

The role of trait-based approaches in understanding stream fish assemblages

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SUMMARY

1. The use of trait-based approaches to examine the ecology of stream fish assemblages is increasing. However, selection of traits that will be useful in testing spatial or temporal hypotheses about ecological organisation is currently limited by availability of data, rather than empirical evaluation.

2. We analysed two data sets of stream fish assemblages to compare taxonomy and trait-based approaches. The Wabash River temporal data set is based on 25 years of boat electrofishing collections over a 230-km river distance. The Indiana Department of Environmental Management data set of stream collections in the state of Indiana was selected to represent a spatial database. We compared several trait-based approaches: reproductive guilds, life history variables, biomonitoring metrics, ecosystem-based functional guilds and feeding and ecosystem interaction guilds.

3. Analyses of fish assemblages that are designed to detect how environmental variation structures fish assemblages can expect similar results using taxonomic or trait-based approaches. Results of trait-based approaches will vary according to the spatial extent of the region and the number of unique entities of trait groups for a given data set. However, taxonomic analyses accounted for more variation than any trait-based analyses.

Keywords: assemblage structure, functional organisation, species traits, stream fishes, trait-based approach

Introduction

Studies that examine the relationships between fish assemblages and environmental variables traditionally have used analyses of species (Grossman *et al.*, 1998) rather than trait-based groups. Descriptions of assemblage structure using species abundances (taxonomy) provide strong support for analyses of correlations with environmental variables at multiple scales (Taylor, Winston & Matthews, 1993; Matthews, 1998; Angermeier & Winston, 1999). For example, differences in local-scale habitat variables may result in variation among local fish assemblages (Gorman &

Karr, 1978). As spatial scale increases from reaches to whole streams, regional variables (e.g. hydrology and geomorphology) provide explanation of fish assemblage variation (Angermeier & Winston, 1999). At catchment and larger scales, variation of species abundances can be explained based on biogeographic and range-size factors (Hocutt & Wiley, 1986; Williams *et al.*, 1993). However, prediction of assemblages using taxonomy neglects the structure and function of ecosystem processes.

Trait-based approaches to understanding ecological organisation provide a link between ecological function and environmental variation at assemblage-level scales (Goldstein & Meador, 2005; Frimpong & Angermeier, 2010; Webb *et al.*, 2010). Studies of species traits in stream community ecology have been valuable for explaining assemblage structure among

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drainages (Gatz, 1979; Hoeinghaus, Winemiller & Birnbaum, 2007), continents (Lamouroux, Poff & Angermeier, 2002), streams with varying hydrological regimes (Poff & Allan, 1995) and to evaluate habitat degradation (Goldstein & Meador, 2005). In addition, the functional assemblage structure of stream organisms varies predictably with river distance in response to variation in nutrient sources and physical attributes that change with stream size (Vannote *et al.*, 1980). However, the selection of traits that allow prediction of spatial and temporal changes in assemblages with environmental variation is currently limited by availability of data (Frimpong & Angermeier, 2010) or perhaps expert knowledge.

Analyses of trait-based categories have limitations and assumptions because they are categorisations of organisms that have ontogenetic and temporal shifts in trophic ecology and habitat use (Hoeinghaus *et al.*, 2007). Hoeinghaus *et al.* (2007) justified their use based on success in development of community assembly rules (Brown, Gox & Kelt, 2000). Further justification is from successful applications of functional group analyses. Hoeinghaus *et al.* (2007) provided a comparison of taxonomy and traits for a Texas spatial data set, and Angermeier & Winston (1999) used similar approaches for conservation application. Although trait-based analyses have been successful in these examples, the use of traits in analyses of assemblages and environmental variation may not always provide better explanation than the traditional taxonomic description of assemblage structure. However, there are few comparisons of trait-based categorisations (Erös *et al.*, 2009).

In this paper, we compare the use of taxonomy and five trait-based categories for two data sets. We examine trait-based approaches as alternatives to taxonomy in fish assemblage classification spatially and temporally along a single river gradient (the Wabash River) and spatially among sites in a larger geographic region comprising multiple catchments (IN, U.S.A.). Our working hypotheses are (i) for fish assemblages in a single river, a trait-based description of assemblage structure will correlate more strongly with river gradients than will a taxonomy-based description of structure and (ii) for analyses of fish assemblages in a larger geographic region, a trait-based description of assemblage structure will correlate more strongly with local habitat variation and water quality variation than taxonomy-based assemblage structure.

Methods

The databases and taxonomic and trait-based approaches

The Wabash River database is based on 25 years of boat electrofishing collections at multiple sites (Pyron, Lauer & Gammon, 2006) that provided information for temporal and spatial analyses. These data were collected in a consistent manner at 500-m long sites in outer bend habitats. The Indiana data set is from a large geographic region and derives from collections by the Indiana Department of Environmental Management (IDEM) using a Probabilistic Monitoring Program (IDEM 2006) at 1220 sites. Although the IDEM data were collected between 1996 and 2007, sampling occurred only once per site. Our analyses tested for spatial or temporal variation in fish assemblages using taxonomy, life history attributes (Winemiller & Rose, 1992), reproductive guilds (Balon, 1975, 1981) condensed by Simon (1999), biomonitoring metrics (Hitt & Angermeier, 2008), functional groups of Poff & Allan (1995) and functional groups of Matthews (1998) with interactions based on feeding and ecosystem interactions described in detail by Higgins & Strauss (2008). Taxonomic data were transformed into traits using weighted abundances in which all individuals (not presence/absence of species) were summed according to their trait membership. We categorised species as listed in Appendix S1. Our approach was to reduce assemblage data using ordinations and test subsequent axes for correlations with river location and year (or environmental variables). The Wabash River analyses used the complete data sets of multiple sites across multiple years, and the Indiana analyses used the complete data set without comparing by collection year, as our primary interest was to compare fish traits and taxonomy explained by environmental variation. Although these analyses can be viewed as confounding spatial and temporal variation, our preliminary analyses and the results of Beugly & Pyron (2010) showed extremely high within-site year-to-year variation and individual year longitudinal river distance variation.

Wabash River analyses

Our analyses tested for temporal and river distance variation among fish assemblages using ordinations of the taxonomic and trait-based categories. We used

reciprocal averaging (RA) multivariate analysis (PC-ORD, McCune & Mefford, 1999) to reduce the dimensions of the data, followed by correlation analyses of subsequent site scores on axes with collection year and site locations. RA is an indirect gradient ordination approach that uses an iterative weighted averaging of site scores and has been useful at identification of environmental gradients in community ecology studies (Angermeier & Winston, 1999; Zeug & Winemiller, 2007). We transformed abundances with $\log(x + 1)$ and selected the option to downweight rare species. We corrected for multiplicity of tests using the false discovery rate of Benjamini & Hochberg (1995), an approach for quantifying type I errors by controlling the expected proportion of false positives, rather than controlling for false positives as with Bonferroni alpha control (Benjamini & Hochberg, 1995; Verhoeven, Simonsen & McIntyre, 2005). We estimated false discovery rates using QVALUE ver. 1 software (Storey, 2002).

Indiana analyses

We first performed ordinations of statewide variation in fish assemblages to explain a habitat quality index [Qualitative Habitat Evaluation Index (QHEI), Rankin, 1989] and water quality variables. QHEI is an assessment of habitat quality based on a composite score from metrics of substrate, instream cover, channel morphology, riparian zone, pool quality, riffle quality and map gradient. QHEI metrics and water quality variables were reduced to fewer, uncorrelated variables by principal component analyses (PCA) using correlation matrices. Significant PCA axes were identified by the broken-stick model (Jackson, 1993). We again used RA multivariate analysis followed by correlation analyses of subsequent axes with PCA scores for habitat quality (QHEI) and water quality.

A second ordination approach used canonical correspondence analysis (CCA) to compare patterns of environmental variables as predictors of fish assemblage structure among sites based on taxonomy and trait-based approaches (Hoeinghaus *et al.*, 2007). Significant variables were identified in CCA using manual selection with 999 Monte Carlo permutations and alpha of 0.05. We did not use the false discovery rate for these analyses because only significant variables were selected in the CCA. Final CCA

ordinations were plotted using only significant environmental variables.

Results

Wabash River analyses

A total of 585 collections varied from 1 to 29 sites per year and resulted in 45 562 individuals in 63 taxa. The ten species with highest abundances were gizzard shad (*Dorosoma cepedianum* Lesueur), common carp (*Cyprinus carpio* Linnaeus), flathead catfish (*Pylodictis olivaris* Rafinesque), river carpsucker (*Carpionodes carpio* Rafinesque), channel catfish (*Ictalurus punctatus* Rafinesque), freshwater drum (*Aplodinotus grunniens* Rafinesque), shorthead redhorse (*Moxostoma macrolepidotum* Lesueur), spotfin shiner (*Cyprinella spiloptera* Cope), golden redhorse (*Moxostoma erythrurum* Rafinesque) and emerald shiner (*Notropis atherinoides* Rafinesque). The first RA axis for taxonomy separated sites with higher abundance of creek chub (*Semotilus atromaculatus* Mitchill) and bluntnose minnow (*Pimephales notatus* Rafinesque) (Fig. 1a). The second axis separated sites with increased creek chub and river redhorse (*Moxostoma carinatum* Cope) from sites with golden shiner (*Notemigonus crysoleucas* Mitchill) and river carpsucker.

The trait-based RA analyses results varied among traits with no apparent similarity among the trait approaches. The first RA axis for Matthews (1998) functional groups separated sites with taxa that physically disturb substrates and that eat eggs and are stone turners (Fig. 1b). The second axis separated sites with increased abundances of invertivore drift feeders from sites with invertivores that crush snails. The first RA axis for Hitt & Angermeier's (2008) biomonitoring metrics separated sites with increased abundances of taxa tolerant to environmental degradation (= tolerant) from sites with increased abundances of taxa intolerant to degradation (= intolerant, Fig. 1c). The second axis separated sites with increased abundances of taxa intolerant to degradation from invertivore–piscivore taxa. The first RA axis for Balon's (1975, 1981) reproductive guilds separated sites with taxa that are nest spawners on rock and gravel (Fig. 1d) while the second axis separated sites with increased abundances of taxa that are internal bearers from sites with increased abundances of nest spawners on miscellaneous substrates. The first RA

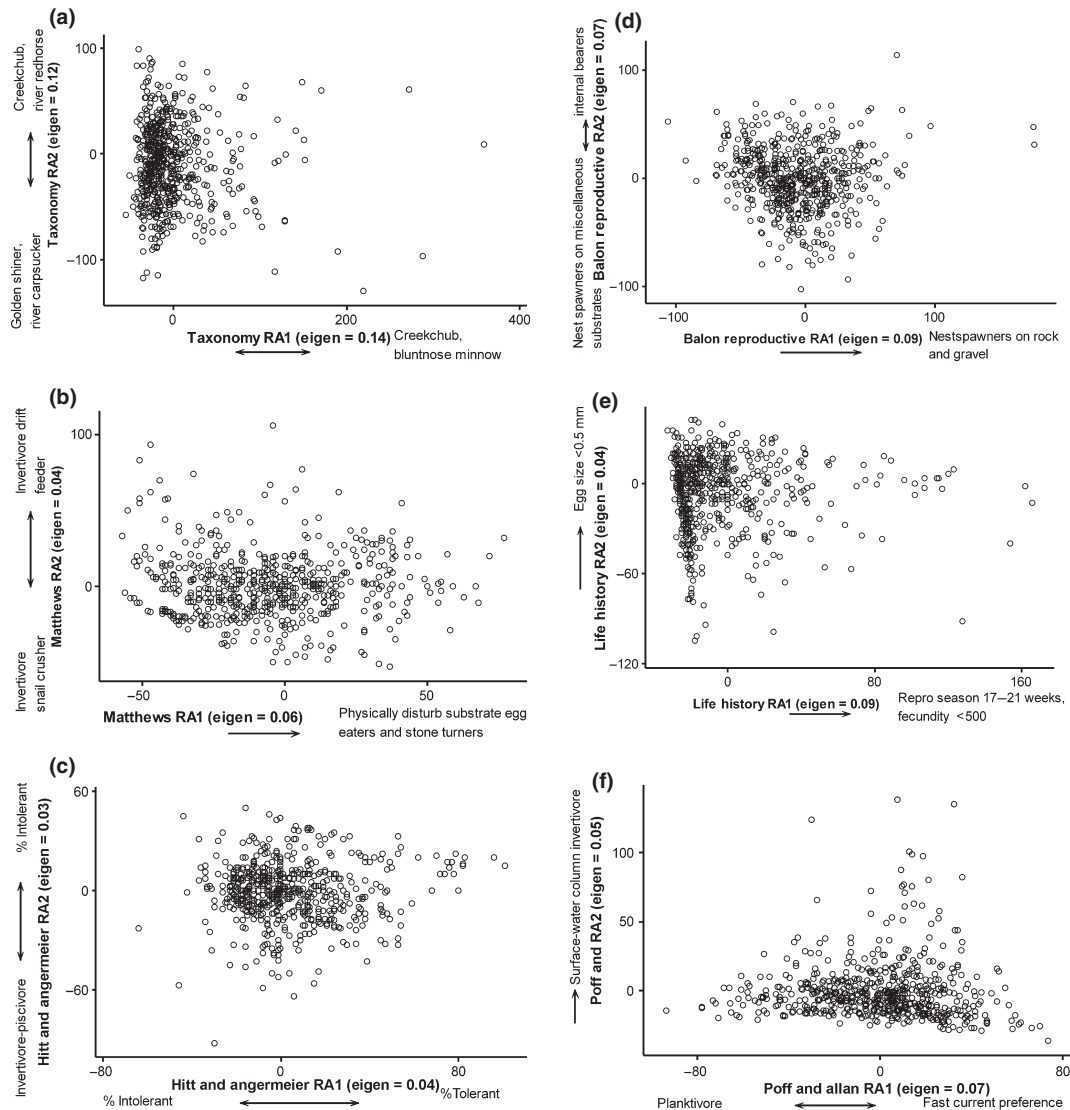


Fig. 1 Reciprocal averaging axes for the Wabash River assemblages using (a) taxonomy, traits of (b) Matthews (1998), (c) Hitt & Angermeier (2008), (d) Balon (1975, 1981) reproductive guilds, (e) Winemiller & Rose (1992) life history traits and (f) Poff & Allan (1995) functional traits. Eigenvalues are in parentheses, and highest loading taxa or traits are listed on figures.

axis for Winemiller & Rose's (1992) life history traits separated sites with increased abundance of taxa with long reproductive seasons and low fecundity (Fig. 1e) while the second separated sites with increased abundance of taxa with small eggs. The first RA axis for Poff & Allan's (1995) functional traits separated sites with increased abundance of taxa that prefer fast current from sites with increased abundance of planktivores (Fig. 1f). The second axis separated sites with increased abundance of surface-water column invertivores.

The strongest correlation between a taxonomic RA axis and year or river location was for RA2 with river

location (0.48; Table 1). Upstream river locations had increased abundances of creek chubsucker (*Erismyzon oblongus* Mitchell), river redhorse and hogsucker (*Hypentelium nigricans* Lesueur) while downstream river locations had increased abundances of golden shiner and river carpsucker (data shown in Figures in Appendix S2). At least one RA axis for each trait-based approach was significantly correlated with river location (Table 1). In the case of Matthews (1998) functional groups, the three RA axes showed increased abundances of benthic pickers, egg eaters and snail crushers in upstream reaches and increased abundances of water column particulate feeders in

Table 1 Correlations from RA multivariate analyses axes for the Wabash River fish assemblage data with year and river location (*q* values in parentheses)

Variable	Year	River location
Taxonomy RA1	0.16 (<0.001)	-0.02 (0.15)
Taxonomy RA2	-0.21 (<0.001)	0.48 (<0.001)
Taxonomy RA3	0.35 (0.001)	0.11 (0.003)
Functional groups (Matthews, 1998) RA1	-0.23 (<0.001)	0.22 (<0.001)
Functional groups (Matthews, 1998) RA2	0.03 (0.12)	-0.13 (0.719)
Functional groups (Matthews, 1998) RA3	-0.20 (<0.001)	0.13 (<0.001)
Biomonitoring metrics (Hitt & Angermeier, 2008) RA1	0.14 (0.01)	-0.25 (<0.001)
Biomonitoring metrics (Hitt & Angermeier, 2008) RA2	0.53 (<0.001)	-0.01 (0.79)
Biomonitoring metrics (Hitt & Angermeier, 2008) RA3	-0.01 (<0.001)	-0.23 (<0.001)
Reproduction (Balon, 1975, 1981) RA1	0.11 (0.003)	0.13 (<0.001)
Reproduction (Balon, 1975; 1981) RA2	-0.41 (<0.001)	0.05 (0.06)
Reproduction (Balon, 1975, 1981) RA3	-0.31 (<0.001)	-0.03 (0.12)
Life History (Winemiller & Rose, 1992) RA1	-0.04 (0.09)	-0.03 (0.12)
Life History (Winemiller & Rose, 1992) RA2	-0.17 (<0.001)	0.21 (<0.001)
Life History (Winemiller & Rose, 1992) RA3	0.22 (<0.001)	-0.26 (<0.001)
Functional groups (Poff & Allan, 1995) RA1	-0.09 (0.012)	0.32 (<0.001)
Functional groups (Poff & Allan, 1995) RA2	0.10 (0.004)	0.03 (0.12)
Functional groups (Poff & Allan, 1995) RA3	-0.46 (<0.001)	-0.001 (0.21)

RA, reciprocal averaging.

downstream reaches. For Hitt & Angermeiers' (2008) biomonitoring metrics, the RA axes showed decreased abundances of invertivores and piscivores in downstream reaches and increased abundances and species richness of percidae taxa in upstream reaches. For Balon's (1975, 1981) reproductive guilds, the analysis showed increased abundance of spawners on sand and non-guarder spawners on rock and gravel in upstream reaches. For Winemiller & Rose's (1992) life history traits, there was increased abundance of species with smaller maturing females in upstream reaches and increased abundance of species with small eggs and high age of maturity in downstream reaches. Finally, for Poff & Allan's (1995) functional groups, there was increased abundance of planktivores in upstream reaches and increased abundance of species with preference for high current velocity in downstream reaches (Appendix S2).

The first and second taxonomic RA axes resulted in significant correlations with year (Table 1). At least one RA axis for each trait-based approach was significant at explaining fish assemblages from year with general trends of increases in tolerant or generalist and decreases in intolerant or specialist traits (Table 1; figures in Appendix S2). The analysis of the first RA axis for Matthews (1998) functional groups with year resulted in decreased abundances of benthic pickers and egg eaters in recent years. The analysis of

the third RA axis for these functional groups with year resulted in decreased abundances of snail crushers and benthic pickers in recent years. The analysis of the first RA axis for Hitt & Angermeier (2008) functional groups with year resulted in higher abundances of tolerant species and lower abundances of intolerant species in recent years. The analysis of the second RA axis for Hitt & Angermeier (2008) functional groups with year resulted in lower abundances of intolerant species and increased abundances of invertivores in recent years. The analysis of the third RA axis for Hitt & Angermeier (2008) functional groups with year resulted in lower abundances of piscivores and increased species richness of percidae in recent years. The analysis of the first RA axis for Balon (1975, 1981) reproductive guilds with year resulted in increased abundance recently of sand spawners and rock and gravel spawners that do not guard eggs. The analysis of the second RA axis for Balon (1975, 1981) reproductive guilds with year resulted in decreased abundance of nest spawners on miscellaneous substrates and increased abundance of internal bearers and guarder substratum choosers of rock attachment. The analysis of the third RA axis for Balon (1975, 1981) reproductive guilds with year resulted in increased abundance of brood hiders on rock and gravel and guarders on plants in recent years. The analysis of the second RA axis for Winemiller & Rose

(1992) life history traits with year resulted in decreased abundance of species with small eggs and high age of maturity recently. The analysis of the third RA axis for Winemiller & Rose (1992) life history traits with river distance resulted in increased abundance of species with high age of maturity recently and decreased abundance of species with small females recently. The analysis of the first RA axis for Poff & Allan (1995) functional groups with year resulted in decreased abundance of planktivores in recent years and increased abundance of species with preference for high current velocity. The analysis of the second RA axis for Poff & Allan (1995) functional groups with year resulted in increased abundance of surface-water column invertivores and species that prefer sand substrates in recent years. The analysis of the third RA axis for Poff & Allan (1995) functional groups with year resulted in increased abundance of herbivore–detritivores and reduced abundance of species that prefer higher current velocity in recent years.

On the basis of these results, we reject our hypothesis that trait-based approaches would provide stronger relationships with river gradients than taxonomic identities. Both approaches were successful at accounting fish assemblage variation in relation to spatial and temporal variation in a single river.

Indiana analyses

The IDEM survey involved a total of 273 335 fishes comprising 139 species. The 10 highest abundance species were central stoneroller (*Campostoma anomalum* Rafinesque), creek chub, bluntnose minnow, longear sunfish (*Lepomis megalotis* Rafinesque), green sunfish (*Lepomis cyanellus* Rafinesque), western blacknose dace (*Rhinichthys obtusus* Agassiz), spotfin shiner, johnny darter (*Etheostoma nigrum* Rafinesque), bluegill sunfish (*Lepomis macrochirus* Rafinesque) and white sucker (*Catostomus commersoni* Lacepède). The PCA for QHEI scores resulted in two axes with broken-stick eigenvalues that were significantly larger than random. The first RA axis for taxonomy separated sites with higher abundance of shovelnose sturgeon and blue sucker (Fig. 2a) while the second axis separated sites with increased starhead topminnow (*Fundulus dispar* Agassiz) and mosquitofish (*Gambusia affinis* Baird & Girard). The first RA axis for Matthews (1998) functional groups separated sites with taxa that are deep burrowers in substrates (Fig. 2b) while the second axis

separated sites with increased abundances of stone turners. The first RA axis for Hitt & Angermeier's (2008) biomonitoring metrics separated sites with increased abundances of intolerant taxa from sites with increased abundances of piscivores (Fig. 2c) while the second axis separated sites with increased abundances of piscivores. The first RA axis for Balon's (1975, 1981) reproductive guilds separated sites with taxa that are nest spawner glue-making nesters from sites with increased abundances of internal bearer taxa (Fig. 2d) while the second axis separated sites with increased abundances of taxa that are internal bearers from sites with increased abundances of guarder substratum choosers that use rocks. The first RA axis for Winemiller & Rose's (1992) life history traits separated sites with increased abundance of taxa with high age of maturity (Fig. 2e) while the second axis separated sites with increased abundance of taxa with low age of maturity. Finally, the first RA axis for Poff & Allan's (1995) functional groups separated sites with increased abundance of planktivore taxa with large shape factor ratio while the second axis separated sites with increased abundance of taxa with small swim factor ratio (Fig. 2f).

The taxonomic RA axes were significantly correlated with PCA axes 1 and 2 for the QHEI (Table 2; Figures in Appendix S2). Sites that had higher QHEI scores had higher abundances of spotted darter (*Etheostoma maculatum* Kirtland), bluebreast darter (*Etheostoma camurum* Cope) and gravel chub (*Erimystax x-punctatus* Hubbs & Crowe) and lower abundances of northern starhead topminnow and western mosquitofish. Sites that were deeper and wider had higher abundances of shovelnose sturgeon (*Scaphirhynchus platyrhynchus* DeKay), blue sucker (*Cycleptus elongates* Lesueur) and skipjack herring (*Alosa chrysochloris* Rafinesque). Sites with decreased depth and width had higher abundances of southern redbelly dace (*Phoxinus erythrogaster* Rafinesque). All trait-based analyses resulted in significant correlations with QHEI PCA axes (Table 2). Although QHEI varied with fish assemblages as expected for several variables (e.g. life history variables), there were multiple results that were not predicted. Here, we mention several exceptionally strong relationships. Matthews (1998) functional group RA3 was correlated with the first QHEI axis such that sites with higher QHEI scores had higher abundances of species that were deep burrowers in soft substrate. The functional

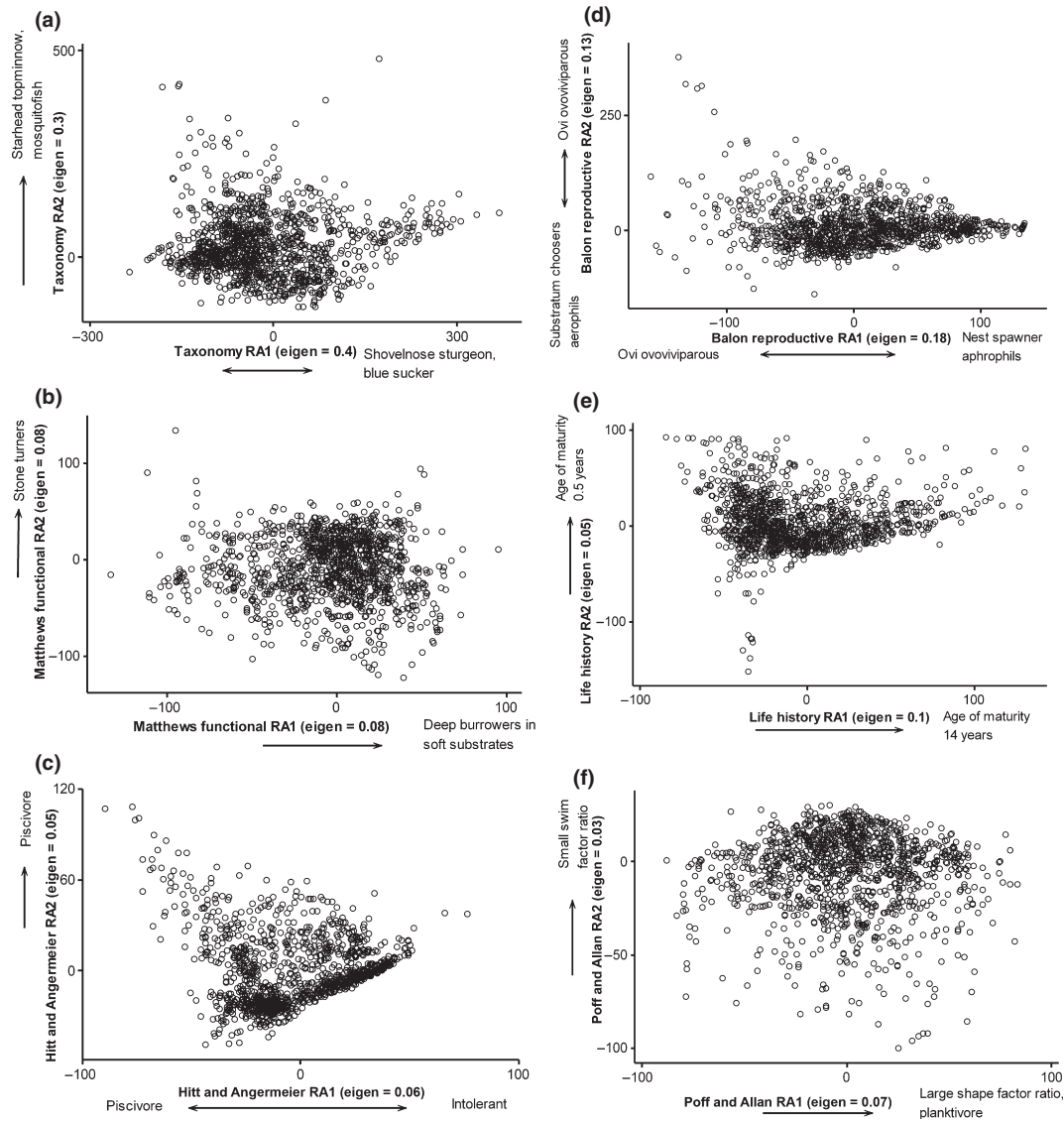


Fig. 2 Reciprocal averaging axes for the Indiana assemblages using (a) taxonomy, traits of (b) Matthews (1998), (c) Hitt & Angermeier (2008), (d) Balon (1975, 1981) reproductive guilds, (e) Winemiller & Rose (1992) life history traits and (f) Poff & Allan (1995) functional traits. Eigenvalues are in parentheses, and highest loading taxa or traits are listed on figures.

groups of Poff & Allan (1995) had significant correlations with two RA axes with QHEI ordinations. Sites that were deeper and wider had higher abundances of species with high shape factors and planktivore species, and sites with higher QHEI scores had increased abundances of species with high swim factor. Balon’s (1975, 1981) reproductive guild RA1 was correlated with the second QHEI axis, such that deeper and wider stream sites had higher abundances of internal bearer species and shallower and narrower sites had higher abundances of plant spawners with adhesive eggs. The first RA axis based on Winemiller

& Rose’s (1992) life history variables was correlated with QHEI PC1. Sites with higher QHEI scores had increased abundances of species that matured at greater age and larger body size. Many taxonomic and trait-based RAs were correlated with water quality PCA axes, although all correlations were <0.3.

The CCA results comparing taxonomic and fish trait data sets resulted in similar patterns to the previous analysis, with stream size variables accounting for most of the variation. All the data sets had significant relationships with the QHEI and water quality variables (Table 3), but taxonomic classifica-

Table 2 Correlations from RA multivariate analyses axes of Indiana fish assemblage data with scores from PCA ordinations of Qualitative Habitat Evaluation Index (QHEI) PCA scores and water quality PCA scores (*q* values in parentheses)

Variable	QHEI PCA1	QHEI PCA2	Water PCA1	Water PCA2
Taxonomy RA1	-0.294 (<0.001)	0.685 (<0.001)	-0.01 (<0.1)	0.15 (<0.001)
Taxonomy RA2	0.566 (<0.001)	0.204 (<0.001)	0.17 (<0.001)	-0.1 (<0.001)
Taxonomy RA3	-0.249 (<0.001)	0.122 (<0.001)	0.011 (0.09)	0.09 (<0.001)
Matthews (1998) RA1	-0.297 (<0.001)	-0.349 (<0.001)	-0.184 (<0.001)	0.04 (0.12)
Matthews (1998) RA2	0.162 (<0.001)	0.185 (<0.001)	-0.03 (0.038)	-0.08 (<0.001)
Matthews (1998) RA3	-0.473 (<0.001)	0.372 (<0.001)	-0.08 (<0.001)	0.21 (<0.001)
Hitt & Angermeier (2008) RA1	-0.373 (<0.001)	0.297 (<0.001)	-0.18 (<0.001)	0.19 (<0.001)
Hitt & Angermeier (2008) RA2	0.334 (<0.001)	0.368 (<0.001)	0.11 (<0.001)	-0.04 (0.023)
Hitt & Angermeier (2008) RA3	0.178 (<0.001)	0.058 (0.007)	0.22 (<0.001)	-0.11 (<0.001)
Balon (1975, 1981) RA1	-0.031 (0.04)	0.555 (<0.001)	0.05 (0.017)	0.07 (0.002)
Balon (1975, 1981) RA2	-0.171 (<0.001)	0.555 (<0.001)	0.05 (0.017)	0.07 (0.002)
Balon (1975, 1981) RA3	0.274 (<0.001)	0.062 (0.005)	-0.04 (0.028)	-0.07 (0.002)
Winemiller & Rose (1992) RA1	-0.474 (<0.001)	0.59 (<0.001)	-0.06 (0.008)	0.16 (<0.001)
Winemiller & Rose (1992) RA2	0.216 (<0.001)	0.065 (0.004)	0.29 (<0.001)	-0.1 (<0.001)
Winemiller & Rose (1992) RA3	0.124 (<0.001)	0.123 (<0.001)	-0.09 (<0.001)	0.05 (0.01)
Poff & Allan (1995) RA1	0.098 (<0.001)	0.582 (<0.001)	0.14 (<0.001)	0.03 (0.048)
Poff & Allan (1995) RA2	0.546 (<0.001)	-0.026 (0.05)	0.14 (<0.001)	-0.14 (<0.001)
Poff & Allan (1995) RA3	-0.138 (<0.001)	0.245 (<0.001)	-0.01 (0.11)	0.05 (0.016)

RA, reciprocal averaging.

tion explained a much greater proportion of variance than the traits classifications (Table 3). The CCA for taxonomy resulted in significance for nearly every environmental variable. There was a strong gradient on the first CCA axis for mean and maximum water depth and canopy cover (Fig. 3). Fish taxa that occurred in highest abundances at these larger and deeper sites with increased canopy cover were black buffalo (*Ictiobus niger* Rafinesque), shortnose gar (*Lepisosteus platostomus* Rafinesque) and blue sucker. Redside dace and starhead topminnow occurred at smaller, shallow sites with decreased canopy cover. The second CCA axis separated sites that were dominated by glide habitat from sites dominated by riffle habitat (Fig. 3). Pugnose minnow (*Opsopoeodus emiliae* Haye) and starhead topminnow occurred in higher abundances at sites on this axis than sites that had increased abundances of threadfin shad (*Dorosoma petenense* Günther) and spotted bass (*Micropterus punctulatus* Rafinesque). All of the trait classifications resulted in first CCA axes with a gradient from small, shallow, less canopy-covered streams to large, deep, canopy-covered streams (Fig. 3). The second axes from CCA analyses of the traits data sets separated sites primarily by riffle habitat. The CCA using Matthews (1998) functional traits resulted in snail crushers and gravel disturbers in highest abundances in larger and deeper sites on the first axis from water

column particulate feeders. Deep burrowers in soft substrates did not co-occur with stone turners. The CCA using Hitt & Angermeier's (2008) biomonitoring metrics resulted in a separation of invertivore-piscivores from intolerant taxa on the first axis (Fig. 4). Piscivores were separated from guarders that deposit eggs on substrates other than rock and gravel. The CCA using Balon's (1975, 1981) reproductive guilds data set resulted in species that were non-guarders with buoyant eggs separated on the first axis from glue-making nesters in higher abundance (Fig. 4). Species that are internal bearers occurred in higher abundance at sites in the ordination that were separated from guarders that choose rocks for attachment of eggs. The CCA using the Winemiller & Rose's (1992) life history traits resulted in separation of species with age of maturity of 14 years from species with age of maturity of 1–5 years and fecundity of 2000–3000 (Fig. 5). Species with age of maturity of 1.5 years were separated from species with female size at maturity of 100–150 mm. The CCA using Poff & Allan's (1995) functional groups separated species with high shape factor ratios that were planktivores from species with high shape factor ratios (Fig. 5). These analyses allow us to reject our hypothesis that trait-based classifications provide stronger explanation of assemblage structure than using taxonomy for a statewide geographic region.

Table 3 Ranks and sums of significant QHEI and water quality variables for Indiana stream fish collections based on percentage contribution to variance (*P* value in parentheses) explained by canonical correspondence analysis (CCA) for taxonomy, and traits of Matthews (1998), Hitt & Angermeier (2008), Balon (1975, 1981), Winemiller & Rose (1992) and Poff & Allan (1995)

	Taxonomy	Matthews	Hitt & Angermeier	Balon repro	Winemiller life history	Poff & Allan
Water depth max	23.6 (0.001)	3.0 (0.001)	1.1 (0.001)	5.8 (0.001)	5.9 (0.001)	2.7 (0.001)
Stream width	6.8 (0.001)	0.1 (0.004)		1.4 (0.001)	0.8 (0.001)	0.3 (0.001)
Aesthetic rating	5.9 (0.001)	0.5 (0.001)	0.3 (0.001)	0.7 (0.001)	0.6 (0.001)	0.3 (0.001)
% Riffle	3.3 (0.001)	1.4 (0.001)	0.7 (0.001)	1.7 (0.001)	0.4 (0.001)	1.1 (0.001)
Water temperature	2.1 (0.001)	0.2 (0.001)		0.5 (0.001)	0.3 (0.001)	0.2 (0.001)
Water depth mean	1.3 (0.002)	0.1 (0.034)	0.2 (0.001)	2.2 (0.001)	0.3 (0.001)	0.2 (0.001)
Subjective rating					0.1 (0.009)	
Canopy cover % open	1.1 (0.001)	0.2 (0.001)	0.1 (0.001)	0.6 (0.001)	0.1 (0.001)	0.1 (0.001)
% Pool	1.1 (0.001)	0.1 (0.001)			0.1 (0.001)	0.1 (0.001)
% Glide	1.0 (0.001)	0.1 (0.003)	0.1 (0.001)	0.3 (0.001)	0.1 (0.002)	0.1 (0.001)
% run	1.0 (0.001)	0.1 (0.011)			0.1 (0.011)	0.1 (0.002)
Dissolved oxygen	1.3 (0.001)	0.2 (0.001)	0.2 (0.001)	0.4 (0.001)	0.1 (0.028)	0.1 (0.001)
Specific conductivity	0.8 (0.004)	0.2 (0.001)		0.2 (0.017)	0.1 (0.036)	
pH	0.6 (0.001)	0.1 (0.003)			0.1 (0.001)	
Turbidity	0.6 (0.023)	0.1 (0.004)	0.1 (0.002)	0.2 (0.016)	0.1 (0.03)	0.1 (0.001)
Variance explained	50.5	6.4	2.8	14.0	9.2	5.4

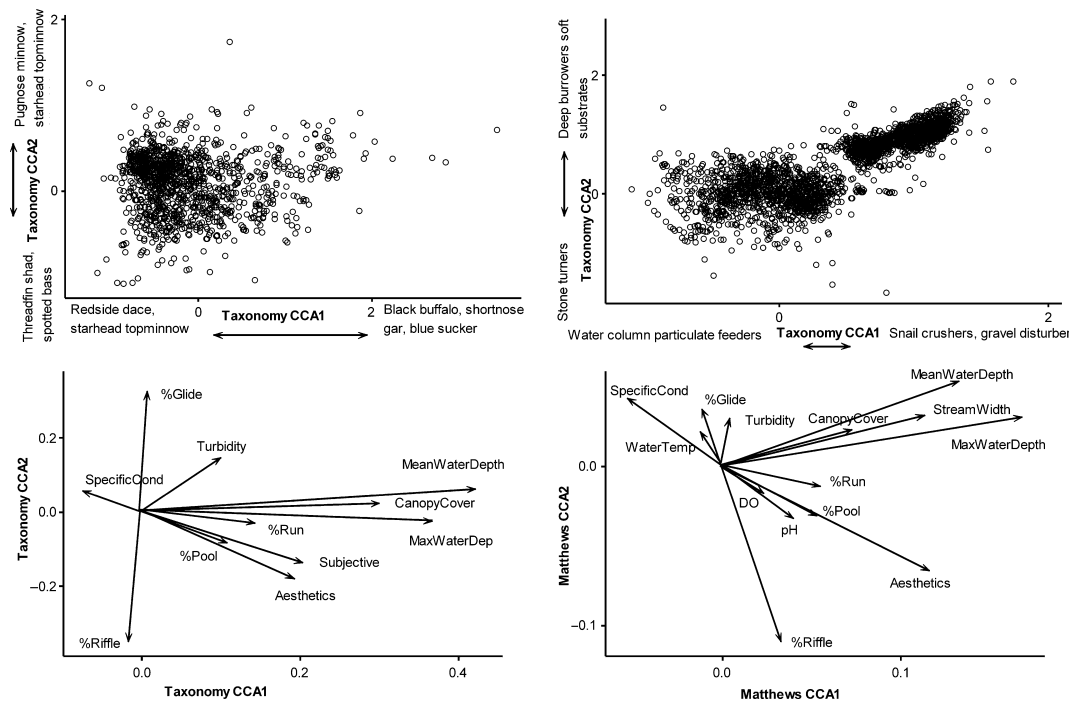


Fig. 3 Canonical correspondence analysis ordination of sites for Indiana fish assemblages taxonomy (left) and Matthews (1998) functional traits (right). Environmental variables are vectors (bottom).

Discussion

A goal of our study was to identify whether the alternative trait-based descriptions of fish assemblages provide different or better discrimination of

environmental attributes and temporal variation than taxonomic descriptions. Our analyses demonstrated that trait-based approaches frequently have similar results or can have increased success when several approaches are used in combination. Single

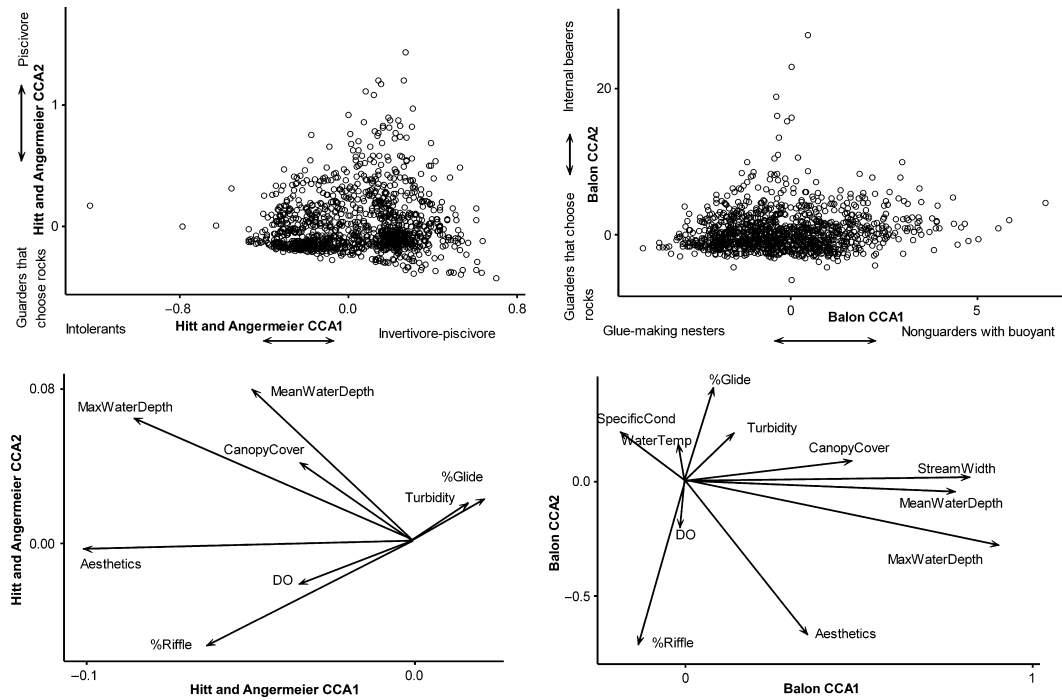


Fig. 4 Canonical correspondence analysis ordination of sites for Indiana fish assemblages using Hitt & Angermeier (2008) biomonitoring metrics (left) and Balon (1975, 1981) reproductive guilds (right). Environmental variables are vectors (bottom).

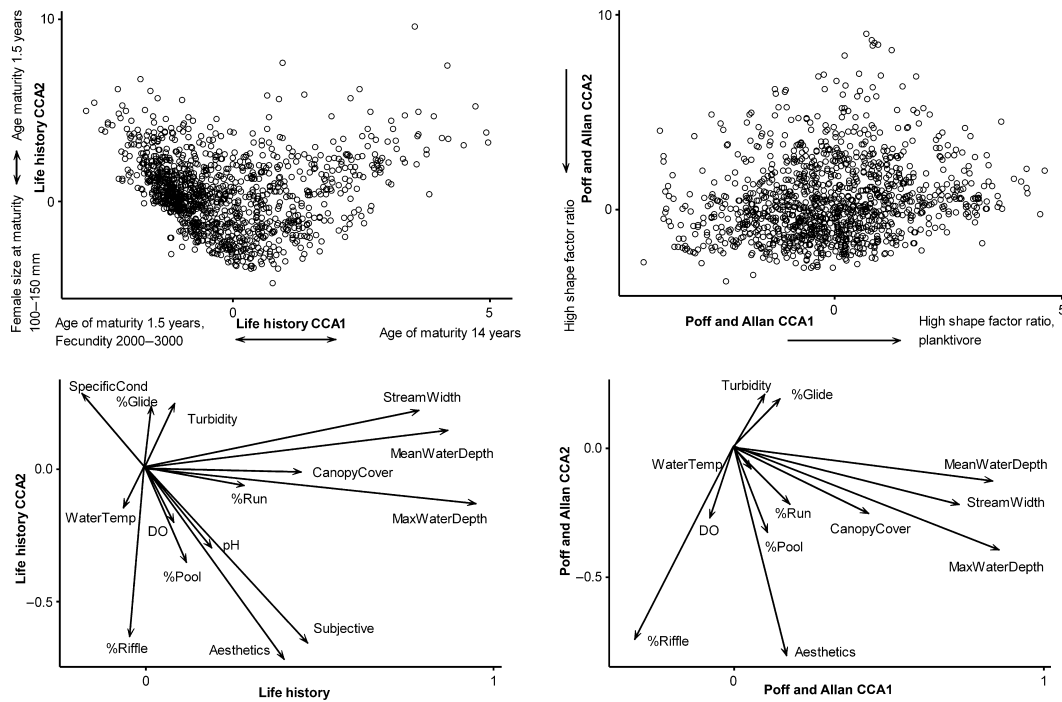


Fig. 5 Canonical correspondence analysis ordination of sites for Indiana fish assemblages using Winemiller & Rose (1992) life history traits (left) and Poff & Allan (1995) functional traits (right). Environmental variables are vectors (bottom).

trait-based approaches accounted for some environmental variation, but using multiple trait approaches often detected variation that was not apparent with a single trait approach. Our main conclusion is that the taxonomy of fish assemblages accounted for greater environmental variation than trait-based classification both in a single river and in a larger region. This concurs with the findings of Erös *et al.* (2009) for fish assemblages in southern Finland.

Analyses in a single river

Although the Wabash River is generally degraded, there is some indication that ecosystem quality has improved in recent decades (Gammon, 1998). However, we found recent declines in this river in intolerant taxa, internal bearers (an invasive mosquitofish) and species that prefer fast current velocity and feed on surface invertivores. Trait categories that increased during the 25-year period were tolerant taxa, nest spawners and herbivore/detritivores. These temporal trends suggest an improved ecosystem quality but do not provide conclusive evidence (Pyron *et al.*, 2008). Our trait-based approach revealed details for temporal patterns among taxa that were not apparent from the taxonomy-based approach (Pyron *et al.*, 2006). Pyron *et al.* (2006) identified changes in assemblages based on taxonomic abundances during the 25-year period, similar to those depicted in Fig. 1a. Beugly & Pyron (2010) found significant relationships for individual sites analysed for temporal change in abundance of fishes grouped by traits, although there was high variation among sites. They interpreted these changes in temporal abundance of fishes grouped by traits as evidence that ecosystem processes were modified from earlier conditions.

We identified significant longitudinal variation in the Wabash River using taxonomic and trait-based approaches. Longitudinal variation in fish assemblages is expected from small tributaries to larger streams as a result of changes in habitats (Vannote *et al.*, 1980), increasing habitat diversity and habitat size (Lowe-McConnell, 1975), species additions via tributaries (Schaefer & Kerfoot, 2004) and because of reduced accessibility of upstream reaches due to of steeper gradients and barriers to movements (Taylor & Warren, 2001; reviewed by Roberts & Hitt, 2010). Although there are distinct changes in the fish assemblages of the Wabash River from upstream to downstream reaches,

anthropogenic influences alter these from the expected natural pattern. Species richness is highest in upstream reaches (Pyron *et al.*, 2006), contradicting the expected pattern, and functional attributes of taxa fit the model of Poff & Allan (1995) for increased hydrological alterations; downstream sites had increased proportions of omnivores, benthic invertivores and taxa with low silt tolerance, groups that are predicted to increase in upstream reaches (Pyron & Lauer, 2004).

State-wide analyses

We found that a statewide analysis using taxonomy of fish assemblages provided a stronger explanation than using traits. The CCA ordinations using taxonomy for Indiana stream fish assemblages resulted in strong gradients for stream size and habitat type. Larger streams had higher abundances of black buffalo, shortnose gar, blue sucker, snail crushers (topminnows) and gravel disturbers (e.g. suckers), invertivore–piscivores, non-guarders with buoyant eggs (cyprinids, freshwater drum), with high age of maturity and high shape factor ratio. Smaller streams had higher abundances of topminnows, water column particulate feeders (small cyprinids), intolerants, glue-making nesters (brook stickleback), with low age of maturity, high fecundity and low shape factor ratio. Similar patterns occurred with habitat type. Threadfin shad and spotted bass tended to occur at sites with increased per cent riffle. These sites were distinct for higher abundance of stone turners (darters, sculpins, madtoms), guarders that deposit eggs on substrates other than rock and gravel and small female size of maturity and high shape factor ratio.

Others have expanded the use of the life history traits from Winemiller & Rose (1992) to further examine ecological phenomena (Vila-Gispert, Alcaraz & García-Berthou, 2005). Their results showed that the three life history endpoints of Winemiller & Rose (1992) are distributed unevenly across North America. Based on Mims *et al.* (2010), the Wabash River catchment and surrounding catchments are dominated by species with an opportunistic strategy (small egg size, short-lived, small body size and low age at maturity). Mims *et al.* (2010) suggested that these geographic patterns are explained in part by selective extinctions during the Pleistocene glaciations. Taxa that were not driven to extinction during this glaciation period survived through migration to

unglaciated locations further south and east. These habitats were subjected to extreme disturbance of variable habitat dessication and hydrological regime, resulting in strong selection for traits that fit the opportunistic life history strategy (Mims *et al.*, 2010). Jacquemin & Pyron (2011) found further evidence for historical effects of glaciation history on taxonomic and functional fish assemblage structure in this region. Local habitats differed significantly with glaciation history, probably contributing towards observed taxonomic and functional occurrence patterns.

Trait-based analyses have inherent problems that are not always present with taxonomy-based approaches. A trade-off of using trait-based approaches is the loss of information by grouping species into discrete ecosystem traits (Wright *et al.*, 2006). Grouping species into categories assumes that the traits are discrete and that all species grouped together are similar in their ecosystem functions. Although similar losses of information can occur with taxonomic analyses of species that are grouped into higher taxa (e.g. family), the issue is always associated with trait approaches. Other difficulties with analyses of trait-based categories include ontogenetic and temporal shifts in trophic ecology and habitat use of fishes (Hoeinghaus *et al.*, 2007). Although analyses of species traits will differ based on spatial extent, geographic location, range sizes of fishes, environmental variables and human impacts, we interpret our results to represent general and robust patterns because of our range of temporal and spatial scales.

Our analyses of temporal and spatial variation in categorical traits have applications for expectations of assemblage variation and for conservation in an increasingly altered landscape. Temporal variation in stream fish assemblages is predicted with local disturbance regimes and human impacts (Detenbeck *et al.*, 1992; Grossman *et al.*, 1998). However, expectations for long-term variation are largely unknown, partly because there are relatively few long-term studies of stream fish assemblages (Jackson, Peres-Neto & Olden, 2001; Pyron *et al.*, 2006). Although trait-based approaches provide potential information about which environmental variables are causing changes to assemblages (Beugly & Pyron, 2010), our current results suggest that taxonomic analyses are more sensitive at detecting temporal changes in an individual stream. We recommend that long-term studies of stream fish assemblages in a single stream utilise taxonomic

analyses supplemented with categorical traits to provide estimates of expected temporal variation.

Hoeinghaus *et al.* (2007) found that taxonomic analyses of Texas fish assemblage structure provided the best explanation of regional-scale environmental variables of temperature extremes and shrub and forest landscape variation. Their functional (trait-based) analyses identified habitat type (riffle, pool) and a measure of local stream stability. Angermeier & Winston (1999) found that variation in ecological composition (categories) was a product of environmental constraints and variation in species composition could be because of environmental constraints or phylogenetic history. Based on our analyses, selection of a taxonomic or trait-based approach should be determined in relation to the hypotheses of interest and the spatial extent of the study. For example, Marsh-Matthews & Matthews (2000) suggested that regional factors give strong explanation for fish assemblage structure in broad-scaled studies. The spatial extent of the study with respect to the geographic range sizes of included species and the presence of faunal breaks appears to be relevant to selection of an appropriate analytical approach. Our results from the Indiana traits data set analyses were not as strong as with taxonomy, perhaps because of lower categorical trait β diversity among river basins at this scale (Higgins, 2010). This is a typical pattern that occurs with lower number of functional trait groups than the number of taxa (Heino *et al.*, 2007). We conclude that trait-based analyses provide information about fish assemblage variation that is different from taxonomic analyses (Hoeinghaus *et al.*, 2007). The use of species traits provides additional explanation of local habitat variation in situations with higher trait β diversity among river basins. Taxonomic analyses are useful at discrimination among catchments, geographic distributions and river gradients. We recommend taxonomic approaches when examining stream fish assemblages, particularly for long-term analyses. Trait-based approaches appear to be useful compared to taxonomy in studies with large spatial extent where there is high turnover of species traits among catchments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Categorization methods.

Appendix S2. Supplement figures that show relationships for fish traits (and taxonomy) with year and river location for Wabash River data, and relationships for fish traits (and taxonomy) with habitat (QHEI) for Indiana data.

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