in individual metrics in response to variation in others. For example, Ludsin et al. (2001) examined the relationship between system productivity and fish species richness in Lake Erie (USA) using simple univariate linear regression. Similarly, Lubinski et al. (2008) assessed relationships between fish species richness, diversity, and evenness measures and lake-specific environmental variables using ordinary least-squares linear regression. For the purposes of this study, all univariate fish assemblage descriptors were grouped to create a multi-index matrix thought to index overall fish biodiversity.

## Statistical analysis

Canonical analysis of principal coordinates (CAP) was used to examine relationships between each individual primary variable and the matrices of secondary and tertiary variables, as well as the relationships between secondary and tertiary matrices. The CAP procedure is a multivariate data reduction technique that identifies axes running through a cloud of data points that have the strongest correlation with another set of variables (Anderson and Robinson 2003). Because the CAP analysis essentially ordinates one data matrix in consideration of another, it is a constrained analysis that uses an a priori hypothesis to construct correlations between matrices. Furthermore, it is flexible and meaningful in that it can be performed using any ecological distance measure (Anderson and Willis 2003). The CAP approach to constrained ordination is essentially a three-step process that includes a principal coordinates analysis (PCO), selection of *m* principal coordinate axes, and an ensuing canonical correlation analysis based on a matrix of explanatory variables. When relating a multivariate matrix to a single variable matrix, the CAP analysis produces a single canonical correlation representing the strength of the association between the canonical (i.e., CAP) axis and the explanatory variable. When relating two multivariate matrices, multiple canonical correlations are produced so as to represent the strength of the association between multiple axes maximizing the linear correlation between data matrices (M.J. Anderson, University of Auckland, personal communication).

Separate CAP analyses were applied to examine correlations between primary variables and respective secondary and tertiary matrices, and between secondary and tertiary matrices. The CAP analysis sought to find correlations between axes representing most of the variation in the water quality, primary productivity, and biodiversity matrices relative to each individual primary variable, with the constraint that the secondary and tertiary matrices were thought to be responses of the explanatory variables. In relating the suites of secondary variables to the biodiversity metrics, the CAP analysis sought to find correlations with the constraint that biodiversity responded to the suites of secondary variables. All CAP analyses were performed using the PERMANOVA+ add-on for the PRIMER-E statistical software package (PRIMER-E Ltd, Plymouth, United Kingdom; Clarke and Gorley 2006) with a Euclidean distance measure. Statistical significance for all CAP analyses was set at $\alpha=0.05$.

## Results

### Primary variables

The study lakes varied greatly in their primary environmental variables (Table 1). Maximum depth ranged from 0.5 to 8.6 m (mean=2.8 m), degree of lake-river interconnectedness ranged from 0 to 14 km (mean=2.5 km), and percentage of row-crop agriculture ranged from 0% to 77% (mean=47%). Lake surface area ranged from 0.01 to 5.7 $km^2$ (mean= 0.74 $km^2$). Lakes within the Delta National Forest and the White River National Wildlife Refuge were surrounded primarily by bottomland hardwood forest (mean percentage agriculture in 1000 m band=1.4%) whereas lakes outside protected areas were surrounded primarily by agricultural land (mean percentage agriculture in 1000 m band=59%).

### Secondary variables

The study lakes also varied in their water quality and primary productivity variables (Table 1). Secchi visibility and turbidity, both indices of overall water transparency, averaged 50 cm (range=15–105 cm) and 29 NTU (range=4.7–113 NTU), respectively. DO concentration and DO saturation averaged 6.2 mg $l^{-1}$ (range=1.5–11 mg $l^{-1}$) and 82% (range=19–147%), respectively. Water temperature averaged 29°C (range= 26–34°C). pH was variable across lakes (range=5.2–9.5) but averaged slightly alkaline (7.2). Chlorophyll-*a* and phycocyanin fluorescence averaged 286 FU (range= 65–964 FU) and 2.5 FU (range=0.3–9.6 FU), respectively. The chlorophyll-*a*:phycocyanin ratio averaged 160 (range=19–426).

The water quality matrix was significantly correlated with the primary productivity matrix ($m=2$; $p<0.05$; Fig. 2). The CAP procedure identified two canonical axes that captured most of the association between the water quality variables and the primary productivity variables. The first and second canonical correlations, indicating the strength of the association between the matrix of water quality variables and the matrix of primary productivity variables, were $\delta_1=0.50$ and $\delta_2=0.29$, respectively.

### Fish collections

Over the multiyear sampling period, over 93,100 fish representing 71 species were collected during 128 h of electrofishing. Analyses were conducted with data from different years combined after a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) with a Bray-Curtis similarity measure indicated no significant among-year differences in assemblage composition for lakes sampled across years ($p=0.31$). Excluding threadfin shad and gizzard shad, bluegill (*Lepomis macrochirus*) were collected most frequently (34% of the catch by number), followed by longear sunfish (*Lepomis megalotis*; 10%), orangespotted sunfish (*Lepomis humilis*; 9%), smallmouth buffalo (*Ictiobus bubalus*; 7%), largemouth bass (*Micropterus salmoides*; 7%), brook silverside (*Labidesthes sicculus*; 5%), and bigmouth buffalo (*Ictiobus cyprinellus*; 4%).

**Table 1** Descriptive statistical properties of primary variables, secondary variables, and fish biodiversity variables collected from 54 oxbow lakes in the Mississippi Alluvial Valley, 2006–2010

| Variable | Mean | SD | CV | Min | 25th | Median | 75th | Max |
|---|---|---|---|---|---|---|---|---|
| Primary | | | | | | | | |
| Depth (m) | 2.8 | 1.7 | 61 | 0.50 | 1.6 | 2.3 | 3.9 | 8.6 |
| Surface area ($km^2$) | 0.74 | 1.2 | 159 | 0.01 | 0.1 | 0.22 | 0.73 | 5.7 |
| Agriculture (%) | 47 | 26 | 56 | 0 | 32 | 54 | 68 | 77 |
| Connectivity (km) | 2.5 | 2.9 | 120 | 0 | 0.2 | 1.7 | 3.5 | 14 |
| Secondary | | | | | | | | |
| Secchi (cm) | 50 | 21 | 43 | 15 | 35 | 49 | 66 | 105 |
| Temperature (°C) | 29 | 1.7 | 5.7 | 26 | 28 | 30 | 31 | 34 |
| DO (mg $l^{-1}$) | 6.2 | 1.9 | 31 | 1.5 | 5 | 5.9 | 7.1 | 11 |
| DO saturation (%) | 82 | 25 | 30 | 19 | 67 | 78 | 97 | 147 |
| pH | 7.2 | 0.64 | 9 | 5.2 | 6.8 | 7.1 | 7.6 | 9.5 |
| Turbidity (NTU) | 29 | 23 | 81 | 4.7 | 14 | 24 | 32 | 113 |
| Chlorophyll-*a* | 286 | 187 | 66 | 65 | 174 | 238 | 361 | 964 |
| Phycocyanin | 2.5 | 2.1 | 84 | 0.3 | 1.1 | 1.7 | 3.2 | 9.6 |
| Chl-*a*:Phyco | 160 | 97 | 60 | 19 | 93 | 145 | 207 | 426 |
| Fish biodiversity | | | | | | | | |
| $S_{raw}$ | 25 | 7.8 | 32 | 12 | 19 | 24 | 28 | 44 |
| $S_{rare}$ | 13 | 3.1 | 24 | 6 | 11 | 13 | 15 | 23 |
| $S_{Margalef}$ | 3.7 | 1.2 | 31 | 1.9 | 2.9 | 3.4 | 4.3 | 6.7 |
| $S_{Menhinick}$ | 1.2 | 0.38 | 32 | 0.44 | 0.89 | 1.2 | 1.4 | 2.1 |
| H′ | 2.1 | 0.40 | 20 | 0.63 | 1.8 | 2.1 | 2.3 | 2.8 |
| $F_{\alpha}$ | 5.5 | 2.1 | 39 | 2.3 | 4.1 | 5.3 | 6.6 | 12 |
| E | 0.35 | 0.11 | 30 | 0.12 | 0.27 | 0.34 | 0.43 | 0.62 |
| J | 0.65 | 0.11 | 17 | 0.23 | 0.58 | 0.66 | 0.73 | 0.82 |
| d | 0.41 | 0.15 | 36 | 0.21 | 0.30 | 0.36 | 0.51 | 0.88 |
| 1-D | 0.25 | 0.12 | 47 | 0.12 | 0.17 | 0.21 | 0.33 | 0.77 |

*SD* standard deviation, *CV* coefficient of variation, *Min* minimum, *25th* 25th quantile, *75th* 75th quantile, *Max* maximum. Of the secondary variables, *Secchi* Secchi visibility, *DO* dissolved oxygen, and *Chl-a:Phyco* chlorophyll-*a*:phycocyanin ratio. Chlorophyll-*a* and phycocyanin were measured in relative fluorescence units. Fish biodiversity metrics included raw species richness ($S_{raw}$), rarefied species richness ($S_{rare}$), Margalef's species richness ($S_{Margalef}$), Menhinick's species richness ($S_{Menhinick}$), Shannon's diversity (H′), Fisher's diversity ($F_{\alpha}$), Buzas and Gibson's evenness (E), Pielou's evenness (J), Berger-Parker dominance (d), and Simpson's dominance (1-D)

## Fish biodiversity metrics

Metrics of species richness and diversity were highly variable across the study lakes (Table 1). Columbus Lake had the greatest observed $S_{raw}$ (44), while Enterprise Lake had the smallest $S_{raw}$ (12). Bobber Lake was the most even in terms of Buzas and Gibson's evenness index (0.62) and Anthrax Lake was the least even (0.12). All other richness and diversity metrics are derived from these basic measurements of raw species richness and evenness and thus show similar patterns of variability.

## Hierarchical variable relationships

Statistically significant relationships existed between the primary variables and the respective secondary matrices, and between the primary variables and the fish biodiversity (tertiary) matrix (Fig. 2). Significant relationships were also detected between the secondary matrices and the biodiversity matrix (Fig. 2).

Water quality and primary productivity were correlated with the primary variables. Depth showed the strongest correlation with the water quality matrix ($\delta$=0.79; $p$<0.05). Surface area ($\delta$=0.40; $p$<0.05) was also correlated with the suite of water quality variables. However, the degree of lake-river interconnectedness and percentage of agricultural land were not significantly correlated with the water quality matrix. In each case, the CAP procedure selected $m$= 2 to 6 principal coordinates that accounted for 67–99% of the variability in the resemblance matrix constructed from the normalized water quality variables. Depth was the only primary variable that was significantly correlated with the primary productivity matrix ($\delta$=0.68; $p$<0.05). In this case, the CAP

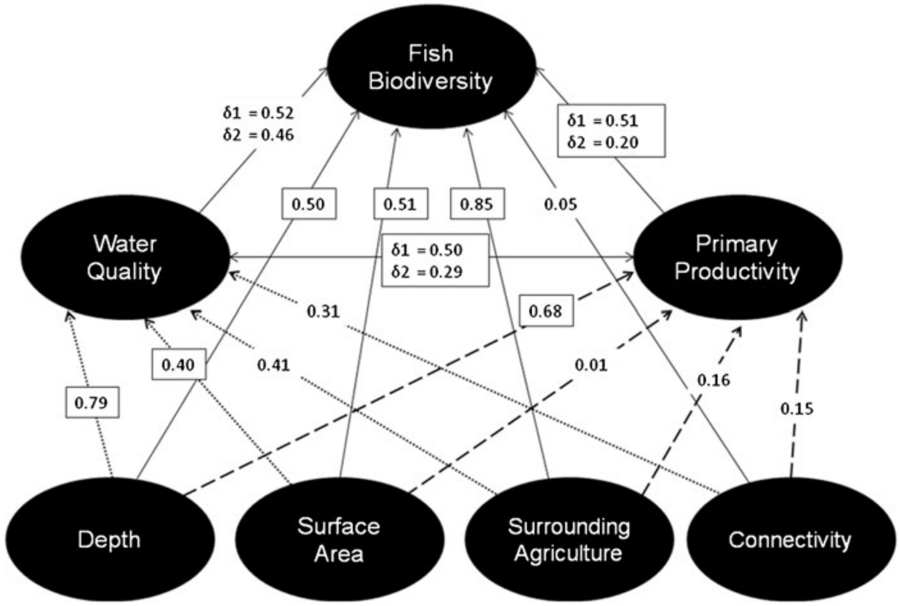


**Fig. 2** Canonical correlations between hierarchical oxbow lake ecosystem components. Depth, surface area,% agricultural land, and connectivity were assigned as primary variables. Suites of water quality variables (temperature, Secchi visibility, dissolved oxygen concentration, dissolved oxygen saturation, turbidity, and pH) and primary productivity variables (phycocyanin fluorescence, chlorophyll-*a* fluorescence, and ratio of chlorophyll-*a* to phycocyanin) were assigned as secondary variables. Fish biodiversity variables (raw species richness, rarefied species richness, Margalef's species richness, Menhinick's species richness, Shannon's diversity, Fisher's diversity, Berger-Parker dominance, Simpson's dominance, Buzas and Gibson's evenness, and Pielou's evenness) were assigned as tertiary variables. Dotted lines show correlations between primary variables and the suite of water quality variables. Dashed lines show correlations between primary variables and the suite of primary productivity variables. Solid lines show correlations between primary variables and fish biodiversity, between groups of secondary variables, and between secondary variables and fish biodiversity. Relationships between variables were assessed using canonical analysis of principal coordinates. Boxed correlations are statistically significant at $\alpha=0.05$

procedure selected $m=2$ principal coordinates that accounted for 94% of the variability in the resemblance matrix constructed from the normalized primary productivity variables.

As for the relationship between each primary variable and the matrix of biodiversity variables, the percentage of agricultural land showed the strongest correlation with fish biodiversity ($\delta=0.85$; $p<0.05$), followed by lake surface area ($\delta=0.51$; $p<0.05$) and depth ($\delta=0.50$; $p<0.05$). In each case, the CAP procedure selected $m=1$ to 9 principal coordinates that accounted for 95 to 98% of the variation in the resemblance matrix constructed from the fish biodiversity variables. Fish biodiversity was generally greater in large, deep lakes with lower proportions of watershed agricultural land. The degree of lake-river interconnectedness was not significantly correlated with the fish biodiversity matrix.

Of the secondary matrices, only the primary productivity matrix was significantly correlated with the fish biodiversity matrix ($m=2$; $p<0.05$). As primary productivity values increased, fish biodiversity generally decreased. The CAP procedure identified two canonical axes that captured most of the association between the primary productivity matrix and the fish biodiversity matrix. The first and second canonical correlations, indicating the strength of the association between the matrix of fish biodiversity variables and the matrix of primary productivity variables, were $\delta_1=0.51$ and $\delta_2=0.20$, respectively. The canonical correlations between the water quality matrix and the fish biodiversity matrix ($\delta_1=0.52$; $\delta_2=0.46$) were not statistically significant.

## Discussion

Our results suggest that the selected primary variables were important in controlling the variation in the secondary and tertiary matrices. Results did not meet initial expectations as stronger correlations were found between the primary variables and fish biodiversity, than between the secondary matrices and fish biodiversity; however, this is not to say that secondary variables are not important in affecting fish biodiversity. Overall, maximum depth and the percentage of agricultural land were the most important variables, influencing water quality, primary productivity, and fish biodiversity variables in floodplain lakes.

## Depth, secondary variables, and fish biodiversity

Depth is a major determinant over the abiotic environment and thus is likely a significant force in the organization of floodplain lake fish assemblages. Depth is largely responsible for the thermal, chemical, and light stratification and for patterns of water transparency and planktonic photosynthesis dynamics in freshwater lakes (Dodson 2005; Nõges 2009). Potential impacts of water transparency on the fish assemblage under the influence of depth are well-summarized by the piscivory-transparency-morphometry (PTM) model of Rodríguez and Lewis (1997). The PTM model predicts that relative abundance of sight-feeding piscivores and abundance of fishes with low-visibility tactile-feeding adaptations should vary predictably as water transparency declines following reductions in lake depth and subsequent resuspension of sediments (Hamilton and Lewis 1990; Rodríguez and Lewis 1997). Variation in the abundance of different groups of fishes may have a marked effect on metrics of species richness, diversity, dominance, and evenness.

Fish biodiversity is likely directly and indirectly affected by depth and the forces that it exerts on secondary variables. Depth likely augments habitat heterogeneity in that deeper lakes may have a vertical stratification of complex habitats (Gorman 1987). A greater complexity of habitats could permit exploitation by a greater number of species. Deeper lakes provide greater environmental stability, increased habitat persistence, and are usually exempt from adverse environmental conditions and periodic desiccation that may affect shallow lakes (Zeug et al. 2005; Shoup and Wahl 2009). Shallow lakes that experience periodic desiccation and other harsh environmental conditions likely have depauperate fish assemblages limited to species suited for rapid colonization such as orangespotted sunfish and western mosquitofish (*Gambusia affinis*) and fishes tolerant of poor water quality. Conversely, deeper, more environmentally stable lakes may support richer and more sensitive fish assemblages (Jester et al. 1992).

## Agriculture, secondary variables, and fish biodiversity

Numerous other studies have identified agricultural practices as influencing habitat degradation (e.g., Lucas 1985), water quality (e.g., Hall et al. 1999), and overall fish assemblage characteristics (e.g., Walser and Bart 1999). Most impacts of agricultural land on secondary variables are negative. Without proper watershed management (e.g., implementation of best management practices), floodplain lakes may experience an increase in suspended sediment loads and nutrients in the water column, thus increasing water column respiration and contributing to decreased dissolved oxygen concentrations (Cooper 1987; Cooper and McHenry 1989; Miranda et al. 2001; Roozen et al. 2003; Schweizer and Matlack 2005).

Sedimentation and its effects on water quality variables are perhaps the most notable impact of agricultural use in floodplain-river systems. Floodplain lakes within the Mississippi Alluvial Valley experienced a 50-fold increase in sedimentation rates with the clearing of land for agricultural purposes (Wren et al. 2008). Percent of agricultural land may couple with the effects of depth to influence water quality variables. Lakes with high sedimentation rates would experience accelerated lake-shallowing and eventually be subject to environmental conditions typical of shallow lakes (i.e., increased turbidity, large fluctuations in DO) and an unfavorable shift in fish assemblage characteristics (Miranda 2010).

## Surface area, secondary variables, and fish biodiversity

In the present study, lake surface area was only weakly, but nonetheless significantly, correlated with the water quality and fish biodiversity matrices. It is probable that stronger and additional correlations between surface area and the water quality and primary productivity matrices are dampened by the combined effects of the other primary environmental variables. For example, reductions in surface area are typical of floodplain lakes undergoing successional processes of depth reduction and increased isolation (Miranda 2005; Shields et al. 2010). The relationship between biodiversity and area is well known and has had many ecological applications (e.g., the theory of island biogeography; MacArthur and Wilson 1967). In floodplain lakes, the species-area relationship is likely a function of surface area and a balance between immigration (colonization) and local extinction events. Area itself may have no direct effect on fishes (Wright 1983); rather, greater area is commonly correlated with greater habitat complexity, and a lake with greater habitat heterogeneity is theoretically able to support more species able to exploit all available habitats. Although surface area is an important factor affecting fish biodiversity, it is likely of little concern to most lake managers simply because little can be done to alter the direct effects of surface area on other floodplain lake variables.

### Connectivity, secondary variables, and fish biodiversity

Lake-river connectivity was likely an extremely influential component of floodplain ecosystem dynamics prior to major landscape modifications in the region (Junk et al. 1989). Previous studies have shown that connectivity affects water quality and primary productivity variables (Knowlton and Jones 1997; Galat et al. 1998), and affects fish diversity and assemblage structure (Miranda 2005; Zeug et al. 2005; Shoup and Wahl 2009; Miyazono et al. 2010). Therefore, connectivity was expected to be strongly associated with the secondary habitat variables and with fish biodiversity. Yet, the degree of lake-river interconnectedness was the least-correlated primary variable.

It is probable that any linearity in the effects of connectivity on other floodplain lake variables was masked by the effects of other primary variables or by the coarseness of our method of measuring connectivity. Alternatively, it may be that the effects of connectivity are reflected more in fish assemblage composition than in fish biodiversity metrics. Fish biodiversity in a more-connected lake may be similar to that of an isolated lake; however, the fish assemblage itself may be substantially different. Riverine species may simply replace lacustrine species in well-connected lakes, changing overall fish assemblage composition but generally leaving fish biodiversity unaffected, or affected minimally so that our sampling could not detect the change. Further research is needed in understanding the effects of connectivity on fish biodiversity and overall assemblage composition in floodplain lakes, as well as in the development of a more accurate index of lake-river connectivity.

### Primary productivity, water quality, and fish biodiversity

The observed trend of decreasing fish biodiversity in lakes with higher productivity was surprising considering the species-energy hypothesis. This hypothesis suggests that energy availability generates and maintains gradients of species richness and diversity (Hawkins et al. 2003). In general, the biodiversity of a given community is limited by the energy supply supporting that community. Similar to the species-area relationship (MacArthur and Wilson 1967), the larger the total resource base, the greater the likelihood that there will be a greater variety of resource types, thus theoretically supporting a greater diversity of species (Wright 1983). Mittelbach et al. (2001), however, found a unimodal relationship between species richness and primary productivity in most aquatic systems, suggesting that high productivity may be associated with stressful conditions that limit species diversity.

Because patterns of local diversity are dependent on local abiotic factors (Tales and Berrebi 2007), we expected strong and significant correlations between the water quality matrix and the fish biodiversity matrix. Instead, a relatively weak and non-significant interaction was observed. The lack of a stronger interaction could have been a function of sampling design. Some of the measured water quality variables have wide diurnal fluctuations, thus, some of the variance in the water quality matrix is likely due to variation in the timing of sample collection. Increased variability in the water quality matrix could have distorted relationships with fish biodiversity. For example, there are often notable diurnal changes in DO concentration, DO saturation, and temperature, especially in shallow systems (Dodson 2005; Miranda 2005). This variance cannot be avoided even when water quality samples are collected at fixed stations or times because day-to-day changes in cloud cover and wind action can change local conditions.

Ecological applications

Results herein provide the framework for a conceptual model that identifies the individual and collective influences of variables from different scales on each other and ultimately on oxbow lake fish biodiversity. This conceptual model is centered on the relationships between depth and the secondary and tertiary variables and between the percentage of agricultural land and the secondary and tertiary variables. Although hierarchically distant from fish biodiversity compared to water quality and primary productivity variables, depth and the percentage of agricultural land should be carefully considered as the focus of floodplain lake management schemes. Results can also be viewed as a feedback model of floodplain lake management in that primary variables can be manipulated for conservation and restoration purposes and secondary and tertiary variables can be used to monitor the success of such efforts. Similarly, the model may be useful in adaptive management of floodplain ecosystems. Although we have taken a reductionist approach to the analysis by examining the interactions between individual ecosystem components, results will ultimately foster the development of a more holistic approach to floodplain ecosystem conservation and management.

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