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Environmental influences on fish assemblage variation among ecologically similar glacial lakes

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Abstract The composition and structure of fish communities are affected by a variety of factors, both within the aquatic ecosystem and from the surrounding watershed. Many studies have examined what structures fish assemblages over broad spatial and environmental gradients. However, the influence of local environmental attributes on the observed variation in fish assemblages is less understood across finer spatial scales, where broad-scale climatic and anthropogenic factors are relatively similar. We used multiple linear regression to examine the relationships between environmental variables and various aspects of fish assemblages (including trophic function, community indices, and species composition) in 90 glacial lakes from northern Indiana, USA, from 1990 to 2010. Trophic structure and species composition were primarily related to water quality, whereas trophic level increased and omnivores declined as Secchi depth increased and phosphorus concentrations decreased. Species richness and diversity, in contrast, were positively linked to lake size and depth. We also found unique relationships among fish assemblages and environmental variables between samples collected using gill nets and night electrofishing, which may result from these gears sampling different assemblage components – therefore, relationships that were apparent in both sampling techniques (e.g., Secchi depth effects on trophic structure) may be the most robust and useful for improving aquatic ecosystem management on local scales.

Keywords Non-metric multidimensional scaling · Inland lakes · Secchi depth · Species richness · Trophic group · Species diversity

Introduction

Variation in the number, abundance, and trophic function of species in lentic assemblages can be driven by complex relationships with diverse environmental variables

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encompassing different spatial scales. Specifically, variation in aquatic communities may be linked not only to the physical attributes of the system (e.g., habitat structure, lake depth and size), but also environmental or climatological factors such as temperature and productivity (Carpenter et al. 1985; Wehrly et al. 1998; Deines et al. 2015). However, community variation among systems has been mainly examined in relation to only a few dominant environmental variables or across relatively broad spatial scales (Hall et al. 1999) which are not intended or able to detect and describe variation in community structure due to local, fine-scale processes (Chu et al. 2015).

By definition, local conditions drive variation in fish assemblages among systems across finer spatial scales. For example, larger and more complex aquatic systems can yield higher species richness, diversity, and evenness (Heck and Wetstone 1977; Friedlander and Parrish 1998). Further, anthropogenic land use in a lake's immediate catchment can alter sediment runoff and nutrient loading patterns and thereby lead to decreases in both water clarity and quality, changing abundances of vegetated or oxygenated habitats, and altering prey availability (Beckett et al. 1992; Hall et al. 1999; Meador and Goldstein 2003; Scavia et al. 2014). These can, in turn, influence the productivity and trophic structure of aquatic systems by decreasing the foraging success of higher trophic level predators and the amount of available niche space (Paine 1966; Persson et al. 1988; Walser and Bart 1999; Mehner et al. 2005). Examining these relationships while controlling for broad climatic gradients could therefore improve the ability to detect local environmental influences regulating fish assemblage structure in lakes.

The structure and function of biotic communities can be quantified and assessed using a variety of methods, including measures quantifying the numbers and types of species (e.g., Eadie and Keast 1984), trophic functionality expressed as overall community trophic level (Wilbur et al. 1974; Gaston et al. 1998; Nordström et al. 2010), or representation by different functional groups (e.g., insectivores, omnivores, and piscivores; Grabarkiewicz and Davis 2008). More complex assessments of multivariate species abundances can be used to examine patterns in community composition among or within systems (West et al. 2003; Wehrly et al. 2012). Often, species numbers or functional groups are used as indicators of overall assemblage function, stability, and health (Carpenter et al. 1985), where increased richness or food web complexity may reduce the invasibility of native ecosystems (Finke and Denno 2004) or dampen the effects of trophic cascades (Davis et al. 2005). In addition, different sampling techniques target different habitats and may vary in species or size-selectivity (Sullivan et al. 2015), which could result in differential assemblage characterizations that respond dissimilarly to environmental variables. Both sampling and quantitative methods to describe communities may thus encapsulate different aspects of community structure, but could contain some informational overlap, meaning variation in their potential relationships to environmental conditions may be difficult to interpret. Relationships that are consistent across gears or metrics may be the most robust and meaningful, while contrasting patterns may identify biases due to sampling or statistical methodology (Sullivan et al. 2015).

Better insights into the most consistent and influential fine-scale relationships driving community assembly and trophic structure may provide important information for enhancing or sustaining ecosystem stability and services. To better understand how local environmental conditions contribute to variation among fish assemblages, we examined 90 glacial lakes in northern Indiana, USA. These systems have similar geological origins, allowing us to control for historical effects and more accurately assess subtle variations in fish assemblages. Specifically, we examined how a suite of local environmental variables, including measures of lake morphology, lake catchment, and water quality, influenced variation in these fish assemblage metrics across lakes. We find significant influences of water quality and some evidence for the impacts of land use on the trophic structure of fish assemblages, whereas assemblage diversity was more strongly influenced by lake morphometry, suggesting different aspects of habitat interact to drive even subtle variation in fish assemblage structure among inland lakes.

Methods

Study area

Our study sites consisted of a census of 90 glacial lakes in northern Indiana surveyed by the Indiana Department of Natural Resources from 1990 to 2010 sampled using either night electrofishing or gill nets (Fig. 1). These lakes were created from the recession of glaciers following the end of the Wisconsin glaciation approximately 11,000 years ago (Eschman 1985). Most study lakes

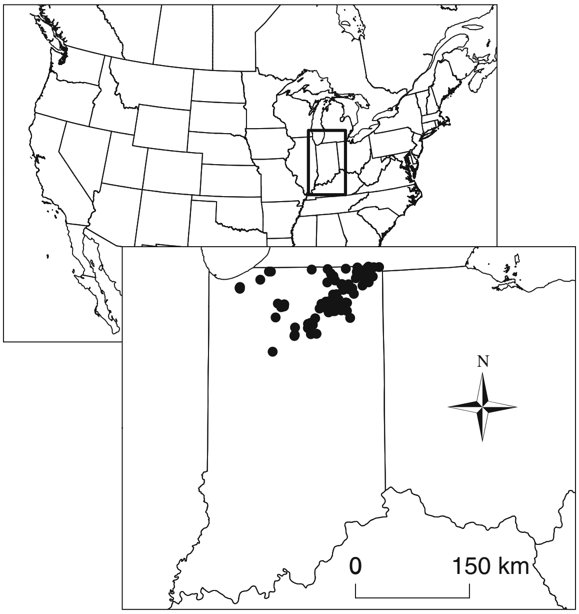

Fig. 1 Lakes where fish assemblages and water quality were sampled in northern Indiana from 1990–2010. In total, 90 lakes were included in all statistical analyses

were moderately-sized (mean area: 0.48 km^2), shallow (mean maximum depth: 13.5 m), mesotrophic to eutrophic systems (range summer chlorophyll-a:1.0–117.0 mg L^{-1}; see Online Resource 1, Table S1 for more details) near the southern edge of the extent of glacial lakes in the Midwest United States (e.g., Wehrly et al. 2012). In addition, sample lakes are proximately located (maximum distance between lakes 186 km; latitudinal span 40.77° to 41.76°) and have relatively similar fish assemblages (primarily warm-water species) and surrounding land use (primarily agriculture), which allowed us to assess how more subtle variation in both the terrestrial and aquatic environment may contribute to local variation in community structure.

Environmental variables

We characterized study lakes using a suite of abiotic variables that represented three different aspects of the abiotic environment: lake morphometry, lake catchment, and within-lake water quality (Online Resource 1, Table S1). Lake morphometry and catchment information was collected from the United States Geological Survey (USGS) National Hydrography Dataset (USGS 2004), the Indiana Department of Natural Resources (IDNR 1966; IDNR 1993), and the National Land Cover Dataset (NCLD) 2001 version 2 (Homer et al. 2007; see Perry 2011 for more information on quantifying catchment and morphometric variables). Water quality data were collected by the Indiana Clean Lakes Program through Indiana University, which sampled a random subset of lakes during summer (late June to early August) from 1990 to 2010. In total, 18 environmental variables were developed prior to analysis (Online Resource 1, Table S1).

Lake morphometry, lake catchment, and water quality characteristics can all have important impacts on fish assemblage structure in inland lakes. Lake size, depth, bed slope, and shape likely determine habitat structure (especially near shore) and availability; therefore larger, more complex lakes may provide additional or more diverse niche space for fish communities (Brucet et al. 2013). Catchment size and catchment land use influence nutrient and other allocthonous inputs to lakes, and therefore may be expected to alter the trophic structure and composition of food webs by affecting lower trophic processes (McGoff et al. 2013). Water quality influences both habitat availability and food web structure, as increased temperature, low oxygen, and poor water clarity may exclude sensitive or thermally-limited species, while phosphorus inputs, zooplankton abundance, and algal abundance may influence resource availability to different trophic guilds (Hayden et al. 2014). Therefore, we selected a set of abiotic and biotic environmental variables from a larger set of lake morphometry, lake catchment, and water quality variables to use as predictors of fish community structure. We first fit a global model and eliminated all potential explanatory variables with variance inflation factors greater than four to minimize multicollinearity among predictors (Burnham and Anderson 2002) while including those variables likely to influence fish assemblage trophic structure, composition, and diversity. The final set of lake morphometry variables selected included lake surface area (km^2), maximum depth (m), the ratio of maximum to mean depth, and shoreline development index (a measure of lake shape, where perfectly circular lakes have an SDI of unity. Selected lake catchment variables included total lake catchment area (km^2) and the proportions of the catchment composed of wetlands and agricultural land use. Selected water quality variables included mean phosphorus concentration (mg L^{-1}; mean of samples taken from epilimnion at 1 m depth and hypolimnion 1 m from lake bottom), chlorophyll-a (Chl-a) concentration (μg L^{-1}; mean of epilimnetic and hypolimnetic samples), zooplankton abundance (number L^{-1}; 63 μm mesh vertical net tow from depth at 1 % light intensity to surface), the proportion of the water column that remained oxygenated in summer (>1.0 mg L^{-1}), water temperature at 2 m depth (°C), and Secchi depth (m) (for more information on lake sampling, see http://www.indiana.edu/~clp/). By including variables across spatial scales, we sought to determine which environmental processes were most important in shaping different aspects of fish assemblages in our study lakes.

Fish sampling

Fish and water quality sampling occurred over the same 20 year period (1990–2010), although both types of data were not necessarily collected from the same lake in the same year (median difference = 2 years, range 0–9 years); therefore, we assumed that relative differences in water quality and fish assemblage structure were consistent among lakes during this time period. When multiple years of data were available, we selected data from the most recent year. Data from two different sampling techniques (night electrofishing and gillnetting) were separately analyzed to avoid errors induced by attempting to combine data from gears with different biases and assumptions, and also to examine whether relationships between environmental variables and fish assemblage varied between gears (Sullivan et al. 2015). All lakes that had a minimum effort of 30 min of electrofishing (mean = 59.7 min, median = 45 min, range 30–330 min) or two gillnet sets (mean = 5 nets, median = 4 nets, range 2–18 nets) were used for analyses, resulting in 88 lakes sampled via night electrofishing and 88 lakes sampled via gillnetting (totaling 90 lakes between the two sampling techniques). All fish samples were collected during standardized annual surveys performed by the Indiana Department of Natural Resources. Briefly, electrofishing was conducted at night using pulsed DC current (5–6 amps, 530 V, 60 pps with two netters) along transects lasting 15 min in duration. Gill nets (76 × 18 m) comprising five, 15 m panels (1.3, 2.5, 3.8, 5.1, and 6.4 cm square mesh) were set overnight beginning in depths less than 2 m and extended into deeper waters perpendicular from shore. Effort (number of transects or number of net sets) was scaled with lake surface area (see Sullivan et al. 2015 for complete details on fish sampling). Species that were rare (present in less than 1 % of lakes), or recently introduced through intentional or unintentional stocking (e.g., walleye *Sander vitreus* Mitchill, white perch *Morone americana* Gmelin) were removed from the data set to ensure that they did not bias later statistical analyses (Online Resource 1, Table S2; see below). These criteria removed 27 species from night electrofishing and 16 species from gillnetting catches.

Data analysis: fish assemblage response variables

For each gear, we defined fish assemblages using metrics that characterized the trophic structure, richness, diversity, and ordination-derived multivariate species composition in each lake (see details below). We first estimated the relative abundance of each species in each lake captured in each gear by calculating the proportional abundance of each species (i.e., the number of each species divided by the total catch from that gear). To evaluate assemblage trophic structure, we assigned both a trophic level and a trophic group to each species sampled from the study sites. We assigned trophic levels to each species based on the values determined from diet literature through an algorithm designed by FishBase (Froese and Pauly 2015). Species that did not have individual trophic levels were assigned the mean value of their genus. Fish species were also assigned to one of three trophic groups: insectivore (I), omnivore (O), and piscivore (P), as identified by the U.S. Environmental Protection Agency (Grabarkiewicz and Davis 2008). After we assigned both a trophic level and a trophic group to each fish species, we calculated the weighted mean trophic level of each study lake, where weights represented the numerical abundance of each species found in a lake and gear type. We also calculated the total proportional abundance of fish sampled from each study lake that was composed of each of the different trophic groups (I, O, and P).

For each lake and sampling method, we also quantified total species richness, Shannon-Wiener diversity, and Shannon-Wiener evenness. Shannon-Wiener diversity (H′) was calculated as

$$H' = -\Sigma(p_i \times \ln(p_i)) \tag{1}$$

where p_i is the proportion of individuals of species *i*. Shannon-Wiener evenness (J) was calculated as

$$\mathrm{J} = \mathrm{H}'/\ \ln(S) \tag{2}$$

where S is the total number of fish species. To account for variation in sampling effort among lakes, species richness, diversity, and evenness were rarefied to a standard amount of effort (either 30 min of electrofishing or 2 gillnet sets) using the bootstrapping approach outlined in Sullivan et al. (2015). We calculated all of these measures using R version 3.1.1 statistical computing software (R Core Team 2014).

Finally, we developed species composition response variables through multivariate ordination analyses, distilling among-lake patterns of multivariate relative abundance data into fewer interpretable variables. Species composition is often spatially autocorrelated (i.e., sites closer to one another have more similar assemblages than distant sites), and such autocorrelation can potentially introduce biases in analyses of environmental effects on spatially structured assemblages. Therefore, we first tested for significant spatial autocorrelation in the assemblages of each sampling technique using Mantel tests of assemblage Bray-Curtis distances against great circle distances among lakes (R package 'geosphere'; Hijmans 2016). Fish species relative abundances in gill net catches were positively autocorrelated globally (Mantel's $r = 0.26$, $P = 0.001$), whereas relative abundances in night electrofishing catches were positively autocorrelated at short distances (<8 km; $r = 0.17$, $P = 0.009$). To account for this, we obtained residuals of species relative abundances from the Mantel correlations (R package 'ecodist'; Goslee and Urban 2007) and transformed these residuals so that the minimum value equaled one to avoid negative distances. These transformed residual distances were then used in a resulting non-metric multidimensional scaling (NMDS) ordination with a maximum of 200 iterations (R package 'vegan'; Oskansen et al. 2013) to develop a small number of interpretable and spatially independent variables assessing species composition among lakes. We determined the final number of axes for each gear by using all axes that reduced ordination stress (a measure of model fit, where stress <0.20 is considered acceptable) by at least 0.05. This resulted in three axes for each sampling method (see Results), and hence three additional response variables (axis scores) per lake. To determine which species were driving assemblage structure differences among lakes after accounting for spatial autocorrelation in assemblage structure, we used Spearman correlations with Bonferroni correction to correlate each NMDS axis with the gear-specific species relative abundances.

Data analysis: multiple linear regression

We used multiple linear regression with model selection based on Akaike's Information Criterion (AIC) to determine which environmental variables were most important for explaining variation in each fish response variable (i.e., trophic level, proportion of omnivores, piscivores, and insectivores, species richness, Shannon-Wiener diversity, Shannon-Wiener evenness, and NMDS axes). Some transformations of response and explanatory variables were required to meet normality assumptions of linear regression in each gear. In both gears, proportion omnivores was cube-root transformed; lake area, catchment area, SDI, phosphorus concentration, Chl-*a*, and zooplankton density were natural log transformed; and proportion agriculture and proportion wetlands were arcsine-square root transformed. Additionally, Shannon-Wiener evenness was Box-Cox transformed ($\lambda = 10.4$; R package 'MASS'; Venables and Ripley 2002) for gillnet catches. To allow for direct comparison of variable importance among environmental variables, we standardized all explanatory variables to mean of zero and standard deviation of one, thus all coefficients could be interpreted as the change in the response with a one standard deviation change in the explanatory variable (Burnham and Anderson 2002).

We first fit linear models including all environmental variables as additive continuous covariates to each of our response variables. Similar to the NMDS analyses, we sought to account for spatial autocorrelation in our response variables by first using Moran's I tests and creating spatial correlograms depicting the strength of autocorrelation (Moran's I) among lakes for each response variable (R package 'ncf'; Bjornstad 2016). When significant spatial autocorrelation was detected, we used spatial eigenvector mapping (SEVM; R package 'spdep'; Bivand et al. 2013; Bivand and Piras 2015) to create additional spatial covariates to include in the multiple linear regression to account for any spatial autocorrelation (Diniz-Filho et al. 2003; Griffith and Peres-Neto 2006; Bivand and Piras 2015). Using this method, only gill net richness exhibited significant spatial autocorrelation under the global Moran's I test (Moran's $I = 0.05$, $P = 0.04$), whereas gill net diversity exhibited marginal spatial autocorrelation (Moran's $I = 0.04$, $P = 0.06$), and both required only a single spatial eigenvector to reasonably account for any spatial autocorrelation (see *Results*).

Once a global model including all environmental and spatial (as needed) variables was developed, forward and backward stepwise model selection based on AIC was employed to reach a preferred model with the lowest AIC value for each response. Conserving explanatory variables between gears allowed us to compare the relative importance of each variable both within and between sampling techniques for the same response variable, in addition to the explanatory power of different models (Burnham and Anderson 2002). All model selection was performed using R package 'MASS' (Venables and Ripley 2002).

Results

Fish sampling

In total, 56 species were sampled from the 90 study lakes, with 55 of these collected using night electrofishing and 34 collected using gill nets (Online Resource 1, Table S2). Electrofishing catches had a higher overall average trophic level and proportion of insectivores, while gill nets captured a higher average proportion of omnivores and piscivores (Table 1). When considering the community structure of our study sites, the average species richness per 30 min of electrofishing was almost twice that of two overnight gill net sets, but gillnetting had a higher average diversity and evenness across lakes.

We used three NMDS axes (stress = 0.113) to evaluate species composition using electrofishing (Online Resource 2, Table S5, Fig. S1). NMDS axis 1 described fish communities along an insectivore-piscivore gradient and was strongly positively correlated with largemouth bass (*Micropterus salmoides* Lacépède) abundance and negatively correlated to abundances of bluegill (*Lepomis macrochirus* Rafinesque; Online Resource 2, Table S5). NMDS axis 2 was similarly aligned along a trophic level gradient, and was positively correlated with yellow perch (*Perca flavescens* Mitchill), pumpkinseed (*Lepomis gibbosus* Linnaeus), lake chubsucker (*Erimyzon sucetta* Lacépède), and redfin pickerel (*Esox americanus americanus* Gmelin), and negatively correlated with piscivorous largemouth bass and spotted gar (*Lepisosteus oculatus* Winchell). Finally, variation in NMDS axis 3 was associated with a number of lower trophic level species, including negative correlations with abundances of redear sunfish (*Lepomis microlophus* Günther), redfin pickerel, and lake chubsucker, and positive correlations with gizzard shad (*Dorosoma cepedianum* Rafinesque), common carp (*Cyprinus carpio* Linnaeus), and longear sunfish (*Lepomis megalotis* Rafinesque) (Table 2; Online Resource 2, Table S5).

There were also three useful NMDS axes describing species composition sampled using gill nets (stress = 0.193; Online Resource 2, Table S6, Fig. S2). The first axis was negatively correlated with abundances of longnose gar (*Lepisosteus osseus* Linnaeus), redear sunfish, warmouth (*Lepomis gulosus* Cuvier), yellow bullhead (*Ameiurus natalis* Lesueur), and bluegill, but positively correlated with omnivores including gizzard shad and white sucker (*Catostomus commersonii* Lacépède). In contrast, axis 2 was positively correlated with abundances of yellow perch and largemouth bass, and negatively correlated with abundances of black crappie (*Pomoxis nigromaculatus* Leseur) and golden shiner (*Notemigonus crysoleucas* Mitchill). The third axis was negatively correlated with abundances of yellow perch, while being positively correlated with abundances of largemouth bass, yellow bullhead, and bowfin (*Amia calva* Linnaeus) (Online Resource 2, Table S6).

Table 1 Summary of trophic and community response variables for fish assemblages sampled using either night electrofishing or gillnetting across 90 study lakes in northern Indiana, with mean, standard deviation (SD), minimum, 25th quartile, median (Med.), 75th quartile, and maximum values

	Night electrofishing							Gill net						
Variable	Mean	SD	Min	25th	Med.	75th	Max	Mean	SD	Min	25th	Med.	75th	Max
Trophic level	3.69	0.17	3.08	3.59	3.68	3.78	4.17	3.42	0.26	2.53	3.31	3.48	3.58	3.96
Insectivore	0.65	0.15	0.24	0.57	0.66	0.76	0.91	0.45	0.20	0.00	0.32	0.49	0.61	1.00
Omnivore	0.05	0.09	0.00	0.00	0.02	0.05	0.50	0.19	0.21	0.00	0.03	0.12	0.31	0.94
Piscivore	0.30	0.14	0.09	0.20	0.28	0.37	0.75	0.35	0.17	0.00	0.24	0.33	0.44	0.87
Richness	11.6	3.1	6.0	9.0	12.0	14.0	20.0	6.2	2.3	1.0	4.8	7.0	8.0	11.0
Diversity	1.35	0.30	0.79	1.12	1.33	1.56	2.08	1.48	0.42	0.00	1.24	1.60	1.76	2.12
Evenness	0.56	0.11	0.30	0.49	0.56	0.64	0.84	0.84	0.13	0.00	0.81	0.88	0.92	1.00

Table 2 Coefficients (standard error) of environmental variables from AIC-selected multiple linear regressions predicting fish assemblage metrics from $n = 88$ lakes sampled using night electrofishing. Coefficients significant at $P < 0.05$ are bolded. Model R^2, F-statistics (with number of explanatory variables p and n-p-1 d.f.), and P-values are also provided. Insec: proportion of insectivores; Omni, proportion of omnivores; Pisci: proportion of piscivores; Div: Shannon-Wiener diversity; Eve: Shannon-Wiener evenness; MDS: non-metric multidimensional scaling axes. See Online Resource 1, Table S1 for description of explanatory variables

Response	Lake Area	Max D.	M:M D.	SDI	Ag	Wetld	Catch. Area	Phos.	Chl-*a*	%Ox	Temp	Zoop.	Secchi	R^2	$F_{p,n\text{-}p\text{-}1}$	*P*
Trophic level								**0.04 (0.02)**	-0.03 (0.02)					0.06	2.76	0.069
Insec								-0.03 (0.02)					**0.04 (0.01)**	0.15	7.48	0.001
Omni			-0.03 (0.02)			-0.03 (0.02)			0.05 (0.03)				-0.03 (0.02)	0.25	7.03	<0.001
Pisci				0.03 (0.01)				**0.04 (0.01)**			-0.03 (0.01)			0.11	3.56	0.018
Richness		**0.78 (0.32)**		0.60 (0.37)			0.59 (0.37)							0.23	8.25	<0.001
Div		0.06 (0.03)		**0.09 (0.03)**	-0.05 (0.04)	-0.06 (0.04)					**-0.09 (0.03)**	**-0.09 (0.03)**		0.25	4.42	<0.001
Eve			0.02 (0.01)		-0.02 (0.01)			-0.02 (0.01)			**-0.03 (0.01)**	**-0.03 (0.01)**	-0.02 (0.01)	0.27	4.91	<0.001
MDS1		0.22 (0.14)		0.21 (0.14)				0.18 (0.13)			**-0.41 (0.13)**			0.15	3.64	0.009
MDS2								**-0.21 (0.09)**				**-0.35 (0.09)**		0.23	12.39	<0.001
MDS3	0.19 (0.12)		-0.15 (0.09)	-0.16 (0.11)			**0.25 (0.11)**				0.12 (0.09)	**-0.18 (0.09)**	**-0.23 (0.07)**	0.29	4.72	<0.001

Multiple linear regression: night electrofishing

Considering significant relationships, our final models explained between 6 and 29 % of the variation in our electrofishing-based fish assemblage response variables (Table 2). Variation in the trophic structure of electrofishing catches was largely driven through relationships with water quality variables. Specifically, Secchi depth was significantly positively related to the proportion of insectivores (Fig. 2a), whereas phosphorus concentration was significantly positively related to the proportion of piscivores. Community complexity was influenced by a combination of lake morphometry and water quality. Richness was positively related to maximum depth (Fig. 3c), whereas diversity was related to SDI, the index of lake shoreline complexity. Both diversity and evenness were negatively related to temperature and zooplankton abundance, indicating warmer, more zooplankton-rich lakes tended to contain less diverse and even assemblages. Finally, assemblage composition was largely driven by variation in water quality. NMDS axis 1 was negatively related to temperature, whereas axis 2 was negatively related to phosphorus and zooplankton. Axis 3 was positively related to catchment size, and negatively related to both zooplankton abundance and Secchi depth.

Multiple linear regression: gill net

We were able to explain 7 to 38 % of the variation in fish assemblage metrics calculated from gill net catches (Table 3), often with more complex models than selected for night electrofishing catches and surprisingly few similarities between the final models selected for the two sampling techniques. Gillnet trophic structure was influenced by a suite of lake morphology, catchment, and water quality variables. Trophic level and piscivore abundance increased with maximum depth, water column oxygenation, and catchment wetlands (Fig. 4b), but trophic level decreased with shoreline complexity and piscivore abundance decreased with Secchi depth. Insectivore abundance increased with both catchment agriculture and wetlands, in addition to Secchi depth (in fact, this was the only consistent relationship between sampling techniques; Fig. 2), while omnivore abundance exhibited the opposite relationships (Fig. 2d), in addition to decreasing with lake area and increasing with shoreline complexity. Gillnet richness was positively related to lake area (Fig. 3b) and negatively related to

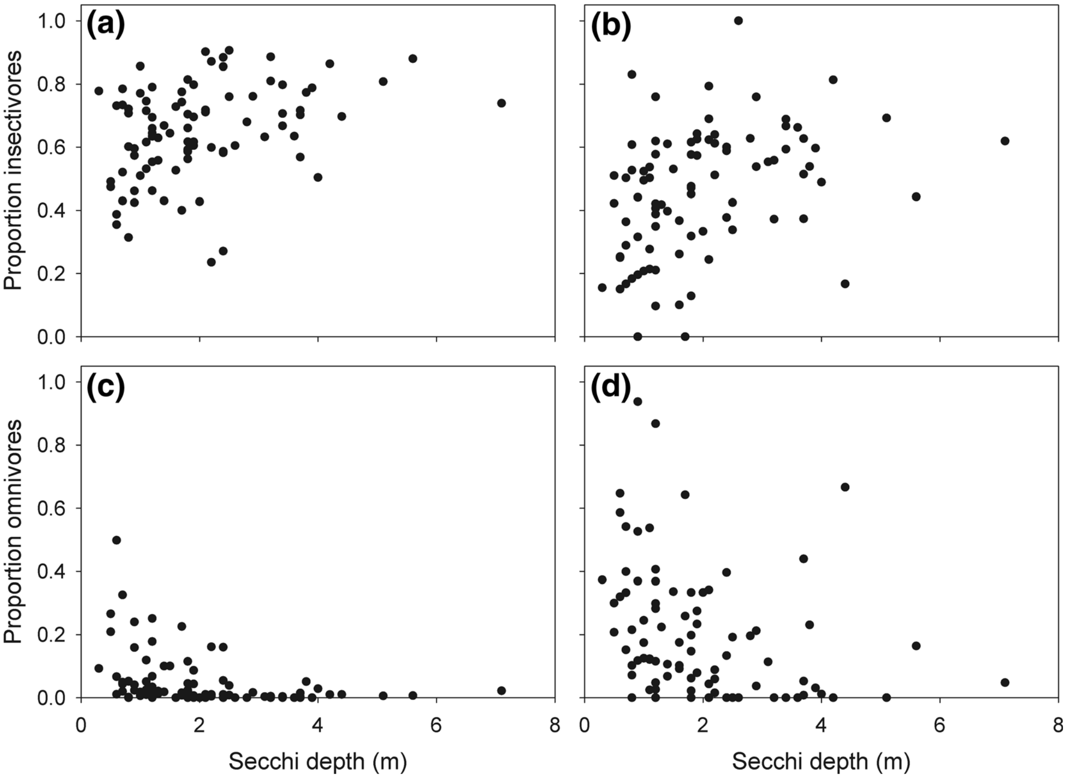

Fig. 2 Relationships between Secchi depth (m) and the proportion of insectivores (**a** and **b**) and omnivores (**c** and **d**) comprising night electrofishing (**a** and **c**) and gillnet (**b** and **d**) samples

Secchi depth. While diversity was also positively linked to lake area (Fig. 3c), it also increased with catchment agriculture and wetlands (Fig. 4c) and decreased with the ratio of maximum to mean depth. Evenness, in contrast, was negatively related to lake area, in addition to phosphorus and water column oxygenation, and also positively related to shoreline complexity. Gillnet catch composition was similarly influenced by large numbers of variables. NMDS axis 1 was negatively related to proportional wetlands coverage in the catchment (Fig. 4d), total catchment area, and Secchi depth, whereas axis 2 was positively related to agriculture and temperature but negatively related to zooplankton abundance. Lastly, axis 3 was negatively related to lake area and positively related to shoreline complexity.

Discussion

By examining a large number of aquatic systems that exist within relatively similar latitudes and catchments, we were able to identify the environmental variables influencing variation in fish assemblages across a relatively fine spatial scale. Most of our study lakes were in catchments dominated by intensive agriculture which has been shown to have strong effects on assemblages through impacts on water and habitat quality (Wichert and Rapport 1998). However, we still detected significant influences of lake water quality and morphometry on various aspects of fish assemblages beyond the effects of catchment size and land use. These relationships demonstrate the large number of environmental influences on fish assemblage structure and function in lentic systems, even when viewed at fine spatial resolution.

Environmental relationships with fish assemblage structure

The trophic structure of fish assemblages were most affected by water quality, particularly Secchi depth (gill nets) and phosphorus concentration (night electrofishing). Secchi depth reflects a suite of other biotic and abiotic variables (e.g., total suspended solids, plankton abundance) that reflects a number of abiotic and biotic

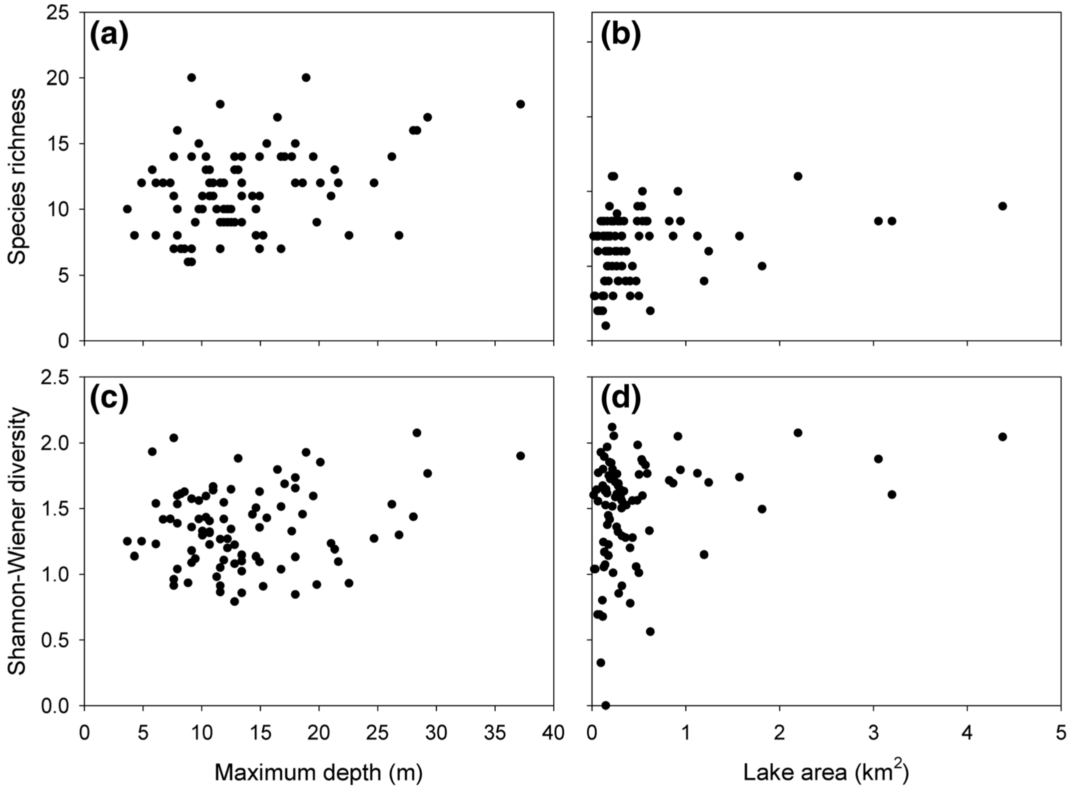

Fig. 3 Relationships between night electrofishing species richness, Shannon-Wiener diversity, and maximum lake depth (**a** and **c**), and gillnet species richness, Shannon-Wiener diversity, and lake area (**b** and **d**) observed across 90 northern Indiana glacial lakes

processes in lakes (e.g., sediment loading, phytoplankton production and consumption; Tilzer 1988), while increased phosphorus often promotes eutrophication of freshwater systems (Lathrop and Carpenter 2013). In this study, most of the sample lakes were meso- to eutrophic, therefore, variation in these factors likely represent the level of system eutrophication. In addition, the relatively limited variability in lake trophic state suggests that our models were able to detect subtle effects of eutrophication on lake trophic structure even among generally highly eutrophied systems. Decreases in Secchi depth (or increases in phosphorus) consistently led to larger proportions of omnivorous species (e.g., cyprinids) and lower proportions of insectivorous species (e.g., percid, centrarchid, and catostomid species). These findings are similar to patterns observed in some mesotrophic and eutrophic lakes, which shifted from percids to cyprinids as total phosphorus levels increased (Jeppesen et al. 2000; Olin et al. 2002). Increased numbers of omnivorous and zooplanktivorous cyprinids, in addition to species with destructive foraging behaviors like common carp (*Cyprinus carpio* Linnaeus), may reduce zooplankton and macrophyte densities and decrease water clarity, thus altering water quality due to higher-level processes (Jeppesen et al. 1997; Jeppesen et al. 2000). Systems with inherently poor water clarity also suffer from reduced macrophyte abundance (Chambers and Kaiff 1985; Jeppesen et al. 1999), which could alter benthic invertebrate production and limit resources available to primarily insectivorous fish species (Beckett et al. 1992; Miller and Crowl 2006; Nolby et al. 2015).

Wetlands have been consistently implemented as water quality control measures across the world (Verhoeven et al. 2006), as they prevent excess nutrients and sediments from entering connected waterways, thereby reducing lake turbidity and algal growth (Johnston 1991). We observed strong effects of catchment wetlands on fish assemblages in gill nets, as increases in the proportion of wetlands in lake catchments increased mean trophic level and decreased omnivore abundance, likely through similar mechanisms as described with the impacts of Secchi depth. We should also note that increases in catchment wetlands, at least as

Table 3 Coefficients (standard error) of environmental variables from AIC-selected multiple linear regressions predicting fish assemblage metrics from $n = 88$ lakes sampled using gill nets. Coefficients significant at $P < 0.05$ are bolded. Model R^2, F-statistics (with number of explanatory variables p and n-p-1 d.f.), and P-values are also provided. Insec: proportion of insectivores; Omni, proportion of omnivores; Pisci: proportion of piscivores; Div: Shannon-Wiener diversity; Eve: Shannon-Wiener evenness; MDS: non-metric multidimensional scaling axes; SEV: spatial eigenvector. See Online Resource 1, Table S1 for explanatory variable definitions

Response	Lake Area	Max D.	M:M D.	SDI	Ag	Wetld	Catch. Area	Phos.	Chl-*a*	%Ox	Temp	Zoop.	Secchi	SEV	R^2	$F_{p,n-p-1}$	*P*
Trophic level		**0.10 (0.03)**		**-0.07 (0.03)**		**0.10 (0.02)**	0.05 (0.03)			**0.09 (0.03)**		0.04 (0.03)			0.28	5.35	<0.001
Insec					**0.06 (0.03)**	**0.06 (0.03)**				-0.04 (0.02)			**0.08 (0.02)**		0.23	6.11	<0.001
Omni	**-0.08 (0.03)**			**0.10 (0.03)**	**-0.08 (0.03)**	**-0.14 (0.03)**						0.05 (0.03)	**-0.08 (0.02)**		0.38	8.30	<0.001
Pisc		**0.049 (0.02)**			-0.03 (0.02)					**0.07 (0.02)**		0.03 (0.02)	**-0.04 (0.02)**		0.13	2.47	0.039
Richness	**0.68 (0.22)**		-0.33 (0.23)						-0.37 (0.26)				**-0.61 (0.20)**	**9.89 (2.05)**	0.40	11.11	<0.001
Div	**0.16 (0.04)**		**-0.14 (0.04)**		**0.14 (0.05)**	**0.12 (0.05)**								0.81 (0.43)	0.30	6.91	<0.001
Eve	**-10.05 (3.28)**			**9.12 (3.23)**				**-15.56 (3.01)**		**-8.28 (3.08)**		4.01 (2.52)			0.32	7.65	<0.001
MDS1				0.22 (0.14)		**-0.34 (0.13)**	**-0.35 (0.14)**		0.26 (0.16)				**-0.30 (0.11)**		0.35	8.88	<0.001
MDS2			0.19 (0.13)		**0.35 (0.14)**		-0.23 (0.14)	-0.28 (0.15)		-0.27 (0.13)	**0.25 (0.13)**	**-0.33 (0.14)**			0.22	3.27	0.004
MDS3	**-0.34 (0.12)**			**0.37 (0.16)**											0.07	3.40	0.038

a proportion of the total catchment area, necessarily reduce the proportion of agriculture or urban development in lake catchments, thus this variable may reflect more than the sole effects of wetlands on lake fish assemblages. Even so, relatively small changes in catchment wetlands (2–7 % of catchment area) can have large effects on nutrient loading to receiving systems (20–50 % reductions; reviewed in Verhoeven et al. 2006). We suggest that these influences on water quality will indeed scale up to influence fish assemblages – based on our results, increasing wetlands by ~5 % could yield a 10–15 % decrease in omnivore abundance and a 0.10 increase in trophic level, often desired outcomes for fisheries managers (Verrill and Berry 1995; Pace et al. 1999). The construction and conservation of wetland areas and riparian buffers thus appears to be a useful strategy to not only manage water quality (Verhoeven et al. 2006) but to also influence the trophic structure of fish assemblages, even with fairly small projects (1–5 % of catchment area).

In both gears, species richness and diversity were influenced by a metric that represented lake size – lake area in gill nets or maximum depth in night electrofishing. Species richness is structured by evolutionary and environmental variables which determine the rates of speciation, extinction, and immigration of different species (MacArthur and Wilson 1967; Viana et al. 2014). We attempted to control for variation in richness due to evolutionary history by examining lakes with relatively similar geological histories, which suggests variation we observed in richness is likely due to environmental differences among lakes (Eschman 1985). Increased habitat size and energy availability may allow for increased trophic specialization and niche sharing, thereby promoting species co-existence and increasing assemblage richness and diversity (Mason et al. 2008; Wagner et al. 2014), while small or degraded sites are often dominated by generalists (Rich 2003). Larger lakes also tend to encompass larger catchments, and therefore exhibit increased connectivity to other aquatic systems (Riera et al. 2000), which may promote immigration of additional species or mitigate local extirpation risks, leading to increased species richness and diversity in these larger, more connected systems (MacArthur and Wilson 1967). Measures of dispersal and connectivity were not considered here, but are important to maintaining species richness in other lentic systems (Guimarães, et al. 2014; Nolby et al. 2015). Therefore, the link between system size and assemblage diversity and

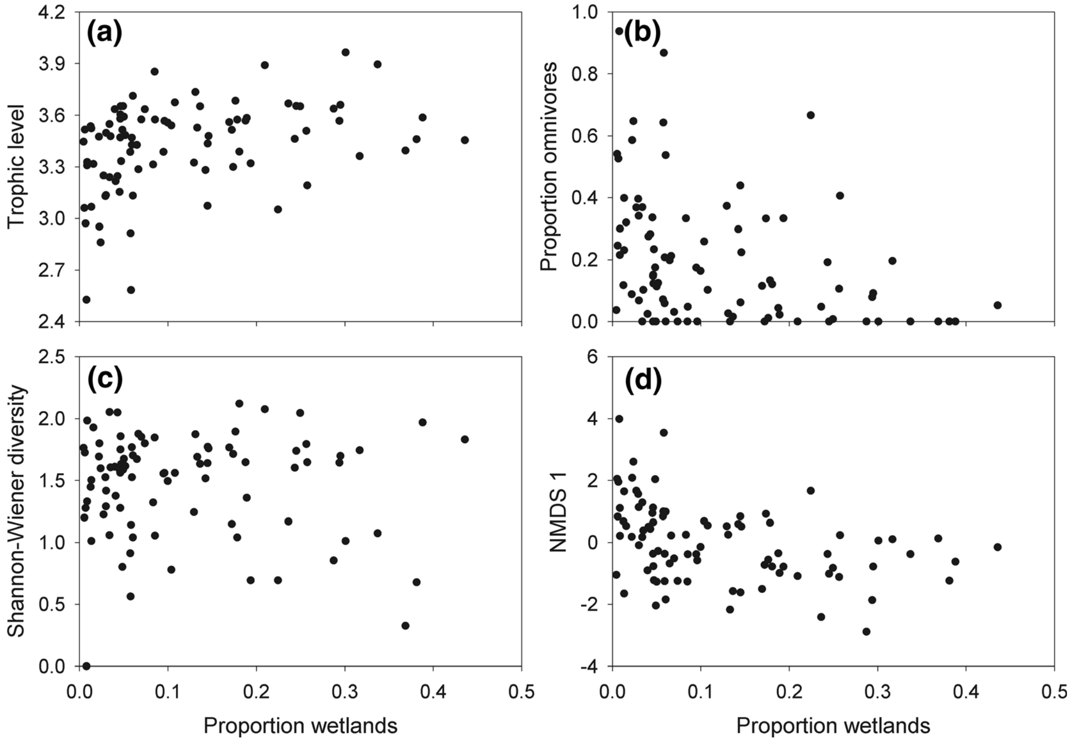

Fig. 4 Relationships between metrics of gill net assemblage structure and the proportion of wetlands in the lake catchment, including: **a** mean trophic level, **b** proportion of the assemblage composed of omnivores, **c** Shannon-Wiener diversity, and **d** non-metric multidimensional scaling (NMDS) axis 1, which correlated negatively with trophic level, insectivores, and evenness, and positively with omnivores

richness appears to operate through similar mechanisms of habitat availability and species dispersal even at fine spatial scales among small inland lakes.

Fish assemblage evenness was also generally influenced by metrics of lake morphometry (e.g., lake area) but was also often related to water quality, including negative relationships with phosphorus and oxygenation (in gill nets), and temperature and zooplankton abundance (in electrofishing). Species evenness represents a balance between the number of different species and the relative numerical dominance of certain species in the assemblage, where lakes that are dominated by few species have relatively low evenness (Fausch et al. 1990). Evenness declining with increases in phosphorus, oxygen, zooplankton, and temperature may represent a shift from assemblages dominated by omnivorous or zooplanktivorous cyprinid species tolerant to eutrophic conditions, as often seen in eutrophic lakes (Persson et al. 1991; Olin et al. 2002), to assemblages more evenly distributed among insectivorous and zooplanktivorous species less tolerant to lake eutrophy, as observed in Danish (Jeppesen et al. 2000) and U.S. lakes (Tango and Ringler 1996), suggesting changes in assemblage dominance will occur with changes in lake water quality.

Most NMDS axes related similarly to environmental variables as variables related to trophic structure, being largely influenced by water quality and catchment characteristics. The structure of species functional groups in streams is more strongly driven by local-scale processes as compared to taxonomic variation across broader regional scales (Hoeinghaus et al. 2007). The similarities in important assemblage structuring factors in lakes suggest a similar mechanism, where assemblage trophic structure best defines relative differences among systems, rather than the number or distribution of species, and is most strongly regulated by variance in water quality and concomitant variability in catchment size or land use. For example, night electrofishing NMDS axis 1 ordinated along a bass to bluegill gradient, and was explained primarily by temperature, suggesting warmer temperatures may exclude bass from nearshore areas, as bass exhibit cooler thermal optima for growth than bluegill (Beitinger and Fitzpatrick 1979). Gill net axis 3, representing a gradient between yellow perch and largemouth bass, yellow bullhead, and bowfin, was influenced by lake size and SDI, suggesting smaller, more homogenous lakes contain more yellow perch capable of utilizing both nearshore and pelagic habitats, and fewer species reliant on structured nearshore habitats (Lane et al. 1996). Multivariate ordination methods may therefore be a useful tool for describing variation in the structure of fish assemblages while also incorporating important, species-specific information that allows for deeper investigations of the role local-scale variation in environmental conditions plays in affecting fish assemblage structure.

Differences between sampling techniques

There were several relationships between potential explanatory variables and fish assemblage response variables that were captured differentially between sampling techniques. For example, land use was strongly related to gill net trophic structure, but not at all to trophic structure of night electrofishing catches. In addition, water column oxygenation was important to species relative abundances in gill net catches, but temperature and zooplankton were more important to relative abundances in night electrofishing catches. These differences are potentially due to differential species-specific selectivities between the sampling gears. Gill nets were set in different habitats (e.g., deeper waters further offshore) than the areas sampled via electrofishing and therefore the two methods likely sample different aspects of the fish community (Menezes et al. 2012; Sullivan et al. 2015). The more offshore species sampled with gill nets may be less affected by nearshore variation in, for example, surface water temperature (Magnuson et al. 1979) and more by variation in lake depth or bottom structure. Nearshore electrofishing catches are also often dominated by littoral, schooling species and may represent a more biased sample of fish assemblages (Menezes et al. 2012). Therefore, gillnet catches could more accurately represent the response of fish assemblages to environmental variation or manipulation, such as variation in nutrient loading from different land use practices. Gill nets also more effectively sample coolwater species (e.g., northern pike *Esox lucius* Linnaeus, yellow perch) that may be more responsive than species commonly caught using night electrofishing (e.g., *Lepomis* species, common carp) to changes in environmental conditions (Leach et al. 1977; Grabarkiewicz and Davis 2008). In the face of such uncertainty, relationships describing similar patterns in both gears (i.e., the effects of Secchi depth on trophic structure) or similarities in the scale of important variables (i.e., lake morphometry influences on diversity, or water quality influences on trophic structure) may be more robust, while relationships occurring in only one gear may be influenced by such bias and require further examination before asserting their importance.

Conclusions

In contrast to past studies demonstrating how broad-scale factors may structure fish assemblages over large latitudinal gradients, we have shown that fine-scale processes can drive more subtle variation in fish assemblage structure among similar systems. An increased understanding of these local dynamics can better inform management practices, as well as provide more detailed implementation strategies to resource managers. For instance, such fine-scale factors are more likely to be available for closer monitoring or control by local resource managers, and therefore provide more practical and accessible means for fisheries management. More broadly, our results suggest that fish assemblages are structured through complex relationships among a number of abiotic factors. Having a more thorough understanding of these abiotic interactions reveals how local environmental conditions influence the structure and function of aquatic ecosystems.

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Compliance with ethical standards

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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