REGIONAL INFLUENCE OF LANDSCAPE FEATURES AND PROCESSES ON FLUVIAL FISH ASSEMBLAGES

By

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ABSTRACT

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Habitat fragmentation, degradation and loss are dominant reasons for global declines in biodiversity of fishes in stream systems, and humans have drastically modified landscapes drained by streams due to activities including urbanization and agriculture. Such human land uses are known to change stream habitats through inputs of excess nutrients, sediments, or toxics and through changes in stream flow and thermal regimes, and human land uses have been shown in many studies to negatively affect stream habitats and the fishes they support. Despite this understanding, degradation of stream habitats and fishes continues globally, and freshwater fishes remain one of the most threatened groups of organisms on the planet. Less understood are the specific mechanisms by which land uses affect stream habitats and how these can vary by region, and how additional landscape-scale characteristics may alter effects of human land uses, resulting in regionally-specific responses in stream fishes to stressors. Such differences across regions may render one locale more sensitive to biodiversity loss or fish assemblage change from the same magnitude of anthropogenic disturbance in the landscape and confound efforts to develop and apply specific actions to conserve biodiversity of stream fishes. The goal of this study is to help address these limitations in understanding. In these chapters, I characterize important natural landscape factors and human land uses influencing distributions and abundances of stream fishes across large regions in both Michigan and within five freshwater ecoregions in the eastern portion of the United States. The results show major regional patterns of natural landscape factors and human stressors that affect fluvial fishes and how these factors

vary in influence across regions. This more in-depth understanding of landscape influences on fluvial fish assemblages will allow managers to better account for this regional variability when working to protect and conserve freshwater fisheries and biodiversity of fluvial fish assemblages from both current and future threats.

I dedicate my dissertation to my mother and father. I want to thank you for your endless support, in life and throughout my education. You have always helped me to feel close to home while living far away.

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PREFACE

The major research chapters (i.e. chapter 1, chapter 2, and chapter 3) are prepared as standalone manuscripts to be submitted for publication. For this reason there is some repetition between chapters in the study site descriptions and methods.

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INTRODUCTION

If you have ever drifted along the course of a river in a canoe, paddling around its bends and meanders, you may be fixed on the water or what's below, but the wide vistas your eyes capture are encompassed within the rivers' valley. Although the river may be the life blood of that valley, it is in part an extension of that valley as a whole. Hynes (1975) described that characteristics of the valley including climate, lithology and topology determine many in-stream processes like flow, sediment load, ion concentrations and nutrient loads; based on this, streams derive nearly all of their energy from their valleys. The type of vegetation and soils available in a watershed are partially defined by the climate and lithology of the valley, in turn influencing the amount of allochthonous inputs and types of ions released into the stream. Water chemistry, along with the type and amounts of organic material within a stream, determines rates of decay and establishes the food web that defines the distribution and structure of in-stream biota. These ideas by Hynes (1975) led in part to the proposal of the River Continuum Concept (RCC) by Vannote et al. (1980), a conceptual model or framework linking longitudinal changes in resource gradients of a stream to structural and functional changes in aquatic communities from headwater streams down to mainstem rivers.

The organization of biological communities and physical habitat of stream systems is largely determined by characteristics of the natural and anthropogenic landscapes through which they flow (Hynes 1975; Allan 2004). Localized river conditions, including communities and habitat, change longitudinally from headwaters to river mouths (Vannote et al. 1980), and localized river conditions are also constrained by their spatial arrangement within the topological architecture of a river network (Benda et al. 2004). Punctuated breaks along these river continuums, at river reach confluences, define unique habitat units influenced by their watersheds (Poole 2002; Fausch et al. 2002; Benda et al. 2004). The hierarchical arrangement of river systems within watersheds constrains regional influences like geology, topography, lithology and climactic variables like precipitation and temperature, helping to define the flow and temperature regimes of rivers (Frissell et al. 1986). This hierarchical nature of river systems constrains the influence of environmental factors, defines local biotic processes, limiting the available community species pool and controls distributions and abundances of individual species and community structure (Schlosser 1991; Tonn 1990; Poff 1997; Fausch et al. 2002). Using these qualities of nested river systems and landscape-scale factors on local factors to describe physical habitat, water quality, species abundances and distributions has been described as a landscape perspective of hierarchical riverine networks (Schlosser 1991; Osborne and Wiley 1992; Ward 1998; Fausch et al. 2002; Benda et al. 2004; Grant et al. 2007).

Building on this idea, some of the greatest threats to freshwater ecosystems globally are modifications caused by anthropogenic activities of fluvial systems and their catchments (Allan 2004; Dudgeon et al. 2006; Vörösmarty et al. 2010). Examples of such changes to stream systems include direct modification of stream flows and fluvial habitats from construction of dams and stream-road crossings, water withdrawals, diversions, and channelization of stream habitats and indirect threats that originate from human perturbations in adjacent landscapes that lead to inputs of excess nutrients, sediments, or toxics, altered water chemistry, altered hydrology, and altered thermal regimes (Allan and Flecker 1993; Sala et al. 2000; Duncan and Lockwood 2001; Caissie 2006; Dudgeon et al. 2006; Helfman 2007; Jelks et al. 2008; Olden and Naiman 2010; Carpenter et al. 2011; Esselman et al. 2011). Landscape-scale human disturbances have commonly been described in the literature as having negative effect on stream habitats and fish assemblages include urbanization and agriculture (Wang et al. 1997; Wang et al. 2000; Wang et al. 2001; Walsh et al. 2005), with barriers to fluvial ecosystems like dams and stream road-crossings also being considered a landscape-scale disturbance in more recent investigations (Cooke et al. 2012; Perkin and Gido 2012; Januchowski–Hartley et al. 2013).

Despite understanding of landscape influences on streams, trends in degradation of aquatic ecosystems and loss of freshwater fish biodiversity continue to occur, as both indirect and direct human impacts on freshwater ecosystems continue throughout the United States (U.S.) driven in part by large-scale changes in human land use. A factor that complicates protection of streams is that land use influences on streams may vary regionally due to influences of co-occurring natural landscape factors such as lithology and topography. This can result in regionally-specific trends and/or differences in the types and levels of human land uses affecting stream fishes across regions. There is inherent natural variability across different regions of the U.S., and landscape-level anthropogenic disturbances and their impacts also vary widely throughout the Nation. With regionally-different underlying natural landscape variables like lithology, land cover and climate, fish assemblages with similar membership in one region may respond to anthropogenic disturbances in a different manner than fish assemblages in another region. These differences across regions may render one locale more sensitive to biodiversity loss or fish assemblage compositional change from the same magnitude of anthropogenic disturbance in the landscape. Substantial differences have been seen in fish diversity and abundance across physiographic regions due to changes of human land use (Utz et al. 2010), and differential responses of stream conditions have been quantified with different levels of urban and agricultural land use in different regions (e.g., Walsh et al. 2005, Meador et al. 2005). These studies emphasize species-specific inter-regional variability in fish response to similar anthropogenic stressors (Hugget 2005, Meador et al. 2005, Utz et al. 2010, Esselman et al. 2013). Few studies have attempted to characterize regionally-distinct fish assemblage response to gradients of landscape human disturbance, yet this understanding is essential to develop large-scale policies and practices to protect and conserve fish habitats, fish diversity and fish population abundances in stream ecosystems.

In this dissertation, my aim is to provide new ecological insights into the large scale regional variability of influences that natural landscape factors and human land uses have on structuring fluvial fish assemblages. Fluvial fish assemblages have been utilized as response indicators to fluvial ecosystem condition because fauna are sensitive to environmental disturbance and degradation in their surrounding landscapes (Pont et al. 2006; Stoddard et al. 2008; Esselman et al. 2013). I used fish species and assemblage metrics describing community structure, trophic structure, levels of tolerance, and life history to quantify interregional variability in their response to human stressors and natural landscape factors through a landscape-based approach. This enhanced understanding of the variability of regional responses of fish assemblage metrics to human stressors should inform the development of a multimetric index of biotic condition (MMIs) for fish, for large regional studies assessing stream condition and integrity. This will provide insight into specific types and locations of threats to regional fish assemblage distinctness. This knowledge will aid managers in improvement of regional prescriptive management action to protect fish assemblage biodiversity into the future.

I begin by considering regional differences in stream thermal regimes across Michigan and the association of specific fish species to multiple facets of a thermal regime to assess which attributes of stream temperature are affecting fish assemblages and how this varies across the state. I use a covariance structure analysis to consider how landscape factors mediate effects on specific fish species and community structure through dominant characteristics of stream temperature. I next consider interregional differences in fish metric response, like feeding guilds, levels of tolerance and life history characteristics, to the effects of human land uses across five freshwater ecoregions in the eastern U.S. Finally, I evaluate dominant natural landscape factors and human land uses influencing five biodiversity indices and how these influences vary across five freshwater ecoregions. My research provides a framework and new methods to elucidate regional differences in major human stressors and their effects on fluvial fish assemblage structure. Further, findings from my study will inform landscape-scale conservation measures across my large study regions and provide prescriptive regional management actions to preserve regional fish assemblage distinctness.

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CHAPTER ONE

MULTIPLE FACETS OF A STREAMS THERMAL REGIME: EFFECTS OF STREAM TEMPERATURE ON MICHIGAN'S FLUVIAL FISH ASSEMBLAGES.

Abstract

Stream thermal regimes are one of the most important factors characterizing distributions and abundances of fishes, and thermal characteristics are themselves influenced by landscape factors. Understanding the role of landscape factors on thermal characteristics and indirectly on fishes is important for managing current stressors to aquatic habitats and to plan for changes that can occur in landscape conditions resulting from changes in land use and climate. The goal of this study was to better understand how landscape factors and stream thermal regimes structure fluvial fish assemblages in Michigan. Objectives include: 1) characterize how thermal regimes vary throughout stream reaches in Michigan, describing prominent characteristics of thermal regimes and characterize major landscape–scale factors controlling these thermal characteristics, 2) test which thermal characteristics stream fish are responding most strongly to and describe if there are regional differences in response across Michigan, and 3) evaluate the way in which landscape factors affect fish through major facets of thermal characteristics. Indicator species analysis was used to evaluate relationships among various metrics characterizing stream thermal regimes and fish measures included taxa richness, Shannon's diversity, and Pielou's evenness. Results showed region–specific patterns in fish species association with different thermal metrics. Covariance structure analysis (CSA) indicated that fish species responses were regulated by maximums and variability in summer stream temperatures which were determined

by percent forest cover in the catchment and mean July air temperature in the catchment. . Our results provide new insights on regional differences in controls on stream fish assemblages and species–specific responses by indirect effects of landscape factors and direct effects of multiple prominent stream thermal metrics. This offers opportunities for improving conservation and management of stream systems and fish resources in the face of current and future changes in land use and climate.

Introduction

A thermal regime is one of the most important characteristics of stream habitat, influencing distributions and abundances of fluvial fishes (Magnuson et al. 1979; Brazner et al. 2005; Buission et al. 2008). Absolute magnitudes of water temperatures and temperature variation directly and differentially affect individual fish species by triggering key events such as spawning, hatching as well as growth throughout ontogeny (Schlosser 1991; Matthews 1998; Helfman 2007). Due to the ectothermic physiology of fish, a thermal regime plays a large role in streams, controlling population density (Inoue and Nakano 2001); determining range of species (Quist et al. 2004; Buission et al. 2008), influencing metabolism, growth and fecundity (Lobon–Cervia et al. 1996), and affecting behavior (Taniguchi et al. 1998). Temperature may also act as a physicochemical habitat filter (Poff et al. 1997), limiting availability of specific thermal habitats as well as fish movements to those habitats. In addition to direct influences on fish, stream temperatures may also have a myriad of indirect effects on particular fish species as they control predators, prey, competitors, and food web interactions.

Many different facets characterize thermal regimes of streams. Stream thermal regimes include average, maximum, and minimum temperatures within a particular system expressed over days, seasons, and/or years. Thermal regimes, however, also include variability in temperatures, expressed as daily, seasonal, and/or annual fluctuations (Caissie 2006; Olden and Naiman 2010). Additionally, other elements of stream thermal regimes include timing of thermal events, frequency and duration of critical temperatures, and the rate of change between temperature extremes (Poff et al. 1997; Olden and Poff 2003; Chu et al. 2010). Together these multiple facets characterize the thermal regime of a stream and also constrain available physical habitat for fishes.

Stream thermal regimes are influenced by numerous natural factors, including climate, which is a primary determinant of river temperatures (Poole and Berman 2001; Caissie 2006). Climate, along with other landscape–scale drivers, exerts spatially–explicit controls on thermal characteristics across climatic and environmental gradients (Wehrly et al. 2003). Typically, streams warm from headwaters to river mouths, with potentially wide variability in diversity and quality of thermal habitats (Vannote et al. 1980). That variability can be influenced by local conditions, or by spatial topology affecting the access of fish to thermal refugia (Matthews and Berg 1997; Martin and Petty 2011). At broad to fine geographic scales, latitude, elevation, surficial geology, and soils also contribute to differences in thermal characteristics within rivers, while site–specific variation in stream temperature can be influenced by localized conditions such as groundwater inputs, stream channel dimensions, and shading (Wehrly et al. 1997; Poole and Berman 2001; Caissie 2006; Wehrly et al. 2006).

The organization of local stream communities is largely determined from the natural and anthropogenic landscapes in their surrounding catchments in a hierarchical fashion from landscape factors influencing physical habitat that in turn effect local community structure (Hynes 1975; Allan 2004). Anthropogenic activities, including urbanization, forest management, agriculture, and groundwater withdrawal, alter stream temperatures and thermal variability (Wang et al. 1997; Allan 2004; Caissie 2006; Wehrly et al. 2006). Barriers like dams and road crossings also affect stream thermal regimes and fluvial fish assemblages by warming or cooling streams , fragmenting habitats that inhibit movement, and altering stream flow (Lessard and Hayes 2003; Hayes et al. 2008; Wang et al. 2011b; Januchowski–Hartley et al. 2013).

The thermal regime of a stream has varied influences on thermal habitats and stream fishes operating at both local and catchment spatial scales. Influences on stream temperature, operating over multiple spatial extents, affect the thermal regime of a stream in a hierarchical fashion. This is known as a landscape perspective (Schlosser 1991; Allan and Johnson 1997; Johnson and Gage 1997; Ward 1998; Wiens 2002). This nested hierarchy of morphological units is constrained by processes operating at higher levels within the catchments like regional climatic variables such as precipitation and temperature, but it is also influenced by local processes that help to define the thermal regime of a river (Frissell et al. 1986; Benda et al. 2004; Parsons and Thoms 2007). This hierarchical arrangement of dendritic river ecosystems constrains the influence of environmental factors, defines local biotic processes, limiting the available community species pool and controlling distribution and abundance of individual species and community structure (Tonn 1990; Schlosser 1991; Fausch et al. 2002). This complex suite of hierarchical factors help to shape the thermal regimes of river systems across multiple biogeographic regions, providing the necessary thermal characteristics that support and structure cold, cool and warm water fish assemblages (Jackson et al. 2001; Wehrly et al. 2003). Proactive conservation of fish assemblages that protect common species, preserve regional distinctiveness of rare fishes like species of greatest conservation need (SGCN), and management to ensure sustainable fisheries in the face of both current and future threats to steam systems is a daunting challenge. The hierarchical relationships between landscapes, physical habitat and how the structure of fish assemblages is affected are difficult to test and require a better understanding of how landscapes affect fish and how they are mediated by physical habitat like stream temperature.

The goal of this study is to characterize multiple facets of thermal regimes of streams and quantify how landscape-level factors affect stream fish in a hierarchical structure. We address four specific objectives. First, we characterize how thermal regimes vary among stream reaches in Michigan, describing prominent characteristics of thermal regimes and characterizing major landscape–scale factors controlling these thermal characteristics. Second, we test which thermal characteristics stream fishes are associated with and describe if there were regional differences in these associations across Michigan. Third, we evaluate the hierarchical process by which landscape factors affected fish, mediated by major facets of the thermal characteristics of the streams. Finally, we describe regional patterns in SGCN fish species diversity, distributions, and relationships between temperature metrics and rare fish species.

Methods

Study area.—This study was conducted in the state of Michigan which covers an area of 149,000 km^2 (Figure 1.1). We divided our study area into three regions to better account for natural landscape patterns and to account for regional differences in distributions of fish species. Study regions were delineated by aggregated ecological drainage units (EDUs) for Michigan (MDNR, unpublished); these regions are described as Upper Peninsula (UP), Northern Lower Peninsula (NLP), and Southern Lower Peninsula (SLP, Figure 1.1). For this study, data from 233 stream reaches were evaluated, (see details for reach definition below), and each reach had both stream fish data and stream temperature data. Ninety-seven reaches were located in the UP, 62 in the NLP, and 74 in the SLP (Figure 1.1).

Natural land cover in Michigan is dominated by forests (forest land cover in catchments of study sites averaged 46% and ranged from 0.53% to 98%) based on the 2001 National Land Cover Dataset (NLCD, Homer et al. 2004, Table 1.1). The two major human land uses include agriculture and developed land cover classes. The agriculture category was comprised of pasture/hay and cultivated crops land use classes and had a mean of 19% in study reach catchments. The category for developed lands included land use classes of low, medium, high intensity developed land, and open developed lands with an average of 7.78% in study catchments, (Table 1.1). Land cover patterns vary throughout the state, with more agriculture and urban land use occurring in the SLP and more forests in the NLP and UP. Surficial lithology is an important control on stream thermal regimes in Michigan by indirectly regulating the potential of groundwater contribution to stream base-flow depending on lithology material size. Surficial lithology varies widely across the state and these landforms in Michigan are primarily comprised of coarse–textured materials (mean = 85% in catchments of study sites), with fine–textured materials being less common (Soller and Reheis 2004; Cress et al. 2010, Table 1.1). Geology also varies, generally in a north to south gradient over the state, with more coarse geology occurring in the UP and NLP and more fine geology occurring in the SLP.

Stream layer, stream catchments and landscape data.—The stream layer used was the 1:100,000 National Hydrography Dataset Plus Version 1 (NHDPlusV1) national streams layer (USEPA and USGS 2005). We defined a stream reach as a section of a stream that extends 1) from the stream origin to the first downstream confluence or junction with a lake or reservoir, 2) from an upstream confluence or lake/reservoir outflow to the next downstream confluence or lake/reservoir junction, or 3) from an upstream confluence or lake/reservoir outflow to the river mouth where it meets the Great Lakes (Brenden et al. 2006; Esselman et al. 2011; Wang et al. 2011a). Two types of catchments associated with stream reaches were used in this study: local catchments and entire upstream network catchments. The local catchment is defined as all land that drains directly into an individual stream reach without being transported via other fluvial pathways represented in the NHDPlusV1 and referred to from here after as a local catchment. The network catchment is all land upstream of and draining into a given reach including the local catchment.

Landscape data and catchment area were summarized at the local and network catchments for corresponding NHDPlusV1 stream reaches. Land cover types from the NLCD (Homer et al. 2004) were grouped into classes and summarized, but only the 4 highest proportions of total land cover types were considered for analyses (e.g., urban, forest, agriculture, and wetlands; Table 1.1). Percentage of catchment in surficial lithology classes (e.g., coarse, fine) were grouped and summarized (Soller and Reheis 2004; Cress et al. 2010, Table 1.1). Reach elevation and gradient were calculated from the National Elevation Data (NED, Gesch 2007). Base–flow index, which represented hydraulic potential characterizing the percentage of groundwater contribution to stream flow, was modeled by the U.S. Geological Survey (USGS, Wolock 2003, Table 1.1). Average mean July air temperature was summarized for the climatological period from 1981 to 2010 by the PRISM Climate Group and attributed to the stream reach (Daly et al. 2008; PRISM 2013, Table 1.1). Variables were chosen based on known prominent landscape-scale factors that have strong natural and human influences on stream physical condition, stream habitats (e.g. Esselman et al. 2011) and fluvial fish (e.g. Esselman et al. 2013)

Fish data.—Fish data for study sites were sampled following MDNR Streams Status and Trends sampling protocols (Wills et al. 2008) using single pass electrofishing during the summer months of years between 1990 to 2010.. A stream backpack shocker or tow barge shocker was used for sampling depending on stream size and water depths (Wills et al. 2008). Lengths of streams sampled were determined by catchment area and by site specific mean stream widths. Streams with catchment area < 105 km^2 were defined as small streams and streams with catchment area between 105 km^2 and 465 km^2 were defined as medium streams. For a small stream < 4.6 m wide, a stream length of 152 m was sampled. For a small stream ≥ 4.6 m wide a stream length of 244 m was sampled. A length of 366 m was sampled for medium stream (Wills et al. 2008). Large and very large stream sites were excluded from analyses because data collected using gear for sampling these systems (e.g., boomshocker) were deemed incompatible with data collected using small to medium stream sampling methods (e.g., backpack and barge shockers). All fish were identified to species except for some cottids, centrarchids, and juvenile petromyzontids which were identified to genus or family level. Fish that were only identified to genus or family level were used to calculate relative abundance of species at sites but were not included in taxon–specific summaries. We calculated the relative abundance (number of total individuals collected/100m stream length) for each species at each sampling location (Table 1.2). Taxa richness, Shannon's diversity, and Pielou's evenness indices were also calculated for all study sites (Shannon 1948; Pielou 1975, Table 1.3).

Instream temperature data.—Temperature data were collected at study sites following MDNR Stream Status and Trend sampling protocols (Wills et al. 2008) between 1990 and 2011. Sample sites that were within 10 km downstream of a major dam were not included in this study (U.S. Geological Survey 2012). All instream temperature data were collected every hour using temperature data loggers that collected data at least from May through September. Temperature data loggers were deployed at each site in the thalweg of the stream or in an area likely to remain wetted through the sampling period. Once temperature data were downloaded, records were graphed and inspected visually to identify periods when the logger may have been out of the water or missing data points. Any site with less than 5 days consecutive collection of stream temperature or high degree of variability (e.g., recording dry periods) were excluded from analyses. All of the 233 sites evaluated in this study had corresponding instream temperature data for the entire months of June, July, and August.

Instream temperature metrics.—Temperature data were summarized into 69 different metrics characterizing magnitude and variability in stream temperature conditions (Table C1.1, Chu et al. 2010; Arismendi et al. 2013). From these, a subset of metrics was selected for further analysis based on ecological interpretability and their availability for all study sites. For example, metrics calculated for the months of May and September were excluded from analyses because not all study sites had data collected during these time periods. Also, moving day averages calculated over 1 and 3 day time periods were found to be highly correlated with moving day averages over longer time periods and excluded from analyses because longer time periods are assumed to capture a broader range in conditions. Following these selection steps, 22 temperature metrics were used for further analysis (Table 1.4). Before analysis, temperature metrics were natural log transformed to help meet the assumption of linearity.

Analysis.—To reduce the dimensionality of the temperature data and to identify major patterns in temperature for the study area, principal component analysis (PCA, Legendre and Legendre 2012) was performed on a correlation matrix of the 22 temperature metrics from our study sites (Table 1.5). Resulting factors with eigenvalues greater than 1 were retained for interpretation. To aid in interpretation, Varimax rotation was applied to resulting axes, and individual variables weighted by an absolute value of 0.6 or higher were considered for interpretation of the PCA axes (Table 1.5)

Indicator species analysis (ISA).—We used Indicator Species Analysis (ISA) to calculate an indicator index (IndVal) that identifies associations between specific fish taxa (Table 1.2) and temperature metrics (Dufrene and Legendre 1997). ISA determines the strength of associations between pairs of variables, with one variable characterizing species distributions across a range of sites and a second variable characterizing an environmental factor that may control differences in species distributions. The indicator index is a measure of specificity for the relative abundance of a fish species for a particular temperature metric group or site-grouping (DeCaceres and Legendre 2009; DeCaceres et al. 2010). To be considered a good indicator, a species must have a high relative abundance at a majority of sites and a high or low association at sites with the environmental characteristic of interest. In this way, results of ISA reveal indicator species along with environmental characteristics potentially important in controlling species distributions across sites.

To describe state-wide and regional trends in associations between fish and temperature metrics we used widely distributed fish species. Fish that did not occur at more than 10% of study sites were not included in the ISA analysis to reduce the influences of species with small ranges, rarity in occurrence or detection. Fish and temperature metrics that were outside of three standard deviations from the mean were excluded before running the ISA to preserve large regional trends and patterns seen in the datasets. To run ISA, we first identified values indicating the top and bottom 50% of each of the 22 temperature metrics, characterizing site groups. Next, the indicator analysis was run using the function “IndVal.g” in the “indicspecies” package in R

(DeCaceres and Legendre 2009; R Core Team 2011) to calculate the indicator value index. The indicator value index is composed of two metrics: the probability of a site belonging to a site-group combination when the species has been found at that site and how frequently the species is found at sites belonging to the site-group (Dufrene and Legendre 1997; DeCaceres et al. 2010). The indicator value ranges from 0 to 1, with higher values representing a greater association with a particular site-group. Statistical significance of the association was evaluated with a permutation test that uses the maximum Sqrt IndVal for the test value. We ran 100 random permutations. Species with p-values < 0.05 were considered significant indicators of a particular site-group. We performed ISA on our statewide data set and within each of the three regions to identify statewide and regional differences in relationships between species and temperature metrics (Figure 1.1).

Covariance structure analysis.—Covariance Structure Analysis (CSA) is a multivariate statistical technique that quantifies sources of variance in complex systems and allows for the testing of hierarchical relationships among variables structured by a priori hypotheses of interrelationships (Bollen 1989; Maruyama 1997). In this study, we used CSA to investigate relationships between fish metrics, stream thermal characteristics, and landscape features. With CSA, correlations among landscape variables can be accounted for, while also accounting for direct influence of landscape variables on fish metrics and indirect influence via thermal characteristics of the stream (Maruyama 1997; Riseng et al. 2004; Infante et al. 2006). CSA cannot be used to prove causality, but it can be used to compare hypothesized interrelationships among variables and test if those models are consistent with the sampled data (Bollen 1989; Maruyama 1997).

Two inputs are required to perform a CSA, a model of hypothesized relationships among all variables of interest (Figure 1.2) and the actual sampled data. CSA results include estimates of the overall fit of the hypothesized model to the actual sampled data as well as estimations of the strengths of relationships among variables (Maruyama 1997). Estimates provide information on the direct effects that one variable has on another and on the indirect effects that one variable has on another as it acts through one or more variables as constrained by relationships depicted in the hypothesized model (Maruyama 1997).

A single CSA model was developed for this study, with paths representing hypothesized relationships among variables (Figure 1.2). The model developed for this study compares the indirect influence of landscape features including study region, coarse and fine lithology, catchment area, percent forest land cover and mean July air temperature on fish through effects of the two most dominant metrics of the thermal regime in a stream, as informed from PCA (i.e., summer maximums and summer ranges); while also accounting for direct effects of coarse and fine lithology and catchment area on fish taxa and community metrics. We developed this model based on current understanding of dominant controls on stream fish and thermal regimes. Fine and course surficial lithology were chosen for the CSA model to represent differences in lithology across the study sites but also as a surrogate of hydraulic potential (Wolock 2003). For example, surficial lithology has been shown to influence instream temperature in Michigan due to the relationship between lithology, hydraulic potential and the percentage of groundwater contribution to base–flow in glaciated regions (Baker et al. 2003). Modeling the direct effects of fine and coarse surficial lithology on fish as well as indirect effects via metrics of the thermal regime allowed us to estimate the relative importance of other influences of surficial lithology compared to their effects through stream temperature. It is well recognized in stream systems that as metrics of stream size increase, like catchment area and correlates (e.g., stream order, stream volume, stream width), there is an increase in area and diversity of available habitat and a propensity for greater fish species diversity and abundance (Angermeier and Schlosser 1989 Goldstein and Meador 2004; Infante et al. 2006; Thornbrugh and Gido 2010). Forest land cover and mean July air temperature have been recognized as influential on stream temperatures in Michigan (Wehrly et al. 2006; Steen et al. 2008). The CSA allows us to estimate hierarchical influences of landscape directly on stream temperature metrics as well as their mediating effects on fish indirectly through stream temperature.

AMOS 21.0 (IBM Corporation 2012) was used to perform the CSA using maximum likelihood estimation to fit sampled data to the hypothesized model. There were 30 total model runs to predict the effects of landscape factors through two stream temperature metrics and fish descriptors. Correlations among landscape factors were modeled based on evaluation of Pearson correlation coefficients; R^2 values less than 0.15 (and $P \geq 0.05$) were considered uncorrelated in the CSA model (Table 1.6). Fish descriptors tested in the model included metrics characterizing assemblages (richness, diversity, and evenness) as well as taxon–specific summaries suggested as being sensitive to temperature metrics by the ISA.

Based on the hypothesized model and sampled data, two types of outputs were used to evaluate the CSA model. A model selection process was used to test if the sampled data (e.g. fish taxa and community metrics, 2 stream temperature metrics) fit the a priori hypothesized model structure through a variety of minimum fit statistics criteria for further evaluation. Model fit was evaluated by chi–squared (χ^2) and its associated probability ($P > 0.05$), degrees of freedom (df), chi–squared divided by degrees of freedom (χ^2/df), the root mean square error of approximation (RMSEA ≤ 0.05), the Tucker Lewis index (TLI > 0.9), and the normed fit index

(NFI > 0.9) following Riseng et al. (2004), Infante et al. (2006), Arbuckle (2010), and Infante and Allan (2010). The amount of variability in fish species explained by the models was evaluated with squared multiple correlation coefficients (R^2). Significance of the effects was assessed with the 95% bias–corrected confidence intervals generated from Monte Carlo bootstrap procedure and *t*–distribution based on the degrees of freedom for the models following Arbuckle (2010). Variables were deemed significant at $\alpha \leq 0.05$. All variables were properly transformed to meet assumptions of normality before analysis.

Results

Patterns in fish species diversity and distribution.—A total of 61,551 fish specimens representing 91 species in 19 families were collected from the study sites, with 57 species collected from UP streams, 65 species from NLP streams, and 79 species from SLP streams (Table 1.2). Fish species ranged in percent of site occurrence from 0.4% to 66%. Forty–four species of fish were found in all three study regions, and 25 species were found within just one of the study regions. Eleven species of fish had a site occurrence of greater than 27% across study sites including, White Sucker, Creek Chub, Eastern Blacknose Dace, Brook Trout, Central Mudminnow, Mottled Sculpin, Johnny Darter, Brown Trout, Rainbow Trout, Longnose Dace, and Common Shiner with a sharp decline in species occurrence at study sites for the eighty additional species (Table 1.2). The most widely–distributed fish species was the White Sucker *Catostomus commersonii*, found at 66.1% of the 233 study sites, with a median of 5 individuals per 100 m and 75% and 25% quantiles equal to 11 and 1, respectively (Table 1.2).

Patterns in SGCN fish species diversity and distribution.—Of the 44 fish Species of Greatest Conservation Need (SGCN) listed for the state of Michigan (Eagle et al. 2005), only 18 were collected from the 233 study sites (Table 1.2). Striped Shiner *Luxilus chrysocephalus* was the most widely–distributed SGCN species across study sites, with a site occurrence of 11.6%, a median of 3.30 fish collected at sites and with 75% and 25% quantile values equal to 6 and 1 individuals per 100 m, respectively. Slimy Sculpin *Cottus cognatus*, was the most locally abundant SGCN collected (e.g., 12.7 median catch of individuals/100 m), but it was found at only 12 study sites. Six species were found at a single site: Lake Sturgeon *Acipenser fulvescens*, Lake Chubsucker *Erimyzon sucetta*, Bigmouth Shiner *Notropis dorsalis*, Spotted Sucker *Minytrema melanops*, River Redhorse *Moxostoma carinatum* and Pugnose Minnow *Opsopoeodus emiliae*. SGCN species richness across the three study regions in Michigan ranged from 8 to 13, with the highest SGCN species richness found in the SLP and the fewest in the NLP (Table 1.2).

Patterns in stream temperature metrics.—The PCA of stream temperature variables resulted in four axes explaining 89% of the variation across the study sites (Table 1.5). Axis 1, explaining 39% of the variation, was weighted positively by temperature magnitudes represented by maximum monthly temperatures, and maximum 7, 14, 21 and 30 day moving average of maximum temperatures. We interpreted this axis as showing high values for summer maximum temperatures. Axis 2 explained 25% of the variation in the sites and was positively weighted by temperature variability characterized by monthly average daily range and 7, 14, 21 and 30 day moving average of range in daily temperatures. Axis 3 explained 13% of the variation across study sites and was positively weighted by the timing of summer maximum range in temperatures captured by the Julian day maximum values of 7, 14, 21, and 30 days moving average of daily range in temperatures. Axis 4 explained 12% of the variation across study sites and was positively weighted by the timing of the summer maximum temperatures characterized by Julian day of maximum values of 7, 14, 21, and 30 days moving average of daily maximum in temperatures. The higher amounts of variation explained by Axis 1 and 2 compared to Axis 3 and 4 suggest that summer maximum temperature and temperature variability are prominent dimensions of the thermal regime in Michigan streams represented by our data.

Based on the above results, we selected two temperature variables that weighted strongest on the first two PCA axes in CSA analysis. These included maximum of 30 days moving average of daily maximum in stream temperature and maximum of 30 days moving average of daily range in stream temperature. Hereafter they were referred to as summer maximums and summer ranges.

Indicator species for key stream temperature metrics.—Of the twenty-seven fish species tested in the ISA, twelve species had associations with specific temperature metrics in Michigan with both affinities for high (i.e., upper 50%) and low (i.e., lower 50%) values of various temperature metrics (Tables 1.7). Of the twelve species that had affinities for temperature metrics, statewide and by regions, nine species had affinities for high summer maximums, three for low summer maximums, six for high variability and five for low variability in stream summer temperatures (1.7). At a statewide level White Sucker, Creek Chub *Semotilus atromaculatus*, and Johnny Darter *Etheostoma nigrum* showed an affinity for streams with high summer maximums, while Brook Trout showed the opposite affinity; higher abundances of Brook Trout were found in streams with low summer maximums. Creek Chub showed an association for high summer range in stream temperatures, indicating a high relative abundance at sites with high variability in daily ranges of temperatures.

The ISA highlighted patterns in taxa associations with temperature metrics at the regional scale versus statewide. For example, the number of fish taxa significantly associated with temperature metrics was 5 in the UP, 9 in the NLP, and 8 in the SLP, with approximately equal numbers of species per region associating with temperature metrics across study sites (1.2%, 1.4%, 1.0%, respectively). This suggests that stream thermal regimes may play almost an equal role, relative to the total number of species per region, in influencing stream fishes in the three study regions (Table 1.7). There is an increase in fish taxa richness from northern latitudes in the UP to southern latitudes in the SLP (Table 1.2). Creek Chub was the only species associated with temperature metrics of maximum or range in temperatures statewide and in all three regions (Table 1.8). Associations for all other species varied regionally. Brook Trout had affinities for low summer maximums statewide in the UP and NLP. In the SLP Brook Trout only occurred at nine out of the 74 sites likely due to the warmer stream temperatures and suboptimal thermal habitats in the SLP. Eastern Blacknose Dace had associations with high summer maximums and summer ranges in the UP. This potentially indicates that stream temperatures may be cooler than optimum stream thermal conditions for Eastern Blacknose Dace during summer months in the UP and may be suggestive of a northern latitudinal range of thermal tolerance for Eastern Blacknose Dace (Table 1.7). Brown Trout *Salmo trutta* had associations to low summer maximums in SLP, suggesting that Brown Trout prefer colder summer stream temperatures in southern portions of stream in Michigan. A few species only showed affinities for one or a few temperature metrics in one region or another and this may be most indicative of the home range of individual fish taxa across Michigan. All twelve fish species that showed a high affinity in the ISA for any stream temperature metric at the statewide level or in any of the three study regions was selected for further analysis, along with taxa richness, diversity, and evenness.

Covariance structure analysis (CSA) model fit and significance.—Fifteen of the 30 models predicting fish metrics from landscape factors and stream temperature metrics fit the hypothesized model based on the set of fit statistics evaluated (Table 1.8). Models that failed to fit the data will not be discussed further (Table 1.8). Of the 15 models that fit the hypothesized model structure, seven models had a significant fit to the data and also were found to have significant relationships between landscape factors, stream temperature metrics, and fish descriptors summarized by standardized total effects (i.e., sum of direct and indirect effects; Table 1.9). Eight models did not have significant relationships between fish descriptors and stream temperature metrics.

Effects of landscape features on stream temperature.—Summer temperature maximums increased significantly with network catchment area and decreased significantly with the proportion of forested land cover in the network catchment (Table 1.10). The mean July air temperature in the network catchment had a significant negative effect on summer temperature ranges (Table 1.10). Catchment area was the strongest predictor of summer maximums of stream temperatures, and mean July air temperature was the strongest predictor of summer range in stream temperatures, range increased with decreasing air temperature (Table 1.10).

Effects of landscape controls and stream temperature on fish species.—In the hypothesized models describing fish descriptors and stream temperature metrics, seven models had significant standardized total effects (Table 1.9). Summer maximums had significant positive standardized total effects on Creek Chub and Bluntnose Minnow, and there were significant negative standardized total effects with summer maximums on Mottled Sculpin and Brown Trout (Table 1.9), which are known to prefer colder water (Eaton and Scheller 1996; Lyons et al. 1996; Wehrly et al. 2003). All specific fish taxa that had significant total effects with maximum stream temperatures were influenced indirectly, either positively or negatively, by the amount of forested land cover in the sites network catchment.

Summer temperature range had significant positive standardized total effects on Creek Chub and Eastern Blacknose Dace. Mean July air temperature in network catchment had a significant positive effect on Creek Chub and Eastern Blacknose Dace (Table 1.9). Of the 12 fish species tested, Creek Chub and Eastern Blacknose Dace were positively affected by the range in summer temperatures, and part of that influence was resulted indirectly from mean July air temperature acting through temperature range. The 12 fish species responding to temperature metrics from the ISA analysis, specific fish species have negative and positive effects caused by two major facets of the thermal regime, maximum stream temperatures and range in stream temperatures during the summer months in Michigan. Mean July air temperature in network catchment had a significant negative effect on Pielou’s evenness (Table 1.9). Of the taxonomic summaries, summer range in stream temperatures had significant negative standardized total effects on Pielou’s evenness. The variability in daily temperature range was found to have negative effects on community evenness. Taxon and evenness in the fish community are also being influenced by landscape level variables, mediated through stream temperature. All significant relationships between summer maximum stream temperatures and range in stream temperature with fish species and community metrics all had low R^2 values.

Discussion

This research showed influences of stream temperature on fishes and influences of landscape factors on stream temperature, which highlights that landscape factors indirectly influence fish via stream temperature. Prominent dimensions of the thermal regime of Michigan streams characterized in our study included summer maximums and variability in summer stream temperature. Fish species that are associated with summer stream temperature have region-specific associations to specific thermal characteristics across study sites. Of the 12 species that showed an association to stream temperature metrics only one species (Creek Chub) showed a consistent response to stream temperature across all study regions, while most species responding to temperature had region–specific responses. All 12 fish species that showed a response to summer stream temperature in the ISA analysis were further investigated during the CSA analysis. Species–specific responses were characterized by the CSA to the two temperature metrics (e.g. maximum 30 day moving average of daily maximums and maximum 30 day moving average of daily range) informed from PCA, which represent the two prominent thermal characteristics (e.g. maximums and variability in summer stream temperatures) in Michigan.

Our results also indicate that these prominent thermal metrics, maximums and variability in summer temperatures, are themselves influenced by regional climate and landscape factors including the amount of forest cover in catchments, mean July air temperature, and catchment area. Thermal metrics do not operate independently but are differentially influenced by specific landscape factors. Therefore, prominent drivers (e.g. regional climate, forest cover, July air temperature) are influencing specific thermal regime characteristics (e.g. maximums or variability in summer stream temperatures) will dictate the spatial extent most appropriate for restoration, and which fish species should respond to conservation and management when incorporating stream temperature. Also specific characteristics of the thermal regime (e.g. maximums versus variability in summer stream temperatures) will be more strongly influenced by land–cover change versus climate change, respectively. This study offers new insights about the importance of summer maximum and variability in summer stream temperatures to specific fish taxa and characterizes how these influences vary regionally. These results have valuable implications when managing for specific fish species, as to differences in regional response of fishes to stream temperature metrics and the scale of specific landscape influences directly on fish and via stream temperature. This provides new insights into how stream fishes may respond to specific stream temperature metrics in the face of changes in land use and climate across Michigan (Wang et al. 2003; Allan 2004) and in the region (Lyons et al. 2010; Wenger et al. 2011; Isaak et al. 2012).

Dominant patterns in thermal regimes throughout Michigan streams.—PCA of 22 temperature metrics revealed four axes representing the major characteristics of thermal regimes in streams in Michigan (Table 1.5). The four axes describe summer maximums and ranges in stream temperature and the timing of the highest maximums and greatest variability in stream temperatures during summer months in Michigan. Despite the fact that temperature data used to calculate metrics were collected during a portion of the year (June through August), it is noteworthy that our analysis revealed four major unique axes that explain variability inherent in thermal regimes including magnitudes, variability and timing of events in Michigan streams. This follows Caissie (2006) who emphasized different spatial and temporal characteristics that affect stream maximums in temperature, the variability in stream temperatures and the timing of these events, daily and seasonally. In the Lower Peninsula of Michigan, Wehrly et al. (2003) found that gradients of summer stream mean temperature and temperature fluctuations were useful in describing differences across streams in fish assemblage structure. Together, these findings underscore the importance of considering additional thermal habitat characteristics that would address thermal magnitudes and variability in stream temperatures along with the timing of these events, when developing new management strategies for streams and thermal habitats for fish in Michigan.

Landscape–scale influences on prominent thermal characteristics.—Our CSA results indicated that maximum and variability in summer stream temperatures across our study sites were correlated with landscape–level controls including catchment area, forest land cover in the network catchment and mean July air temperature in the network catchment. Specifically, summer maximums were positively related to catchment area and negatively related to percent forest cover in network catchments. This result is similar to Chu et al. (2010), who used discriminant function analysis (DFA) to show not only percent riparian forest affected stream temperature in Ontario, Canada, but also that percent surface water and groundwater discharge were influential. Fine and coarse surficial lithology were used in our CSA model to represent differences in geology across Michigan and also used as a surrogate for base–flow or groundwater influence on stream temperatures. Our final CSA model is similar to the model of Wehrly et al. (2006) in the use of similar landscape predictors. They used catchment area, local forest, mean July air temperature, and percent catchment water and wetland land use to describe direct landscape controls on mean July stream temperature in the Lower Peninsula of Michigan. In their study, catchment area had the strongest effect on mean July stream temperature, (temperature increased with area), followed by a negative effect from local forest cover. Our results expanded on Wehrly et al. (2006), by testing the responses of fish to an additional thermal metric that characterizes the range or variability in summer stream temperature, which was negatively associated with mean July air temperature. This highlights that specific facets of stream temperature (e.g. maximums and variability) may be vulnerable to different changes in the landscape in Michigan streams. Maximum summer stream temperatures are potentially most heavily influenced by changes in land cover (e.g. % forest land cover), while the variability in summer stream temperatures may be most vulnerable to climate change (e.g. mean July air temperature, Table 1.9) across Michigan streams.

Prolonged high summer air temperatures may lead to less fluctuation in stream water temperature during summer months, due in part to maximum periods of solar and long–wave radiation exposure (Caissie 2006). Water, with its higher specific heat capacity than air, would stay warmer longer during the summer months, losing less heat than air during longer diurnal photoperiods (Wetzel 2001). Based on this idea, the relationships between variability in summer stream temperatures and July air temperature will change with varying amounts of precipitation and warmer air temperatures, such as those that will occur with predicted changes in climate (Wenger et al. 2011; Isaak et al. 2012). Our results reveal that landscape factors affect maximums and variability in stream summer temperature, and these factors mediate both fish assemblage structure and taxa specific responses to the dominant two characteristics of stream temperature across Michigan. This suggests that a more comprehensive evaluation of the direct and indirect influences of landscape factors on fish is needed, including understanding how landscapes control dominant thermal characteristics, and how landscape processes mediate effects on specific fish species and community structure through characteristics of stream temperature. This is pertinent for managing fish species effectively in the face of changing land use and climate.

Fish response to thermal characteristics and regional differences in response.—Our ISA analyses conducted at both state–wide and regional scales illustrated that different species of stream fish are related to different dimensions of stream thermal regimes, including magnitudes and daily and monthly ranges in stream temperatures and the timing of these events. Wehrly et al. (2003) used two dimensions of stream thermal regimes, stream summer mean temperature and fluctuation in stream temperatures to classify regional patterns in fish distribution in Michigan. In our study, the ISA analysis quantified which fish species responded to specific thermal characteristics (e.g. summer maximums and/or summer variability in stream temperatures), and the response of specific fish species changed across study regions. For instance, Brook Trout was associated most commonly with low maximum summer temperature metrics (e.g., Statewide, UP, NLP) and low temperature variability in the UP and NLP. Brook Trout only occurred at 9 out of 74 (i.e., 12%) sampled sites in the SLP, but had no association with temperature metrics in the SLP. Brook Trout in the SLP may occur only in streams with suboptimal–optimal thermal habitats throughout the summer, but might also need stream connectivity to cooler stream reaches for thermal refugia and long–term persistence in the SLP region in Michigan streams.

In contrast to brook trout, Brown Trout associated with both low maximum summer temperatures and low variability to summer temperatures in the SLP. Brown Trout in the SLP, where mostly warm transitional streams occur, have a strong association with thermal metrics specifically related to cold or cool streams only, across our study sites in Michigan. Creek Chub had associations with high maximum summer temperature metrics and high range in summer temperatures in all study regions and statewide. Creek Chub may have a feeding advantage in warm and warm transitional streams in Michigan because Creek Chub have been shown to have competitive success in feeding over other cool water species like Brook Trout and Brown Trout in Rocky Mountain streams at stream temperatures ≤22°C (Taniguchi et al. 1998). White Sucker also had an affinity for low variability in summer temperatures in the NLP. Our ISA results showed that different groupings of fish species and specific taxa respond to different high and low values of thermal regimes, and therefore, stream temperature is mediating the assemblage structure of fishes and membership of individual taxa via its multifaceted thermal characteristics.

In Michigan, stream temperature in different regions are influenced differently by groundwater recharge, coarseness of landform textures, depth to bedrock, and anthropogenic land uses (Zorn et al. 2002; Baker et al. 2003; Wang et al. 2003; Allen 2004; Wehrly et al. 2006). Utz et al. (2010) found that fishes had region–specific sensitivity to urban and agricultural land use across adjacent geoclimatic regions. Our ISA found different regional associations of specific fish species to temperature metrics. It highlights that of the 12 fish species that had an association with temperature metrics only one species (e.g., Creek Chub) responded similarly to thermal characteristics across our three study regions, and the majority of taxa had region–specific responses to temperature metrics (Table 1.7). This finding is consistent with the finding of Chu and Jones (2011) in that different fish taxa had associations with specific thermal regime classes; 16% of the explained variation in fish assemblage structure was due to spatial or region–specific differences between these thermal classes across their study sites in the Great Lakes Basin of Ontario, Canada. This inter–regional association of specific temperature metrics on individual fish taxa illustrates that there are region–specific aspects of thermal regime in streams controlling fish abundances, distributions and assemblage structure in Michigan streams.

Landscape influences on stream fishes via effects on temperature.—Our CSA provides evidence for indirect effects of landscape–level factors controlling fluvial fish assemblage structure and specific taxa abundances via two facets of a thermal regime, summer stream temperature maximums and summer range in stream temperatures in our study sites across Michigan. Specific species are differentially influenced indirectly by catchment area, percent forest cover in the network catchment, mean July air temperature, through two different facets of the stream thermal regime, summer maximums and summer range in temperatures.

Catchment area has species–specific effects on fish through two different dominant characteristics of the thermal regime, maximum summer temperature and variability in summer temperatures. Catchment area had significant positive effects on Bluntnose Minnow through maximum summer stream temperatures and on Eastern Blacknose Dace through variability in summer stream temperatures. Forest land cover had significant positive effects on Mottled Sculpin and Brown Trout through maximum summer stream temperatures and negative effects on Creek Chub, Common Shiner, and Bluntnose Minnow via summer maximums in stream temperature, quantifying the role that forest land cover has on cooling of streams and association with cold/cool water fish species. Fish species that are influenced by forest cover in the catchment are likely to be most sensitive to changes in summer maximum stream temperatures and affected by changes in land use (Wang et al 2003; Allan 2004).

Mean July air temperature had significant negative effects on Creek Chub and Eastern Blacknose Dace and positive effects on community evenness through variability in summer stream temperatures (i.e., variability decreased with air temperature). Fish that are influenced by mean July air temperature are likely most sensitive to changes in summer variability in stream temperatures and may be most affected by a warming environment and increased precipitation that increases variability in stream temperatures due to effects of climate change (Wenger et al. 2011; Isaak et al. 2012). Studies have described the hierarchical influence of landscape–level factors on stream temperature (e.g., Wehrly et al. 2006) and these landscape–level processes on physical habitat can indirectly mediate fish species abundances and assemblage structure (Infante et al. 2006; Infante and Allan 2010). To our knowledge this is the first study to indicate that summer ranges in stream temperatures mediate taxa specific abundances and community evenness through landscape–level factors. These results are important for setting realistic management goals for specific species. They add new insight on the differential avenues of vulnerability that specific fish taxa may experience from landscape–level factors like land use change or climate change, mediating the effects on fish through specific stream thermal characteristics.

Stream temperature is a major habitat factor that has been used to describe the distribution and abundances of fish species (Inoue and Nakano 2001; Buission et al. 2008). Different factors of the thermal regime like summer mean stream temperatures and fluctuations in summer stream temperatures have been successfully used to classify existing thermal regimes in stream segments in Michigan and describe patterns of fish species distribution (Wehrly et al. 2003; 2006). Summer stream temperatures and range in stream temperatures have also been used to help classify valley segments in Michigan's Lower Peninsula (Seelbach et al. 2006). The evaluation of stream temperature (e.g. maximums and variability in stream temperatures) and incorporation of these thermal regimes into stream management are considered a more holistic perspective of in–stream heat budgets and flow assessments (Poole and Berman 2001; Olden and Naiman 2010). Michigan has unique stream temperature regimes due to its low elevation, glacial landscape, and a high degree of groundwater influence. Results from our study highlight that a more complete evaluation of multiple facets of stream temperature in conjunction with biological data could offer insights into differential responses of stream fish to different characteristics of stream thermal regimes.

Management implications.—Our study has highlighted some potential research and management opportunities. The MDNR's current practice of characterizing stream temperatures is primarily targeted on thermal characteristics important to game fishes versus the entire fish assemblage. MDNR monitors stream temperature during periods of thermal maximums like July and August. Little stream temperature data have historically been collected during the spring and fall seasons. Also, sampling has historically been more targeted toward salmonid species then stratified random sampling across the state. Our results emphasized that thermal maximums in the summer months are important to fish assemblage structure, but the variability in monthly and daily range in stream temperatures also influences fish assemblage structure in Michigan. These results have important implications for thermal habitat availability and suitability for specific game fish species and SGCN species. Under predicted land use and climate changes, there may be substantial effects on prey fish availability for game and SGCN species related to stream temperature changes in Michigan. Environmental changes may also cause changes in condition of specific competition interactions between competing species or in predator–prey relationships due in part to changes in the thermal regime in Michigan streams.

We generated one of the most comprehensive datasets of community fish assemblage with corresponding stream temperature data. Yet the summer seasonality of our dataset was not complete enough to explore the seasonal effects that thermal regime in streams may also have in structuring fish assemblages during critically energy times for fish like during spawning both in the spring and fall or cold temperatures observed during winter. The temporal variability in a streams thermal regime and the specific importance of these changes to the timing of specific fish species life history characteristics like migration and spawning are vital to developing species specific thermal habitat management strategies. Our results highlighted the importance of multiple unique characteristics of a thermal regime to fish species throughout the summer months in Michigan streams but how these unique characteristics change seasonally and their importance to specific fish taxa are essential avenues for future research. This leads to management opportunities to improve data collection and analysis to better utilize all aspects of the in–stream thermal regime that structures fish assemblages. To better manage for changes in fish assemblages mediated by different facets of the in–stream thermal regimes one would need to 1) collect complete seasonal in–stream temperature data covering all accessible months for collection and 2) manage for a richer set of characteristics of the thermal regime that structure fish assemblages including thermal maximums across seasons as well as monthly and daily variability in temperature ranges across seasons.

We had one of the most comprehensive datasets for Michigan, with fish assemblage corresponding with hourly temperature measurements for the summer months. Yet this comprehensive dataset failed to capture enough abundance of SGCN listed fish species to evaluate stream temperature relationships of these rare SGCN fish species. Our analyses also pointed out another potential management opportunity. Long term monitoring programs with a stratified random sampling design were designed to capture abundances of common fish species to represent long term trends in a region. Rare fish species occur rarely in any randomized sampling design because of their low distributions, low species abundances and their difficulty with being sampled. Rare fish species are less likely to be encompassed in analyses preformed on long term monitoring datasets. These datasets are often times the best sampling efforts and best representation of conditions statewide. The problem with long term monitoring datasets is that because they are the best available comparable statewide datasets they are often used to investigate patterns in rare fishes and critical habitats for management. These monitoring programs were not designed to capture the abundances and distribution of rare species. Therefore management of rare fish species using long term monitor datasets for observing trends in changes of biodiversity and abundance of these rare species will not provide an accurate risk or threat assessment for habitats or fish species of greatest conservation need. Specific targeted monitoring of SGCN species and their associated critical habitats, along with other data types (e.g. stream temperature data), would need to be incorporated into data collection procedures to evaluate important physical habitat relationships for rare fishes and help conserve regional distinctiveness in fish biodiversity.

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APPENDICES

APPENDIX 1.A

TABLES

Table 1.1.—Average, maximum, and minimum values of landscape variables for 233 study sites, for the state of Michigan and by three regions, Upper Peninsula (UP), Northern Lower Peninsula (NLP) and Southern Lower Peninsula (SLP). Variables marked with (*) indicate those used in Covariance Structure Analysis.

	Statewide		
	avg	max	min
Landscape variables			
Drainage area (km^2)*	172.72	2206.71	3.34
Coarse lithology (%)*	84.68	100.08	0.00
Fine lithology (%)*	16.30	100.00	0.00
Stream gradient (cm/m)	0.37	2.48	0.00
Mean July air temperature (°C)*	19.93	22.75	17.36
Base-flow index (%)	65.52	87.16	29.38
Catchment land cover (%)			
Urban	7.78	99.16	0.29
Agriculuture	18.80	88.01	0.00
Forest*	45.87	98.41	0.53
Wetlands	18.89	58.63	0.16

Table 1.1 (cont'd)

	UP		
	avg	max	min
Landscape variables			
Drainage area (km^2)*	122.74	945.78	3.34
Coarse lithology (%)*	85.08	100.00	0.79
Fine lithology (%)*	15.76	100.00	0.00
Stream gradient (cm/m)	0.59	2.48	0.00
Mean July air temperature (°C)*	18.71	20.46	17.36
Base-flow index (%)	63.23	74.60	52.52
Catchment land cover (%)			
Urban	2.97	11.90	0.29
Agriculuture	1.78	21.35	0.00
Forest*	63.35	98.41	21.02
Wetlands	26.09	58.63	0.40

Table 1.1.—(cont'd)

	NLP		
	avg	max	min
Landscape variables			
Drainage area (km^2)*	237.06	1030.67	9.95
Coarse lithology (%)*	91.38	100.01	12.01
Fine lithology (%)*	4.35	100.00	0.00
Stream gradient (cm/m)	0.21	1.19	0.00
Mean July air temperature (°C)*	19.91	20.91	18.98
Base-flow index (%)	76.26	87.16	64.04
Catchment land cover (%)			
Urban	7.00	15.69	3.25
Agriculuture	10.36	44.37	0.00
Forest*	50.17	74.74	22.00
Wetlands	16.24	30.88	5.12

Table 1.1.— (cont'd)

	SLP		
	avg	max	min
Landscape variables			
Drainage area (km^2)*	184.33	2206.71	5.23
Coarse lithology (%)*	78.52	100.08	0.00
Fine lithology (%)*	27.03	100.00	0.00
Stream gradient (cm/m)	0.22	1.35	0.00
Mean July air temperature (°C)*	21.57	22.75	19.95
Base-flow index (%)	59.52	79.40	29.38
Catchment land cover (%)			
Urban	14.73	99.16	3.71
Agriculuture	48.20	88.01	0.07
Forest*	19.34	63.98	0.53
Wetlands	11.66	29.97	0.16

Table 1.2.—Fish species collected at study sites (n=233), species codes, percent site occurrence, median and quantiles of catch, and percent site occurrence by 3 Michigan regions, Upper Peninsula (UP), Northern Lower Peninsula (NLP) and Southern Lower Peninsula. Species marked with (*) indicate those used in CSA. Species marked with (†) indicate Species of Greatest Conservation Need (SGCN) in Michigan.

			Catch (individuals · 100 m^{-1})			% of sites found by region		
Fish species (n=91)	Species code	% of sites found	75% quantile	Median	25% quantile	n=57 UP	n=65 NLP	n=79 SLP
White sucker (*Catostomus commersonii*)*	catcom	66.10	11.20	5.30	1.30	53.60	77.40	73.00
Creek chub (*Semotilus atromaculatus*)*	sematr	64.40	24.00	6.70	2.30	51.50	69.40	77.00
Eastern blacknose dace (*Rhinichthys atratulus*)*	rhiatr	57.50	27.40	9.50	2.10	58.80	69.40	45.90
Brook trout (*Salvelinus fontinalis*)*	salfon	48.50	32.20	10.90	2.60	69.10	59.70	12.20
Central mudminnow (*Umbra limi*)*	umblim	48.10	5.30	1.60	0.70	42.30	50.00	54.10
Mottled sculpin (*Cottus bairdii*)*	cotbai	47.60	25.50	12.00	4.10	57.70	46.80	35.10
Johnny darter (*Etheostoma nigrum*)*	ethnig	43.30	10.50	3.30	1.30	29.90	46.80	58.10
Brown trout (*Salmo trutta*)*	saltru	34.80	33.50	9.00	2.60	14.40	67.70	33.80
Rainbow trout (*Oncorhynchus mykiss*)	oncmyk	28.80	36.40	6.60	1.30	36.10	40.30	9.50
Longnose dace (*Rhinichthys cataractae*)*	rhicat	27.90	16.40	5.30	1.80	52.60	21.00	1.40
Common shiner (*Luxilus cornutus*)*	luxcor	27.00	19.70	4.40	1.30	19.60	37.10	28.40
Green sunfish (*Lepomis cyanellus*)	lepcya	24.50	4.50	1.70	0.80	0.00	27.40	54.10
Rock bass (*Ambloplites rupestris*)*	ambrup	24.00	6.10	2.80	1.10	13.40	21.00	40.50
Largemouth bass (*Micropterus salmoides*)	micsal	20.20	1.80	0.80	0.40	4.10	22.60	39.20
Blackside darter (*Percina maculata*)	permac	17.20	4.10	1.80	0.70	8.20	19.40	27.00
Brook stickleback (*Culaea inconstans*)	culinc	16.30	3.80	1.60	0.70	21.60	17.70	8.10
Hornyhead chub (*Nocomis biguttatus*)	nocbig	16.30	14.80	5.10	1.30	16.50	14.50	17.60
Bluntnose minnow (*Pimephales notatus*)*	pimnot	16.30	8.90	3.10	1.10	10.30	6.50	32.40
Northern hog sucker (*Hypentelium nigricans*)	hypnig	15.90	5.30	2.00	1.00	4.10	17.70	29.70
Pumpkinseed (*Lepomis gibbosus*)	lepgib	15.90	2.30	1.30	0.60	4.10	24.20	24.30
Yellow perch (*Perca flavescens*)	perfla	15.50	1.90	0.70	0.30	11.30	25.80	12.20
Rainbow darter (*Etheostoma caeruleum*)	ethcae	12.90	9.10	3.30	1.10	0.00	11.30	31.10
Burbot (*Lota lota*)	lotlot	12.90	3.20	1.10	0.50	20.60	12.90	2.70

Table 1.2.—(cont'd)

			Catch (individuals · 100 m^{-1})			% of sites found by region		
Fish species	Species code	% of sites found	75% quantile	Median	25% quantile	UP	NLP	SLP
Bluegill (*Lepomis macrochirus*)	lepmac	11.60	4.50	1.40	0.70	2.10	12.90	23.00
Striped shiner (*Luxilus chrysocephalus*)†	luxchr	11.60	6.40	3.30	1.30	14.40	1.60	16.20
Northern redbelly dace (*Phoxinus eos*)	phoeos	11.60	2.80	1.30	0.70	14.40	16.10	4.10
Northern pike (*Esox lucius*)	esoluc	10.30	1.30	0.70	0.30	5.20	11.30	16.20
Smallmouth bass (*Micropterus dolomieu*)	micdol	9.90	3.40	1.80	0.80	5.20	9.70	16.20
Logperch (*Percina caprodes*)	percap	9.40	2.10	1.00	0.30	12.40	11.30	4.10
Grass pickerel (*Esox americanus*)†	esoame	9.00	1.60	0.70	0.30	0.00	3.20	25.70
Coho salmon (*Oncorhynchus kisutch*)	onckis	9.00	15.80	6.00	0.70	18.60	3.20	1.40
Central stoneroller (*Campostoma anomalum*)	camano	8.60	7.10	3.60	1.20	0.00	4.80	23.00
Stonecat (*Noturus flavus*)	notfla	6.40	2.50	1.10	0.60	0.00	0.00	20.30
Fantail darter (*Etheostoma flabellare*)†	ethfla	5.60	6.40	3.00	0.70	7.20	0.00	8.10
Pearl dace (*Margariscus margarita*)	marmar	5.60	8.20	2.60	0.70	9.30	4.80	1.40
Slimy sculpin (*Cottus cognatus*)†	cotcog	5.20	21.20	12.70	4.80	3.10	12.90	1.40
Fathead minnow (*Pimephales promelas*)	pimpro	5.20	1.70	0.80	0.50	4.10	1.60	9.50
Black bullhead (*Ameiurus melas*)	amemel	4.70	0.70	0.70	0.30	1.00	9.70	5.40
Common carp (*Cyprinus carpio*)	cypcar	4.70	2.00	1.30	0.40	0.00	1.60	13.50
Spotfin shiner (*Cyprinella spiloptera*)	cypspi	4.70	4.30	2.00	1.10	0.00	3.20	12.20
Golden redhorse (*Moxostoma erythrurum*)†	moxery	4.70	4.70	1.40	0.90	0.00	3.20	12.20
Golden shiner (*Notemigonus crysoleucas*)	notcry	4.70	1.10	0.70	0.40	3.10	6.50	5.40
Yellow bullhead (*Ameiurus natalis*)	amenat	3.90	1.60	0.30	0.30	0.00	3.20	9.50
Blacknose shiner (*Notropis heterolepis*)	notheterol	3.90	4.40	1.60	0.70	5.20	4.80	1.40
American brook lamprey (*Lampetra appendix*)	lamapp	3.40	3.30	2.00	1.00	2.10	6.50	2.70
River chub (*Nocomis micropogon*)	nocmic	3.40	12.40	7.50	4.00	2.10	4.80	4.10
Iowa darter (*Etheostoma exile*)	ethexi	3.00	2.90	0.80	0.80	2.10	1.60	5.40
Brassy minnow (*Hybognathus hankinsoni*)†	hybhan	3.00	1.60	0.70	0.50	3.10	4.80	1.40
Blackchin shiner (*Notropis heterodon*)	notheterod	3.00	7.10	4.40	2.10	3.10	1.60	4.10

Table 1.2.—(cont'd)

			Catch (individuals · 100 m^{-1})			% of sites found by region		
Fish species	Species code	% of sites found	75% quantile	Median	25% quantile	UP	NLP	SLP
Black crappie (*Pomoxis nigromaculatus*)	pomnig	3.00	0.80	0.60	0.30	0.00	1.60	8.10
Walleye (*Sander vitreus*)	sanvit	3.00	0.30	0.30	0.20	5.20	1.60	1.40
Round goby (*Neogobius melanostomus*)	neomel	2.60	8.10	3.30	2.60	0.00	1.60	6.80
Sand shiner (*Notropis stramineus*)	notstr	2.60	1.00	0.70	0.70	2.10	4.80	1.40
Chinook salmon (*Oncorhynchus tshawytscha*)	onctsh	2.60	1.40	0.90	0.50	0.00	8.10	1.40
Brown bullhead (*Ameiurus nebulosus*)†	ameneb	2.10	0.80	0.40	0.30	1.00	0.00	5.40
Greenside darter (*Etheostoma blennioides*)	ethble	2.10	5.90	3.80	3.70	0.00	0.00	6.80
Longear sunfish (*Lepomis megalotis*)	lepmeg	2.10	7.80	2.50	1.00	0.00	0.00	6.80
Emerald shiner (*Notropis atherinoides*)†	notath	2.10	1.30	1.30	1.20	1.00	1.60	4.10
Mimic shiner (*Notropis volucellus*)	notvol	2.10	9.50	2.60	1.10	0.00	1.60	5.40
Finescale dace (*Phoxinus neogaeus*)†	phoneo	2.10	6.60	1.10	0.70	3.10	3.20	0.00
Pirate perch (*Aphredoderus sayanus*)†	aphsay	1.70	2.30	1.10	0.70	0.00	0.00	5.40
Creek chubsucker (*Erimyzon oblongus*)	eriobl	1.70	33.70	19.00	3.40	0.00	1.60	4.10
Northern brook lamprey (*Ichthyomyzon fossor*)	ichfos	1.70	2.80	1.00	0.60	0.00	3.20	2.70
Redfin shiner (*Lythrurus umbratilis*)	lytumb	1.70	2.60	1.90	1.50	0.00	1.60	4.10
Silver redhorse (*Moxostoma anisurum*)	moxani	1.70	0.80	0.40	0.30	1.00	1.60	2.70
Spottail shiner (*Notropis hudsonius*)	nothud	1.70	1.30	1.00	0.80	1.00	3.20	1.40
Rosyface shiner (*Notropis rubellus*)	notrub	1.70	8.90	4.40	2.00	0.00	1.60	4.10
Bowfin (*Amia calva*)	amical	1.30	1.30	1.30	0.80	0.00	0.00	4.10
Least darter (*Etheostoma microperca*)†	ethmic	1.30	16.10	2.00	1.10	1.00	0.00	2.70
Channel catfish (*Ictalurus punctatus*)	ictpun	1.30	2.00	1.30	0.90	0.00	0.00	4.10
Trout-perch (*Percopsis omiscomaycus*)	peromi	1.30	1.60	1.10	0.70	3.10	0.00	0.00
Lake chub (*Couesius plumbeus*)	couplu	0.90	2.00	1.80	1.50	1.00	1.60	0.00
Threespine stickleback (*Gasterosteus aculeatus*)	gasacu	0.90	1.60	1.10	0.70	1.00	0.00	1.40
Greater redhorse (*Moxostoma valenciennesi*)†	moxval	0.90	1.30	1.00	0.70	0.00	0.00	2.70
Lake sturgeon (*Acipenser fulvescens*)†	aciful	0.40	0.20	0.20	0.20	1.00	0.00	0.00

Table 1.2.—(cont'd)

Fish species	Species code	% of sites found	Catch (individuals · 100 m^{-1}) 75% quantile	Median	25% quantile	% of sites found by region UP	NLP	SLP
Goldfish (*Carassius auratus*)	caraur	0.40	0.30	0.30	0.30	0.00	0.00	1.40
Warmouth (*Chaenobryttus gulosus*)	chagul	0.40	1.60	1.60	1.60	0.00	0.00	1.40
Redside dace (*Clinostomus elongatus*)	clielo	0.40	2.20	2.20	2.20	1.00	0.00	0.00
Gizzard shad (*Dorosoma cepedianum*)	dorcep	0.40	1.60	1.60	1.60	0.00	0.00	1.40
Lake chubsucker (*Erimyzon sucetta*)†	erisuc	0.40	1.30	1.30	1.30	0.00	0.00	1.40
Muskellunge (*Esox masquinongy*)	esomas	0.40	0.20	0.20	0.20	1.00	0.00	0.00
Bigmouth shiner (*Hybopsis dorsalis*)†	hybdor	0.40	0.60	0.60	0.60	1.00	0.00	0.00
Chestnut lamprey (*Ichthyomyzon castaneus*)	ichcas	0.40	4.20	4.20	4.20	0.00	1.60	0.00
Spotted sucker (*Minytrema melanops*)†	minmel	0.40	2.00	2.00	2.00	0.00	0.00	1.40
River redhorse (*Moxostoma carinatum*)†	moxcar	0.40	0.60	0.60	0.60	0.00	1.60	0.00
Black redhorse (*Moxostoma duquesnii*)	moxduq	0.40	3.00	3.00	3.00	0.00	0.00	1.40
Shorthead redhorse (*Moxostoma macrolepidotum*)	moxmac	0.40	0.40	0.40	0.40	0.00	0.00	1.40
Pugnose minnow (*Opsopoeodus emiliae*)†	opsemi	0.40	3.30	3.30	3.30	1.00	0.00	0.00
Sea lamprey (*Petromyzon marinus*)	petmar	0.40	10.70	10.70	10.70	1.00	0.00	0.00
Round whitefish (*Prosopium cylindraceum*)	procyl	0.40	0.60	0.60	0.60	0.00	1.60	0.00
Flathead catfish (*Pylodictis olivaris*)	pyloli	0.40	0.70	0.70	0.70	0.00	0.00	1.40

Table 1.3.—Taxonomic summaries statewide and by regions.

Taxonomic summaries	Statewide		
Variable	mean	max	min
Taxa richness	9.54	28.00	1.00
Shannon's diversity	1.41	2.64	0.00
Pielou's evenness	0.67	1.00	0.00
	UP		
	mean	max	min
Taxa richness	7.67	19.00	1.00
Shannon's diversity	1.28	2.38	0.00
Pielou's evenness	0.67	1.00	0.00
	NLP		
	mean	max	min
Taxa richness	10.47	28.00	2.00
Shannon Weaver diversity	1.41	2.40	0.12
Pielou's evenness	0.64	1.00	0.09
	SLP		
	mean	max	min
Taxa richness	11.20	25.00	2.00
Shannon's diversity	1.59	2.64	0.59
Pielou's evenness	0.70	0.97	0.37

Table 1.4.—Instream temperature metric description, codes, mean, maximums and minimums for variables at 233 study sites, for the state of Michigan and by three regions, Upper Peninsula (UP), Northern Lower Peninsula (NLP) and Southern Lower Peninsula (SLP). Temperature metrics marked with (*) indicate those used in CSA. Temperature units in (°C).

		Statewide		
Instream temperature metric description	Variable code	mean	max	min
Monthly average daily maximum				
June	ADmax6	19.37	27.87	11.27
July	ADmax7	20.42	28.09	11.28
August	ADmax8	19.52	26.10	11.67
Monthly average daily range				
June	ADrange6	3.64	8.86	0.79
July	ADrange7	3.77	8.60	1.32
August	ADrange8	3.35	8.24	0.82
Maximum of 7 days moving average of daily				
range	Max7MovingADRT	5.10	32.02	1.43
maximum	Max7MovingAMaxT	22.25	39.54	12.88
Maximum of 14 days moving average of daily				
range	Max14MovingADRT	4.61	27.37	1.43
maximum	Max14MovingAMaxT	21.49	36.68	12.31
Maximum of 21 days moving average of daily				
range	Max21MovingADRT	4.45	24.51	1.26
maximum	Max21MovingAMaxT	21.10	35.00	11.93
Maximum of 30 days moving average of daily*				
range*	Max30MovingADRT	4.26	23.34	1.18
maximum*	Max30MovingAMaxT	20.83	33.95	11.77
Julian day of maximum of 7 days moving average of daily				
range	JDM7MADRT	181.79	267.17	126.17
maximum	JDM7MAMaxT	196.41	249.17	141.17
Julian day of maximum of 14 days moving average of daily				
range	JDM14MADRT	181.93	266.17	126.17
maximum	JDM14MAMaxT	198.42	238.17	164.17
Julian day of maximum of 21 days moving average of daily				
range	JDM21MADRT	184.35	263.17	131.17
maximum	JDM21MAMaxT	200.25	235.17	164.17
Julian day of maximum of 30 days moving average of daily				
range	JDM30MADRT	184.42	258.17	134.17
maximum	JDM30MAMaxT	199.62	232.17	163.17

Table 1.4.—(cont'd)

Instream temperature metric description	Variable code	UP		
		mean	max	min
Monthly average daily maximum				
June	ADmax6	18.15	25.02	11.27
July	ADmax7	19.46	25.91	11.28
August	ADmax8	18.89	25.47	11.67
Monthly average daily range				
June	ADrange6	3.67	8.85	0.79
July	ADrange7	3.83	8.11	1.43
August	ADrange8	3.45	8.24	1.47
Maximum of 7 days moving average of daily				
range	Max7MovingADRT	5.12	10.95	1.43
maximum	Max7MovingAMaxT	21.36	29.33	12.88
Maximum of 14 days moving average of daily				
range	Max14MovingADRT	4.65	10.18	1.43
maximum	Max14MovingAMaxT	20.55	28.09	12.31
Maximum of 21 days moving average of daily				
range	Max21MovingADRT	4.55	9.90	1.26
maximum	Max21MovingAMaxT	20.21	27.60	11.93
Maximum of 30 days moving average of daily				
range	Max30MovingADRT	4.40	9.20	1.18
maximum	Max30MovingAMaxT	19.95	26.60	11.77
Julian day of maximum of 7 days moving average of daily				
range	JDM7MADRT	178.94	245.17	126.17
maximum	JDM7MAMaxT	198.38	249.17	145.17
Julian day of maximum of 14 days moving average of daily				
range	JDM14MADRT	180.89	247.17	126.17
maximum	JDM14MAMaxT	200.21	238.17	169.17
Julian day of maximum of 21 days moving average of daily				
range	JDM21MADRT	182.85	252.17	131.17
maximum	JDM21MAMaxT	202.85	235.17	167.17
Julian day of maximum of 30 days moving average of daily				
range	JDM30MADRT	183.83	248.17	134.17
maximum	JDM30MAMaxT	201.16	230.17	163.17

Table 1.4.—(cont'd)

Instream temperature metric description	Variable code	NLP mean	NLP max	NLP min
Monthly average daily maximum				
June	ADmax6	19.15	24.53	12.38
July	ADmax7	20.05	26.16	13.24
August	ADmax8	18.71	25.34	12.25
Monthly average daily range				
June	ADrange6	3.98	8.86	1.44
July	ADrange7	4.03	8.60	1.55
August	ADrange8	3.50	7.35	1.15
Maximum of 7 days moving average of daily				
range	Max7MovingADRT	5.92	32.02	2.05
maximum	Max7MovingAMaxT	22.12	39.54	14.42
Maximum of 14 days moving average of daily				
range	Max14MovingADRT	5.33	27.37	1.94
maximum	Max14MovingAMaxT	21.30	36.68	14.09
Maximum of 21 days moving average of daily				
range	Max21MovingADRT	5.05	24.51	1.90
maximum	Max21MovingAMaxT	20.83	35.00	13.63
Maximum of 30 days moving average of daily				
range	Max30MovingADRT	4.82	23.34	1.82
maximum	Max30MovingAMaxT	20.59	33.95	13.41
Julian day of maximum of 7 days moving average of daily				
range	JDM7MADRT	176.54	267.17	136.17
maximum	JDM7MAMaxT	189.95	229.17	141.17
Julian day of maximum of 14 days moving average of daily				
range	JDM14MADRT	176.16	265.17	136.17
maximum	JDM14MAMaxT	193.21	226.17	164.17
Julian day of maximum of 21 days moving average of daily				
range	JDM21MADRT	179.75	262.17	137.17
maximum	JDM21MAMaxT	195.27	223.17	164.17
Julian day of maximum of 30 days moving average of daily				
range	JDM30MADRT	178.28	256.17	135.17
maximum	JDM30MAMaxT	194.89	219.17	169.17

Table 1.4.—(cont'd)

Instream temperature metric description	Variable code	SLP mean	SLP max	SLP min
Monthly average daily maximum				
June	ADmax6	21.12	27.87	15.61
July	ADmax7	22.00	28.09	15.62
August	ADmax8	20.99	26.10	13.92
Monthly average daily range				
June	ADrange6	3.33	7.04	1.18
July	ADrange7	3.46	6.65	1.32
August	ADrange8	3.11	6.77	0.82
Maximum of 7 days moving average of daily				
range	Max7MovingADRT	4.37	9.04	1.54
maximum	Max7MovingAMaxT	23.44	29.29	16.50
Maximum of 14 days moving average of daily				
range	Max14MovingADRT	3.97	8.36	1.46
maximum	Max14MovingAMaxT	22.81	28.66	15.88
Maximum of 21 days moving average of daily				
range	Max21MovingADRT	3.81	8.14	1.45
maximum	Max21MovingAMaxT	22.43	28.61	15.86
Maximum of 30 days moving average of daily				
range	Max30MovingADRT	3.58	7.05	1.33
maximum	Max30MovingAMaxT	22.13	28.25	15.77
Julian day of maximum of 7 days moving average of daily				
range	JDM7MADRT	189.73	267.17	126.17
maximum	JDM7MAMaxT	199.48	243.17	160.17
Julian day of maximum of 14 days moving average of daily				
range	JDM14MADRT	188.09	266.17	127.17
maximum	JDM14MAMaxT	200.63	228.17	171.17
Julian day of maximum of 21 days moving average of daily				
range	JDM21MADRT	190.27	263.17	131.17
maximum	JDM21MAMaxT	201.44	228.67	179.17
Julian day of maximum of 30 days moving average of daily				
range	JDM30MADRT	190.65	258.17	135.17
maximum	JDM30MAMaxT	201.98	232.17	179.17

Table 1.5.—Principle component analysis (PCA) results for 22 instream temperature variables, including interpretations of axes, loading assigned to each variable for each axes, and percentage of variation in data explained by each axis. Instream temperature variable codes are described in Table 1.3. Total amount of variation explained was 89.24%. Temperature metrics marked with (*) indicate those used in CSA.

	Axis 1	Axis 2	Axis 3	Axis 4
Interpertation	Maximum values	Range in values	Julian day range in values	Julian day maximum
Variance explained (%)	39.32	24.96	13.12	11.83
Variable code				
ADmax6	0.92	0.12	0.13	-0.12
ADmax7	0.95	0.16	0.11	0.06
ADmax8	0.93	0.11	0.13	0.16
Max7MovingAMaxT	0.95	0.21	0.10	0.00
Max14MovingAMaxT	0.96	0.20	0.10	0.03
Max21MovingAMaxT	0.97	0.19	0.09	0.06
Max30MovingAMaxT*	0.97	0.18	0.10	0.05
ADrange6	0.14	0.89	-0.13	-0.13
ADrange7	0.23	0.90	0.04	-0.08
ADrange8	0.19	0.89	0.11	0.03
Max7MovingADRT	0.14	0.95	-0.13	-0.11
Max14MovingADRT	0.14	0.96	-0.09	-0.10
Max21MovingADRT	0.15	0.96	-0.08	-0.09
Max30MovingADRT*	0.14	0.97	-0.07	-0.09
JDM7MADRT	0.14	-0.08	0.89	0.03
JDM14MADRT	0.11	-0.04	0.94	0.06
JDM21MADRT	0.14	-0.06	0.93	0.02
JDM30MADRT	0.15	-0.08	0.92	0.06
JDM7MAMaxT	0.03	-0.11	0.06	0.78
JDM14MAMaxT	0.12	-0.08	0.04	0.90
JDM21MAMaxT	0.00	-0.07	0.03	0.92
JDM30MAMaxT	0.01	-0.11	0.02	0.89

Table 1.6.—Pearson product moment correlations between landscape variables for covariance structure analysis (CSA). Mean July air temperature is at the local catchment scale, coarse and fine lithology, forest land cover and catchment area are at the network catchment scale.

	Coarse lithology	Fine lithology	Catchment area	Forest land cover	Mean July air temperature
Coarse lithology	1.00				
Fine lithology	-0.91	1.00			
Catchment area	0.16	-0.19	1.00		
Forest land cover	0.19	-0.21	-0.15	1.00	
Mean July air temperature	-0.06	0.24	0.13	-0.75	1.00

Table 1.7.—ISA values for species associations with instream temperature variables, Statewide (e.g., ISA value > 0.65) and 3 Michigan regions (e.g., ISA value>0.70). Statewide; n=233, Upper Peninsula; n=97, Northern Lower Peninsula; n=62, Southern Lower Peninsula; n=74. Species codes are described in Table 1.2 and instream temperature variable codes are described in Table 3 with .h and .l depicting high and low species associations with the variable, respectively.

Instream temperature variables	Statewide					
	catcom	sematr	rhiatr	salfon	umblim	ethnig
ADmax6.h	0.70	0.75				0.66
ADmax6.l				0.70		
ADmax7.h	0.77	0.79				0.70
ADmax7.l				0.75		
ADmax8.h	0.74	0.78				0.71
ADmax8.l				0.75		
Max7MovingAMaxT.h	0.78	0.79				0.71
Max7MovingAMaxT.l				0.74		
Max14MovingAMaxT.h	0.76	0.77				0.70
Max14MovingAMaxT.l				0.75		
Max21MovingAMaxT.h	0.77	0.78				0.69
Max21MovingAMaxT.l				0.76		
Max30MovingAMaxT.h	0.77	0.78				0.70
Max30MovingAMaxT.l				0.75		
ADrange6.h		0.67				
ADrange7.h		0.74				
ADrange8.h		0.73				
Max7MovingADRT.h		0.74	0.67			
Max14MovingADRT.h		0.73				
Max21MovingADRT.h		0.74				
Max21MovingADRT.l	0.66					
Max30MovingADRT.h		0.77				
JDM7MADRT.h		0.66			0.66	

Table 1.7.—(cont'd)

Instream temperature variables	Upper Peninsula				
	catcom	sematr	rhiatr	salfon	rhicat
ADmax6.h	0.75	0.72	0.72		
ADmax7.h	0.80	0.82	0.77		
ADmax7.l				0.77	
ADmax8.h	0.84	0.81	0.77		
ADmax8.l				0.78	
Max7MovingAMaxT.h	0.86	0.83	0.81		
Max7MovingAMaxT.l				0.78	
Max14MovingAMaxT.h	0.81	0.80	0.79		
Max14MovingAMaxT.l				0.78	
Max21MovingAMaxT.h	0.84	0.83	0.80		
Max21MovingAMaxT.l				0.79	
Max30MovingAMaxT.h	0.84	0.84	0.78		0.70
Max30MovingAMaxT.l				0.73	
ADrange7.h		0.76	0.74		
ADrange8.h		0.72			
Max7MovingADRT.h		0.76	0.74		
Max7MovingADRT.l				0.74	
Max14MovingADRT.h		0.76	0.70		
Max14MovingADRT.l				0.73	
Max21MovingADRT.h		0.78	0.71		
Max21MovingADRT.l				0.74	
Max30MovingADRT.h		0.77	0.72		0.72
Max30MovingADRT.l				0.70	
JDM14MAMaxT.l				0.74	
JDM21MAMaxT.l				0.71	

Table 1.7.—(cont’d)

Instream temperature variables	Northern Lower Peninsula								
	catcom	sematr	rhiatr	salfon	umblim	ethnig	saltru	luxcor	ambrup
ADmax6.h	0.76	0.74							
ADmax7.h	0.79	0.73	0.71						
ADmax7.l					0.76				
ADmax8.h	0.73	0.73				0.75		0.77	
ADmax8.l					0.71		0.74		
Max7MovingAMaxT.h						0.74			
Max21MovingAMaxT.h	0.74	0.70							
Max21MovingAMaxT.l				0.73					
Max30MovingAMaxT.h	0.74	0.70							
Max30MovingAMaxT.l				0.73					
ADrange7.l				0.71					
ADrange8.h						0.73			
ADrange8.l							0.75		
Max7MovingADRT.l	0.71								
Max14MovingADRT.l	0.80								
Max30MovingADRT.l	0.80								
JDM7MADRT.l	0.74		0.79	0.71					
JDM14MADRT.h									0.78
JDM14MADRT.l	0.75	0.85	0.77						
JDM21MADRT.l			0.76						
JDM30MADRT.h					0.72				
JDM30MADRT.l				0.71					
JDM7MAMaxT.l				0.73					
JDM30MAMaxT.l					0.74				

Table 1.7.—(cont'd)

Instream temperature variables	Southern Lower Peninsula							
	catcom	sematr	umblim	saltru	luxcor	ambrup	cotbai	pimnot
ADmax6.h						0.70		0.70
ADmax6.l				0.74				
ADmax7.h		0.72				0.72		
ADmax7.l				0.76				
ADmax8.h		0.77				0.70		
ADmax8.l			0.72	0.71				
Max7MovingAMaxT.h		0.79						
Max7MovingAMaxT.l				0.76				
Max14MovingAMaxT.h		0.79						
Max14MovingAMaxT.l				0.81			0.71	
Max21MovingAMaxT.h		0.80						
Max21MovingAMaxT.l				0.78			0.73	
Max30MovingAMaxT.h		0.80				0.70		
Max30MovingAMaxT.l				0.78			0.73	
ADrange6.h		0.76						
ADrange7.h		0.71						
Max14MovingADRT.h		0.70						
Max21MovingADRT.h		0.74			0.71			
JDM21MADRT.l	0.72							
JDM30MADRT.l	0.75							

Table 1.8.—Fit statistics for CSA models predicting fish descriptor metrics directly for landscape factors and indirectly through metrics of a streams thermal regime. Fit equals yes if X^2 prob > 0.05, RMSEA ≤ 0.05, TLI > 0.9, and NFI > 0.9.

Category	Variable	Summer maximum in stream temperature							
		X^2	df	prob	RMSEA	X^2/df	TLI	NFI	Fit
Taxonomic summaries									
	Taxa richness	16.43	7.00	NSF	NSF	2.35	0.97	0.99	no
	Shannon diversity	16.25	7.00	NSF	NSF	2.32	0.97	0.99	no
	Pielou evenness	10.96	7.00	0.14	0.05	1.57	0.99	0.99	yes
Fish individual species									
	White Sucker	11.88	7.00	0.10	NSF	1.70	0.98	0.99	no
	Creek Chub	7.49	7.00	0.38	0.02	1.07	1.00	0.99	yes
	E. Blacknose Dace	7.81	7.00	0.35	0.02	1.12	1.00	0.99	yes
	Brook Trout	12.46	7.00	NSF	NSF	1.78	0.98	0.99	no
	Central Mudminnow	9.55	7.00	0.22	0.04	1.37	0.99	0.99	yes
	Mottled Sculpin	7.38	7.00	0.39	0.02	1.06	1.00	0.99	yes
	Johnny Darter	11.64	7.00	0.11	NSF	1.66	0.98	0.99	no
	Brown Trout	9.28	7.00	0.23	0.04	1.33	0.99	0.99	yes
	Longnose Dace	22.06	7.00	NSF	NSF	3.15	0.95	0.98	no
	Common Shiner	7.17	7.00	0.41	0.01	1.03	1.00	0.99	yes
	Rock Bass	14.37	7.00	NSF	NSF	2.05	0.98	0.99	no
	Bluntnose Minnow	8.41	7.00	0.30	0.03	1.20	1.00	0.99	yes
		Summer range in stream temperature							
Taxonomic summaries									
	Taxa richness	28.13	7.00	NSF	NSF	4.02	0.93	0.98	no
	Shannon diversity	20.51	7.00	NSF	NSF	2.93	0.95	0.98	no
	Pielou evenness	9.25	7.00	0.24	0.04	1.32	0.99	0.99	yes
Fish individual species									
	White Sucker	15.86	7.00	NSF	NSF	2.27	0.97	0.99	no
	Creek Chub	9.98	7.00	0.19	0.04	1.43	0.99	0.99	yes
	E. Blacknose Dace	6.08	7.00	0.53	0.00	0.87	1.00	1.00	yes
	Brook Trout	14.61	7.00	NSF	NSF	2.09	0.97	0.99	no
	Central Mudminnow	11.54	7.00	0.12	NSF	1.65	0.98	0.99	no
	Mottled Sculpin	8.95	7.00	0.26	0.04	1.28	0.99	0.99	yes
	Johnny Darter	10.69	7.00	0.15	0.05	1.53	0.99	0.99	yes
	Brown Trout	10.17	7.00	0.18	0.04	1.45	0.99	0.99	yes
	Longnose Dace	15.75	7.00	NSF	NSF	2.25	0.97	0.99	no
	Common Shiner	9.48	7.00	0.22	0.04	1.35	0.99	0.99	yes
	Rock Bass	21.54	7.00	NSF	NSF	3.08	0.95	0.98	no
	Bluntnose Minnow	12.14	7.00	NSF	NSF	1.74	0.98	0.99	no

Table 1.9.—Standardized total effects of landscape variable generated through CSA directly and indirectly on individual fish descriptors and indirectly through metrics of the thermal regime (e.g., MaxT = the Maximum of 30 days moving average of daily maximum in stream temperature and ADRT= Maximum of 30 days moving average of daily range is stream temperature). Landscape variables are: Regions= three study regions in Michigan (Figure 1), percent of coarse or fine lithology in the network catchment, network catchment area, percent of forested land cover in the network catchment, and mean July air temperature summarized at the network scale. Variables without values were models that had non–significant fit statistics.

		Standardized total effects						
Variable	R^2	MaxT	Region	Coarse lithology	Fine lithology	Catchment area	Forest land cover	Mean July air
Taxonomic summaries								
Pielou evenness	0.02	0.04	-0.01	-0.09	0.05	0.01	-0.01	0.01
Fish individual species								
Creek Chub	0.10	**0.30**	-0.04	0.01	0.17	0.00	**-0.08**	0.04
E. Blacknose Dace	0.03	0.01	0.00	0.11	0.21	0.15	0.00	0.00
Central Mudminnow	0.02	0.01	-0.01	-0.01	-0.05	-0.11	-0.03	0.01
Mottled Sculpin	0.02	**-0.14**	0.02	-0.01	0.00	-0.03	**0.04**	-0.02
Brown Trout	0.09	**-0.24**	0.03	0.30	0.18	0.13	**0.06**	-0.03
Common Shiner	0.02	0.14	-0.02	0.08	0.02	-0.01	**-0.04**	0.02
Bluntnose Minnow	0.06	**0.17**	-0.03	0.10	0.16	**0.19**	**-0.05**	0.02
	R^2	ADRT	Region	Coarse lithology	Fine lithology	Catchment area	Forest land cover	Mean July air
Taxonomic summaries								
Pielou evenness	0.05	**-0.17**	-0.04	-0.12	0.01	0.00	-0.02	**0.07**
Fish individual species								
Creek Chub	0.08	**0.21**	0.05	0.05	0.25	0.03	0.02	**-0.09**
E. Blacknose Dace	0.07	**0.19**	0.05	0.14	0.25	**0.16**	0.02	**-0.08**
Mottled Sculpin	0.00	-0.02	-0.01	-0.01	-0.02	-0.04	0.00	0.01
Johnny Darter	0.04	0.10	0.03	0.15	0.27	0.14	0.01	-0.05
Brown Trout	0.05	0.03	0.01	0.30	0.16	0.12	0.00	-0.01
Common Shiner	0.01	0.09	0.02	0.10	0.06	0.00	0.01	-0.04

Table 1.10.—Standardized total effects coefficients of landscape variables on stream temperature metrics were analyzed for statistical significance (*t* distribution, α = 0.05) using Monte Carlo bootstrapped SEs. Table includes squared multiple correlation coefficients (R^2) describing variance explained in stream temperature metrics. MaxT = the Maximum of 30 days moving average of daily maximum in stream temperature and ADRT= Maximum of 30 days moving average of daily range is stream temperature.

Variable	MaxT	ADRT
R^2	0.23	0.08
Standardized total effects from		
Region	-0.15	0.26
Coarse lithology	0.02	0.10
Fine lithology	0.20	0.07
Catchment area	**0.35**	0.04
Forest land cover	**-0.27**	0.09
Mean July air temperature	0.14	**-0.43**

APPENDIX 1.B

FIGURES

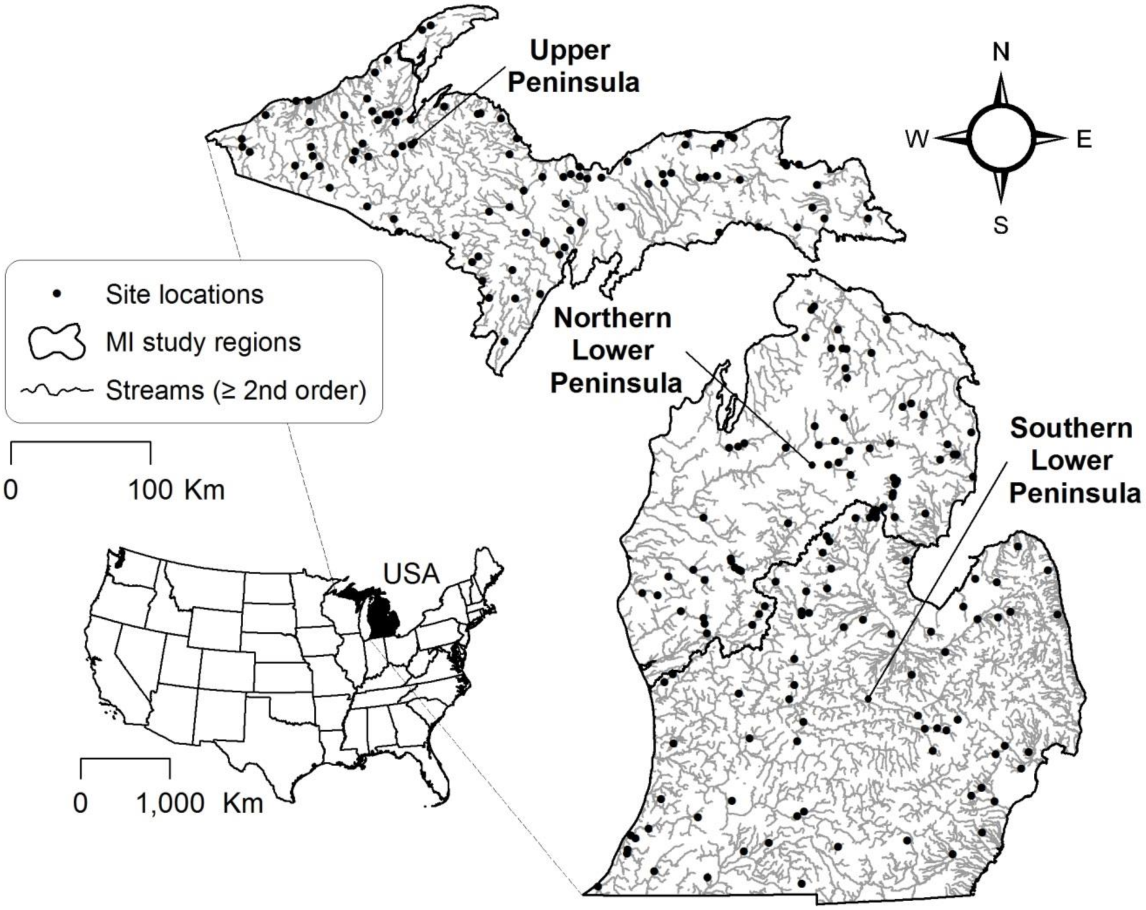

Figure 1.1.—Locations of study sites in Michigan having both fish community and instream temperature data collected from 1990 to 2011 (n= 233).

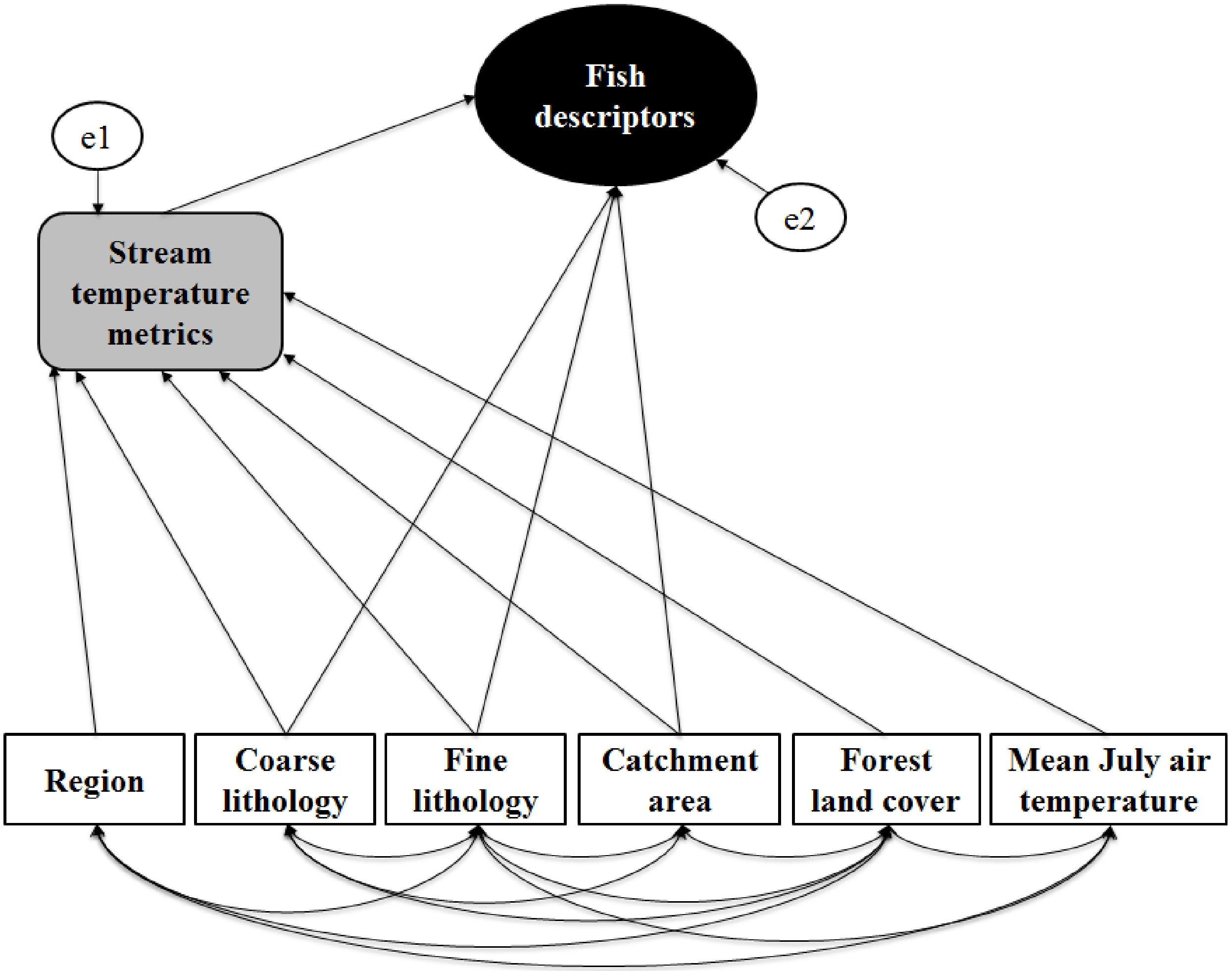

Figure 1.2.—Model developed for covariance structure analysis to evaluate hypothesized relationships among landscape variables and fish assemblage descriptors, with landscape effects modeled directly and indirectly through stream temperature variables (straight arrows), based on theorized influences. Curved arrows among landscape variables indicate correlations supported by Pearson pairwise correlations (Table 1.5).

APPENDIX 1.C

SUPPLEMENTAL TABLES

Table C1.1.—List of instream temperature metric descriptions calculated for 233 sites with matching temperature and fish assemblage data collected from study reaches. Averages (mean), maximums (max) and minimums (min) for each temperature variable, statewide and for each of three regions of Michigan, Upper Peninsula (UP), Northern Lower Peninsula (NLP), and Southern Lower Peninsula (SLP).

					3 Michigan regions								
		Statewide			UP			NLP			SLP		
Instream temperature metric description	Temperature code	mean	max	min	mean	max	min	mean	max	min	mean	max	min
Monthly average daily maximum													
May	ADmax5	15.32	21.33	9.40	14.46	20.33	9.40	15.23	21.33	10.88	16.30	21.09	12.68
June	ADmax6	19.37	27.87	11.27	18.15	25.02	11.27	19.15	24.53	12.38	21.12	27.87	15.61
July	ADmax7	20.42	28.09	11.28	19.46	25.91	11.28	20.05	26.16	13.24	22.00	28.09	15.62
August	ADmax8	19.52	26.10	11.67	18.89	25.47	11.67	18.71	25.34	12.25	20.99	26.10	13.92
September	ADmax9	16.45	23.89	10.90	15.27	19.94	10.90	15.67	19.82	12.35	18.38	23.89	13.86
Monthly average daily mean													
May	ADmean5	13.24	19.00	8.41	12.28	16.07	8.41	13.08	19.00	9.85	14.40	18.39	10.76
June	ADmean6	17.43	26.35	9.70	16.21	23.38	9.70	17.03	22.10	11.19	19.35	26.35	13.84
July	ADmean7	18.41	25.96	10.16	17.41	24.14	10.16	17.90	23.91	12.23	20.15	25.96	14.03
August	ADmean8	17.73	24.68	10.50	17.05	22.31	10.50	16.85	23.27	11.39	19.33	24.68	12.91
September	ADmean9	14.86	21.42	9.32	13.79	18.99	9.32	13.98	18.06	11.40	16.74	21.42	12.79
Monthly average daily minimum													
May	ADmin5	11.42	16.64	6.49	10.40	14.62	6.49	11.13	16.19	8.59	12.77	16.64	9.30
June	ADmin6	15.72	24.92	8.42	14.49	22.00	8.42	15.17	20.14	9.92	17.79	24.92	11.97
July	ADmin7	16.66	24.11	9.11	15.63	22.70	9.11	16.02	22.34	11.11	18.54	24.11	12.79
August	ADmin8	16.17	23.46	9.08	15.45	21.29	9.08	15.21	21.79	10.38	17.88	23.46	12.08
September	ADmin9	13.44	20.49	7.96	12.48	18.16	7.96	12.46	17.14	10.30	15.28	20.49	11.42

Table C1.1.—(cont'd)

					3 Michigan regions								
		Statewide			UP			NLP			SLP		
Instream temperature metric description	Temperature code	mean	max	min	mean	max	min	mean	max	min	mean	max	min
Monthly average daily range													
May	ADrange5	3.90	7.89	1.49	4.06	7.89	1.49	4.09	7.63	1.60	3.53	6.65	2.24
June	ADrange6	3.64	8.86	0.79	3.67	8.85	0.79	3.98	8.86	1.44	3.33	7.04	1.18
July	ADrange7	3.77	8.60	1.32	3.83	8.11	1.43	4.03	8.60	1.55	3.46	6.65	1.32
August	ADrange8	3.35	8.24	0.82	3.45	8.24	1.47	3.50	7.35	1.15	3.11	6.77	0.82
September	ADrange9	3.00	6.87	1.06	2.79	5.78	1.06	3.21	5.92	1.28	3.10	6.87	1.45
Monthly range of means													
May	Rmean5	8.75	17.27	0.27	10.21	17.27	3.91	7.22	14.11	0.27	8.87	14.97	5.72
June	Rmean6	6.64	15.22	0.32	7.00	15.22	2.25	7.59	14.27	0.66	5.37	12.10	0.32
July	Rmean7	6.16	15.07	1.61	6.24	15.07	2.51	6.36	12.36	2.75	5.89	11.96	1.61
August	Rmean8	6.28	14.88	2.60	6.41	14.82	2.60	6.35	13.34	3.32	6.06	14.88	2.77
September	Rmean9	7.71	14.64	0.65	8.06	14.64	0.65	7.53	12.33	2.78	7.44	12.50	3.14
Average daily mean													
Spring	SpADmean	13.24	19.00	8.41	12.28	16.07	8.41	13.08	19.00	9.85	14.40	18.39	10.76
Summer	SuADmean	17.85	25.41	10.16	16.91	23.27	10.16	17.25	22.77	11.61	19.59	25.41	13.59
Maximum daily mean													
Spring	SpMDmean	17.93	23.93	11.01	17.84	23.91	11.01	17.11	23.93	11.80	18.91	23.52	13.26
Summer	SuMDmean	21.87	29.44	12.37	20.84	28.03	12.37	21.62	28.23	14.24	23.43	29.44	16.38
Maximum of 1 days moving average of daily													
range	Max1MovingADRT	6.65	37.04	1.50	6.95	17.53	1.50	7.40	37.04	3.13	5.66	11.84	2.00
maximum	Max1MovingAMaxT	23.87	44.38	14.14	23.11	33.03	14.14	23.75	44.38	15.39	24.90	31.97	17.83
mean	Max1MovingAMeanT	21.48	29.44	12.37	20.62	28.03	12.37	20.93	28.23	14.24	22.98	29.44	16.38
Maximum of 3 days moving average of daily													
range	Max3MovingADRT	5.74	35.49	1.50	5.80	13.49	1.50	6.67	35.49	2.32	4.88	10.18	1.67
maximum	Max3MovingAMaxT	23.13	41.88	13.31	22.27	29.97	13.31	23.04	41.88	15.04	24.24	31.06	17.08
mean	Max3MovingAMeanT	20.91	28.21	12.09	20.01	27.79	12.09	20.41	27.15	13.60	22.41	28.21	15.64
Maximum of 7 days moving average of daily													
range	Max7MovingADRT	5.10	32.02	1.43	5.12	10.95	1.43	5.92	32.02	2.05	4.37	9.04	1.54
maximum	Max7MovingAMaxT	22.25	39.54	12.88	21.36	29.33	12.88	22.12	39.54	14.42	23.44	29.29	16.50
mean	Max7MovingAMeanT	20.12	27.65	11.60	19.22	27.65	11.60	19.61	26.54	13.25	21.66	27.28	15.07

Table C1.1.—(cont'd)

					3 Michigan regions								
		Statewide			UP			NLP			SLP		
Instream temperature metric description	Temperature code	mean	max	min	mean	max	min	mean	max	min	mean	max	min
Maximum of 14 days moving average of daily													
range	Max14MovingADRT	4.61	27.37	1.43	4.65	10.18	1.43	5.33	27.37	1.94	3.97	8.36	1.46
maximum	Max14MovingAMaxT	21.49	36.68	12.31	20.55	28.09	12.31	21.30	36.68	14.09	22.81	28.66	15.88
mean	Max14MovingAMeanT	19.48	26.78	10.96	18.53	26.35	10.96	18.94	25.61	12.98	21.09	26.78	14.40
Maximum of 21 days moving average of daily													
range	Max21MovingADRT	4.45	24.51	1.26	4.55	9.90	1.26	5.05	24.51	1.90	3.81	8.14	1.45
maximum	Max21MovingAMaxT	21.10	35.00	11.93	20.21	27.60	11.93	20.83	35.00	13.63	22.43	28.61	15.86
mean	Max21MovingAMeanT	19.10	26.32	10.89	18.19	25.41	10.89	18.56	25.13	12.58	20.70	26.32	14.20
Maximum of 30 days moving average of daily													
range	Max30MovingADRT	4.26	23.34	1.18	4.40	9.20	1.18	4.82	23.34	1.82	3.58	7.05	1.33
maximum	Max30MovingAMaxT	20.83	33.95	11.77	19.95	26.60	11.77	20.59	33.95	13.41	22.13	28.25	15.77
mean	Max30MovingAMeanT	18.85	26.14	10.71	17.93	24.84	10.71	18.32	24.87	12.40	20.45	26.14	14.20
Julian day of maximum of 1 days moving average of daily													
range	JDM1MADRT	180.08	272.17	123.17	180.52	272.17	125.17	174.95	270.17	126.17	183.83	270.17	123.17
maximum	JDM1MAMaxT	193.10	251.17	139.17	193.35	251.17	139.17	185.43	218.17	141.17	199.20	248.17	159.17
mean	JDM1MAMeanT	195.94	252.17	147.17	198.30	252.17	147.17	188.13	218.17	158.17	199.59	244.17	160.17
Julian day of maximum of 3 days moving average of daily													
range	JDM3MADRT	180.99	269.17	124.17	180.67	250.17	126.17	177.13	269.17	134.17	184.59	265.17	124.17
maximum	JDM3MAMaxT	193.99	251.17	127.17	196.44	251.17	143.17	186.54	219.17	127.17	197.28	244.17	158.17
mean	JDM3MAMeanT	198.50	251.17	146.17	201.67	251.17	146.17	190.72	226.17	159.17	201.17	244.17	159.17

Table C1.1.—(cont'd)

					3 Michigan regions								
		Statewide			UP			NLP			SLP		
Instream temperature metric description	Temperature code	mean	max	min	mean	max	min	mean	max	min	mean	max	min
Julian day of maximum of 7 days moving average of daily													
range	JDM7MADRT	181.79	267.17	126.17	178.94	245.17	126.17	176.54	267.17	136.17	189.73	267.17	126.17
maximum	JDM7MAMaxT	196.41	249.17	141.17	198.38	249.17	145.17	189.95	229.17	141.17	199.48	243.17	160.17
mean	JDM7MAMeanT	200.11	249.17	145.17	202.25	249.17	145.17	195.36	229.17	159.17	201.51	243.17	171.17
Julian day of maximum of 14 days moving average of daily													
range	JDM14MADRT	181.93	266.17	126.17	180.89	247.17	126.17	176.16	265.17	136.17	188.09	266.17	127.17
maximum	JDM14MAMaxT	198.42	238.17	164.17	200.21	238.17	169.17	193.21	226.17	164.17	200.63	228.17	171.17
mean	JDM14MAMeanT	200.51	240.17	145.17	200.75	225.17	145.17	197.59	226.17	164.17	202.68	240.17	176.17
Julian day of maximum of 21 days moving average of daily													
range	JDM21MADRT	184.35	263.17	131.17	182.85	252.17	131.17	179.75	262.17	137.17	190.27	263.17	131.17
maximum	JDM21MAMaxT	200.25	235.17	164.17	202.85	235.17	167.17	195.27	223.17	164.17	201.44	228.67	179.17
mean	JDM21MAMeanT	202.81	232.17	165.17	205.18	230.17	168.17	200.05	232.17	165.17	202.33	229.17	181.17
Julian day of maximum of 30 days moving average of daily													
range	JDM30MADRT	184.42	258.17	134.17	183.83	248.17	134.17	178.28	256.17	135.17	190.65	258.17	135.17
maximum	JDM30MAMaxT	199.62	232.17	163.17	201.16	230.17	163.17	194.89	219.17	169.17	201.98	232.17	179.17
mean	JDM30MAMeanT	201.74	231.17	163.17	202.56	230.17	163.17	198.65	219.17	167.17	203.50	231.17	185.17
julian day of maximum													
of maximum temperature of the summer	JDmaxTmax	194.10	251.17	139.17	195.73	251.17	139.17	187.73	218.17	151.17	197.29	244.17	159.17
of average temperature of the summer	JDmaxTmean	196.57	252.17	159.17	199.30	252.17	159.17	189.85	218.17	159.17	198.62	244.17	160.17
Julian day of maximum of 7 days daily													
maximum	JDMM7MaxT	196.83	249.17	145.17	198.40	249.17	145.17	190.97	229.17	159.17	199.89	243.17	160.17
mean	JDMM7MeanT	200.24	249.17	145.17	202.22	249.17	145.17	195.89	229.17	159.17	201.49	243.17	171.17

Table C1.2.—List of sites with temperature and fish assemblage data collected from study reaches. Each site's stream name, reach code, and region code in which it is located are listed, along with the latitude and longitude of the point marking the upstream end of the sample reach.

Reach code	Stream name	Year	Latitude	Longitude	Region code
12926133	Bird Creek	2010	43.97	-82.97	SLP
13047663	Bullock Creek	2010	43.53	-84.36	SLP
6841567	Cassidy Creek	2010	45.86	-87.84	UP
6860186	Cedar River	2010	45.78	-87.53	UP
13204407	Cheboyganing Creek	2010	43.44	-83.76	SLP
12918875	Cherry Creek	2010	43.52	-82.64	SLP
14443608	Cook's Run	2010	46.17	-88.88	UP
6789873	Cranberry River	2010	46.70	-89.45	UP
6860332	Crooked Creek	2010	45.60	-87.50	UP
6841681	DeHaas Creek	2010	45.60	-87.73	UP
6789339	Duck Creek	2010	46.83	-89.47	UP
12025464	E Br Salmon Trout River	2010	46.79	-87.85	UP
9019265	Eastman Creek	2010	42.38	-86.15	SLP
11940357	Flintsteel River	2010	46.75	-89.13	UP
6841611	Harter Creek	2010	45.71	-87.80	UP
12255214	Hayden Creek	2010	42.26	-85.83	SLP
11937039	Hill Creek	2010	47.31	-88.43	UP
11962270	Hunter's Brook	2010	45.95	-87.24	UP
12942320	Johnson Creek	2010	44.20	-83.78	NLP
12021724	Laughing Whitefish River	2010	46.39	-87.07	UP
6789659	Little Carp River	2010	46.73	-89.87	UP
6789337	Little Iron River	2010	46.83	-89.59	UP
12255574	Little Portage Creek	2010	42.04	-85.43	SLP
6848077	Little River	2010	45.32	-87.58	UP
12261932	Mill Creek	2010	41.87	-85.74	SLP
6857446	N Br Ford River	2010	46.15	-87.75	UP
11937459	Obenhoff Creek	2010	47.11	-88.74	UP
11945791	Onion Creek	2010	46.57	-88.95	UP
11930744	Perch River	2010	46.51	-88.64	UP
13009178	Perry Creek	2010	43.30	-83.64	SLP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
12927361	Pigeon River	2010	43.74	-83.16	SLP
6841565	Pine Creek	2010	45.83	-87.90	UP
12121180	Pine River	2010	44.19	-85.77	NLP
12918323	Rock Falls Creek	2010	43.81	-82.70	SLP
9017617	S Br Macatawa River	2010	42.74	-86.04	SLP
12025490	Salmon Trout River	2010	46.78	-87.88	UP
12927171	Shebeon Creek	2010	43.77	-83.35	SLP
11962262	Silver Creek	2010	45.88	-87.10	UP
11930120	Silver River	2010	46.76	-88.70	UP
11951379	Sission Lilly	2010	46.47	-89.41	UP
11939211	Sleepy River	2010	46.86	-88.92	UP
12258102	Tallahassee Creek	2010	41.83	-84.93	SLP
11952109	Tenderfoot Creek	2010	46.34	-89.48	UP
11946929	Tenmile Creek	2010	46.53	-89.43	UP
11951377	Trout Creek	2010	46.46	-89.03	UP
12936622	White Feather Creek	2010	43.90	-83.97	SLP
12927975	Wiscoggin Drain	2010	43.59	-83.47	SLP
12953314	Au Sable River	2009	44.68	-84.58	NLP
8991910	Big S Br Pere Marquette River	2009	43.82	-86.08	NLP
12498902	Black River	2009	45.08	-84.46	NLP
11959836	Bryan Creek	2009	46.19	-87.57	UP
12498830	Canada Creek	2009	45.24	-84.23	NLP
11959562	E Br Escanaba River	2009	46.29	-87.43	UP
12501809	E Br Maple River	2009	45.55	-84.75	NLP
11937883	Gratiot River	2009	47.34	-88.35	UP
12203110	Haynes Creek	2009	44.71	-83.35	NLP
13175771	Huron River	2009	42.13	-83.36	SLP
12221810	Little Indian River	2009	46.20	-86.53	UP
12501827	Maple River	2009	45.53	-84.77	NLP
12027614	Menge Creek	2009	46.73	-88.50	UP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
11951613	Mid Br Ontonagon River	2009	46.28	-89.24	UP
12953268	N Br Au Sable River	2009	44.83	-84.49	NLP
13046755	N Br Tobacco River	2009	43.96	-84.71	SLP
8990046	Pere Marquette River	2009	43.86	-85.86	NLP
12503387	Pigeon River	2009	45.27	-84.46	NLP
12503419	Pigeon River	2009	45.15	-84.47	NLP
12027134	Ravine River	2009	46.82	-88.19	UP
12021146	Rock River	2009	46.39	-86.92	UP
12953068	S Br Au Sable River	2009	44.54	-84.55	NLP
12952968	S Br Au Sable River	2009	44.62	-84.45	NLP
13030993	Shiawassee River	2009	42.82	-83.73	SLP
12017474	Sucker River	2009	46.67	-85.90	UP
12017476	Sucker River	2009	46.60	-85.93	UP
12017482	Two Hearted River	2009	46.61	-85.60	UP
11930116	W Br Sturgeon River	2009	46.76	-88.74	UP
12953512	Au Sable River	2008	44.66	-84.73	NLP
6859854	Bark River	2008	45.63	-87.26	UP
13027941	Cedar River	2008	43.43	-84.11	SLP
12214737	Davenport Creek	2008	46.07	-85.25	UP
12015636	Days River	2008	45.93	-87.05	UP
11959888	Hunters Brook	2008	46.02	-87.41	UP
12961971	Mcginn Creek	2008	44.84	-83.77	NLP
10850156	Mid Br Rouge River	2008	42.33	-83.25	SLP
12202316	Ocqueoc River	2008	45.46	-84.09	NLP
12952808	Perry Creek	2008	44.66	-84.08	NLP
12503351	Pigeon River	2008	45.40	-84.53	NLP
12014046	Rapid River	2008	46.04	-87.00	UP
12944838	Rifle River	2008	44.31	-84.07	NLP
12021166	Silver Creek	2008	46.40	-87.00	UP
12188951	Silver Creek	2008	46.40	-85.63	UP

Table C1.2.—(cont’d)

Reach code	Stream name	Year	Latitude	Longitude	Region code
11962022	Squaw Creek	2008	45.97	-87.22	UP
12188963	Syphon Creek	2008	46.39	-85.75	UP
12017658	Two Hearted River	2008	46.58	-85.65	UP
12953622	W Br Big Creek	2008	44.63	-84.27	NLP
12014072	W Br Whitefish River	2008	46.10	-86.90	UP
12014514	W Br Whitefish River	2008	46.22	-87.04	UP
12953302	Au Sable River	2007	44.78	-84.76	NLP
12021200	Au Train River	2007	46.38	-86.84	UP
12206528	Bear Creek	2007	46.19	-84.75	UP
12206346	Carp River	2007	46.06	-84.90	UP
12183907	Clear Creek	2007	46.33	-84.70	UP
11948631	E Br Ontonagon River	2007	46.49	-88.89	UP
12206284	Elmhurst Creek	2007	46.12	-84.64	UP
12184125	Grant Creek	2007	46.47	-84.87	UP
13228138	Iron Creek	2007	42.09	-84.01	SLP
12183703	Naomikong Creek	2007	46.46	-84.99	UP
11931042	Rock River	2007	46.57	-88.49	UP
12185431	Roxbury Creek	2007	46.48	-85.01	UP
12502977	Sturgeon River	2007	45.28	-84.60	NLP
9004125	Bear Creek	2006	43.06	-85.47	SLP
12953358	Beaver Creek	2006	44.53	-84.65	NLP
6790993	Black River	2006	46.51	-90.07	UP
6790205	Black River	2006	46.48	-90.00	UP
13007340	Cass River	2006	43.51	-83.34	SLP
13039000	Chippewa River	2006	43.59	-84.90	SLP
11951427	Cisco Br Ontonagon River	2006	46.41	-89.34	UP
11930334	Clear Creek	2006	46.71	-88.65	UP
12222166	Creighton River	2006	46.35	-86.28	UP
11937723	Elm River	2006	47.03	-88.86	UP
12231450	Fish Creek	2006	43.28	-84.97	SLP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
12944334	Gamble Creek	2006	44.41	-84.03	NLP
14443726	Iron River	2006	46.09	-88.64	UP
12021288	Mosquito River	2006	46.49	-86.47	UP
13038808	N Br Chippewa River	2006	43.71	-84.86	SLP
3470497	Rice Creek	2006	42.29	-84.91	SLP
12021058	Rock River	2006	46.45	-86.92	UP
3472663	Spring Brook	2006	42.37	-85.53	SLP
11946997	Trout Creek	2006	46.52	-89.01	UP
12954072	Van Etten River	2006	44.43	-83.34	NLP
11930214	W Br Sturgeon River	2006	46.72	-88.81	UP
13047167	Bailey Creek	2005	43.86	-84.63	SLP
14443816	Brule River	2005	46.01	-88.58	UP
12026122	Carp River	2005	46.52	-87.58	UP
13184584	Clinton River	2005	42.63	-83.22	SLP
13045491	E Br Tittabawassee River	2005	44.18	-84.23	SLP
11930690	Kelsey Creek	2005	46.56	-88.58	UP
12503375	Little Pigeon River	2005	45.28	-84.50	NLP
13182894	Mid Br Clinton River	2005	42.64	-82.93	SLP
10849642	Mid Br Rouge River	2005	42.37	-83.45	SLP
13047477	N Br Salt River	2005	43.73	-84.67	SLP
13184576	Paint Creek	2005	42.69	-83.14	SLP
13040936	Pine River	2005	43.48	-84.53	SLP
13184448	Red Run	2005	42.54	-83.01	SLP
12955128	S Br Au Sable River	2005	44.46	-84.44	NLP
12189217	Tahquamenon River	2005	46.37	-85.42	UP
12026264	Bismark Creek	2004	46.63	-87.51	UP
13045425	Brick Creek	2004	44.22	-84.25	SLP
13039110	Cedar Creek	2004	43.56	-84.90	SLP
12021738	Chocolay River	2004	46.38	-87.26	UP
12961811	Cole Creek	2004	44.89	-83.96	NLP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
13045431	Cooks Creek	2004	44.22	-84.22	SLP
12211124	E Br Munuscong River	2004	46.11	-84.24	UP
13038992	Johnson Creek	2004	43.57	-84.84	SLP
11951401	Marshall Creek	2004	46.41	-89.57	UP
13045511	Mid Br Tittabawassee River	2004	44.18	-84.28	SLP
13015549	Misteguay Creek	2004	43.16	-83.94	SLP
13007330	Mud Creek	2004	43.51	-83.16	SLP
13040090	N Br Chippewa River	2004	43.78	-85.13	SLP
12117876	N Br Manistee River	2004	44.64	-85.03	NLP
9005547	Norris Creek	2004	43.13	-86.12	SLP
9005507	Norris Creek	2004	43.18	-86.05	SLP
12264790	Pokagon Creek	2004	41.91	-86.20	SLP
11930106	Sturgeon River	2004	46.78	-88.62	UP
13019901	Thread Creek	2004	42.87	-83.54	SLP
12961725	Turtle Creek	2004	44.91	-83.88	NLP
13045501	W Br Tittabawassee River	2004	44.18	-84.41	SLP
3471093	Kalamazoo River	2003	42.26	-84.96	SLP
13031047	Shiawassee River	2003	42.80	-83.65	SLP
12502939	W Br Minnehaha Creek	2003	45.35	-84.83	NLP
12026202	Yellow Dog River	2003	46.76	-87.66	UP
12134742	Bigelow Creek	2002	43.45	-85.75	NLP
13057812	Boardman River	2002	44.67	-85.40	NLP
8990078	Little S Br Pere Marquette River	2002	43.79	-85.76	NLP
13006734	Mid Br Cass River	2002	43.55	-83.05	SLP
3470695	Rice Creek	2002	42.06	-84.61	SLP
12951474	S Br Pine River	2002	44.57	-83.51	NLP
13226892	Saline River	2002	42.00	-83.62	SLP
13031417	Shiawassee River	2002	42.81	-83.84	SLP
13057846	Swainston Creek	2002	44.64	-85.54	NLP
12944870	W Br Rifle River	2002	44.25	-84.15	NLP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
12951286	Wallace Creek	2002	44.55	-83.64	NLP
12183695	Ankodosh Creek	2001	46.48	-85.00	UP
12021302	Anna River	2001	46.38	-86.71	UP
13057824	Boardman River	2001	44.65	-85.45	NLP
13045737	Cedar River	2001	44.03	-84.65	SLP
12130638	Clam River	2001	44.15	-85.01	NLP
12214753	Crow River	2001	46.03	-85.61	UP
13030899	Jones Creek	2001	42.90	-83.90	SLP
12951194	McDonald Creek	2001	44.57	-83.48	NLP
13031255	Ore Creek	2001	42.67	-83.77	SLP
10849532	Tarabusi Creek	2001	42.42	-83.36	SLP
13045751	W Br Ceader River	2001	44.07	-84.67	SLP
12951060	W Br Pine River	2001	44.64	-83.57	NLP
12014040	W Br Whitefish River	2001	46.10	-86.90	UP
6790865	Black River	2000	46.56	-90.08	UP
12132510	Hersey River	2000	43.85	-85.44	NLP
12944354	Houghton Creek	2000	44.39	-84.04	NLP
9001717	Prairie Creek	2000	43.11	-84.97	SLP
9004341	Prairie Creek	2000	43.02	-85.02	SLP
12944400	Prior Creek	2000	44.33	-84.07	NLP
12242480	Sebewa Creek	2000	42.75	-84.96	SLP
12944882	Silver Creek	2000	44.18	-84.06	NLP
12132402	Hersey River	1999	43.91	-85.52	NLP
12132432	Hersey River	1999	43.87	-85.49	NLP
12132378	Hersey River	1999	43.93	-85.53	NLP
12132498	Hersey River	1999	43.86	-85.46	NLP
12241372	Looking Glass River	1999	42.87	-84.90	SLP
12255996	Nottawa Creek	1999	42.10	-85.21	SLP
8991986	S Br Pentwater River	1999	43.69	-86.18	NLP
8991416	S Br Pentwater River	1999	43.71	-86.32	NLP

Table C1.2.—(cont'd)

Reach code	Stream name	Year	Latitude	Longitude	Region code
12944820	Vaughn Creek	1999	44.42	-84.03	NLP
12256792	Blue Creek	1998	42.13	-86.37	SLP
12257042	Blue Creek	1998	42.14	-86.41	SLP
12221660	Driggs River	1998	46.35	-86.13	UP
12257022	Mill Creek	1998	42.19	-86.26	SLP
12944330	Oyster Creek	1998	44.44	-84.06	NLP
3396654	S Br Galien River	1998	41.81	-86.69	SLP
12256900	trib Saint Joseph River	1998	42.03	-86.44	SLP
12257058	trib Saint Joseph River	1998	42.05	-86.44	SLP
12221624	Hudson creek	1997	46.42	-86.06	UP
8990202	Martin Creek	1997	43.59	-85.97	NLP
12145326	trib Coldwater River	1997	42.77	-85.37	SLP
6838369	W BrSturgeon River	1997	46.00	-88.06	UP
12017494	E Br Two Heart	1996	46.64	-85.48	UP
12017622	Two Hearted River	1996	46.66	-85.53	UP
11930932	W Br Otter River	1996	46.78	-88.87	UP
12221632	Driggs River	1995	46.41	-86.14	UP
12188975	Tahquamenon River	1995	46.39	-85.80	UP
12134738	Bigelow Creek	1994	43.51	-85.76	NLP
12132824	E Br Little Muskegon River	1993	43.62	-85.23	NLP
12132952	Little Muskegon River	1993	43.50	-85.34	NLP
12133224	Little Muskegon River	1993	43.57	-85.28	NLP
8990450	S Br White River	1993	43.55	-85.77	NLP

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CHAPTER TWO

LANDSCAPE EFFECTS ON FLUVIAL FISH ASSEMBLAGE STRUCTURE: REGIONAL RESPONSES TO HUMAN LAND USES.

Abstract

Anthropogenic activities, including urbanization, agriculture, and dams, cause degradation to stream ecosystems and are a dominant reason for global biodiversity declines in fluvial fish assemblages. While such trends have been well-documented regionally, differences occur in how fish respond to human land uses, resulting in location-specific responses in fishes from the same degree of human land use in one region vs. another. To test for such differences, we conducted our study within five large ecoregions in the eastern United States and evaluated data characterizing stream fish assemblages from > 10,500 locations within the study region. Fishes were summarized by functional and taxonomic metrics describing community structure, trophic structure, levels of tolerance to human stressors, and life history. Natural and anthropogenic landscape factors were evaluated across regions, and prominent human land uses were identified to test for regionally-specific influences on fishes including percent urbanization, percent agriculture, and density of stream-road crossings and dams in stream catchments. After controlling for natural landscape factors (including catchment area, catchment lithology, and elevation of study sites) we used cascade multivariate regression trees (CMRT) to quantify variance explained in fish metrics by landscape factors. Results showed differences in dominant influences by regions, and differences in levels of human land uses influencing fishes within and across regions. Knowledge of such regional differences lends insights into controls on stream

fish assemblages and can aid in developing conservation strategies to prevent biodiversity loss from current and future human land uses.

Introduction

For over a century, freshwater fishes have experienced population declines and range reductions globally due to anthropogenic influences in the environment (Dudgeon et al. 2006; Helfman 2007; Vörösmarty et al. 2010). Many freshwater fishes are critically imperiled in North America and have remained in a similar or worse state of conservation status (i.e., listed as endangered, threatened or vulnerable) over the last two decades (Jelks et al. 2008). Due to these trends, freshwater fishes are considered one of the most imperiled taxa on the planet (Racciardi and Rasmussen 1999; Cooke et al. 2012). Habitat degradation, fragmentation and loss are dominant reasons for declines in biodiversity of freshwater fishes (Sala et al. 2000; Helfman 2007; Jelks et al. 2008; Burkhead 2012), with changes in habitat resulting in part from human land uses in surrounding landscapes. Human land uses may affect fishes by altering stream flows and thermal regimes as well as through inputs of nutrients, sediments, and toxins, all known to degrade habitat for stream fish assemblages (Dudgeon et al. 2006; Helfman 2007; Jelks et al. 2008). Modifications to aquatic habitats, induced by land cover changes are expected to continue into the future, with persistent negative effects on freshwater fishes (Ormerod 2003; Helfman 2007; Jelks et al. 2008).

In fluvial systems, understanding the extent to which human alterations landscapes may affect fishes has advanced greatly in the past few decades due to intensive study of relationships between land cover in catchments and aquatic habitat quality (e.g., Allan et al. 1997; Wiens 2002; Allan 2004). This greater understanding has been accompanied by advancements in the utility and application of bioassessment methods which has improved our understanding of the types and levels of human perturbation that are negatively affecting aquatic habitats and the fishes they support (Barbour et al. 1999; Karr and Chu 1999; 2000 Norris and Thoms 1999). For example, urban land use has been described as a major source of degradation to habitat and declines in biota in stream systems (Paul and Meyer 2001; Allan 2004; Walsh et al. 2005). Studies documenting negative effects of urban land use on habitats and fish in Wisconsin (e.g., Wang et al. 2000; 2001) and declines of endemic fish species with urban land use across stream catchments exist in the southeastern U.S. (e.g., Walters et. al. 2003, Scott 2006). Similarly, agricultural land use is known to negatively affect fish in a variety of ways (Richter et al. 1997; Allan 2004). Percent agricultural land use in catchments was associated with negative effects on fish assemblages in 20 major river basins throughout the conterminous United States (Meador and Goldstein 2003). Further, regional decreases in fish abundance, species richness, and fish biotic integrity have been described for streams in Wisconsin (e.g., Wang et al. 1997; Fitzpatrick et al. 2001) and Michigan (e.g., Roth et al. 1996) resulting from > 30% agriculture in catchments. Besides urban and agricultural land uses, dams and others barriers to fish passage are increasingly acknowledged as operating at a landscape-scale due to their pervasiveness throughout river networks and to the variety of effects they have on stream fishes and habitats (Cooper et al. In Review). Besides reducing network connectivity, dams alter flow and thermal regimes, sediment transport, and water physicochemistry (Olden and Naiman 2010, Cooper et al. In Review), and recent efforts have characterized cumulative effects of multiple barriers, including dams and passageways at stream-road crossings, on stream habitats and fishes (Wang et al. 2011b, Perkin and Gido 2012, Januchoswki-Hartley et al. 2013). Yet despite extensive and advancing understanding of the pervasiveness of anthropogenic landscape effects on streams, degradation of stream habitats and decline in stream fishes continues throughout the U.S. (Allan and Flecker 1993; Dudgeon et al 2006; Jelks et al. 2008; Strayer and Dudgeon 2010).

One factor that confounds the ability to protect streams from degradation resulting from human land uses includes limited understanding of the mechanisms by which landscape factors affect streams including delivery of sediments, nutrients, and/or toxins, and alterations to flow and thermal regimes (Allan 2004). Such diverse and often co-occurring factors like the delivery of materials, and thermal and flow alterations make it challenging to manage for sources of degradation to stream habitats. Stream protection is further complicated because land use influences on streams may vary regionally due to the influences of co-occurring natural landscape factors such as lithology and topography. This can result in regionally-specific trends and/or differences in the types and levels of human land uses affecting stream fishes across regions. Only a few studies have attempted to describe such regional differences in fish responses. For example, Utz et al. (2010) found substantial regional differences in declines of diversity and abundances of stream fishes across physiographic regions in Maryland, attributing these differences in part to geomorphic characteristics of the regions and their ability to buffer effects of urbanization.

The effects of landscape-scale factors like human land use may vary by the specific compositions of fish assemblages, and this factor requires greater understanding for stream protection. Morgan and Cushman (2005) found differences in regional sensitivity of fish species to urban land use in Maryland, due in part to differences in tolerance of fishes between the Eastern Piedmont and Costal Plains physiographic regions. In a similar study, Meador et al. (2005) showed that fish species richness declined with increasing urbanization at sites in both Boston, MA and Birmingham, AL but attributed the observed declines to different factors in

Boston, fluvial specialists were negatively associated with urban land in the absence of endemic species. In Birmingham, endemic fishes were negatively associated with urban land. The authors attributed these results to compositional differences in fish assemblages between the regions and to regionally different mechanisms related to urbanization like water withdrawal and flow alterations. Together, these findings underscore the observations that fish assemblages can respond differently and be more susceptible to human land uses depending on location and types of human stressors (Utz et al. 2010).

Based on the importance of understanding such regional differences in land use effects on conservation and management of fluvial fish, the goal of this study was to characterize regionally-specific differences in fish assemblage relationships to human land uses across five large regions in the eastern portion of the U.S. We had three objectives. First, we characterized prominent anthropogenic landscape factors that could potentially affect fish over large spatial extents. Second, we developed a composite variable of prominent natural landscape factors known to affect fish that could be used to incorporate natural landscape factors into assessments of stream fishes. Finally, we characterized if fish response to human land uses vary by ecoregions in an attempt to describe regional influences for improved understanding of landscape controls on stream fishes.

Methods

Study area.—This study was conducted within five large freshwater ecoregions located in the eastern U.S. These freshwater ecoregions, referred to following as “ecoregions,” were delineated by the World Wildlife Fund and included: the Appalachian Piedmont, Chesapeake Bay, Laurentian Great Lakes, Middle Missouri, and the Upper Mississippi (Abell et al. 2008;

Figure 2.1). Freshwater ecoregions were defined as areas with similar biogeographic history in fish faunas that encompassed major river basins and large basin boundaries; they represented ecologically-relevant units for groupings of fishes based on evolutionary patterns across large landscapes (Maxwell et al. 1995; Matthews 1998; Abell et al. 2000; 2008; Esselman et al. 2011). Freshwater ecoregions were chosen as the spatial units to evaluate in this study to account for broad influences of natural landscape factors across the entire study area on stream fishes and to incorporate a diverse range of natural and human landscape variables to facilitate regional comparisons among ecoregions.

The study area extends from the western Great Plains to the east coastal plains of the U.S. (Figure 2.1). Natural landscape factors within the study area are highly diverse; study ecoregions include previously glaciated landscapes in the Chesapeake Bay and Laurentian Great Lakes and regions that have not been glaciated including the coastal plains and highlands of the Appalachian Piedmont ecoregion. In the eastern and central portion of the study area, the Middle Missouri and Upper Mississippi ecoregions included areas of intensive agriculture, while high percentages of grasslands occur within the western Middle Missouri ecoregion. A high percentage of forested areas are located within the Laurentian Great Lakes, and the Chesapeake Bay ecoregion includes areas of high urban land use.

Stream layer.—The 1:100,000-scale National Hydrography Dataset Plus Version 1 (NHDPlusV1) national streams layer was used as a base layer for geographic representation of streams reaches and their catchments (USEPA and USGS 2005). We define a stream reach as a section of river in the NHDPlusV1 that extends 1) from the stream origin to the first downstream confluence or junction with a lake or reservoir, 2) from an upstream confluence or lake/reservoir outflow to the next downstream confluence or lake/reservoir junction, or 3) from an upstream confluence or lake/reservoir outflow to the river mouth where it meets with a lake, reservoir, or estuary (Brenden et al. 2006; Esselman et al. 2011; Wang et al. 2011a). Catchments summarizing information over two spatial extents were used in this analysis based on the NHDPlusV1. “Local catchments” included all land that drains directly into an individual stream reach without being transported via other fluvial pathways represented in the NHDPlusV1, and “network catchments” included all land upstream of and draining into a given reach via fluvial pathways, including the local catchment.

Natural landscape variables.—A variety of nationally-available landscape datasets were used in this study. All natural and human landscape factors were summarized at the local catchment and then aggregated to the network catchment, representing two spatial extents, then attributed to NHDPlusV1 stream reaches using a geographic information system (GIS, Table 2.1). Natural land cover classes including water, wetland, barren, forest, shrub, and grassland were developed from the National Land Cover Dataset (NLCD, Homer et al. 2004; Table 2.1). Catchment areas were calculated using a GIS. Channel gradient (i.e. slope) and elevation were developed from U.S. Geological Survey (USGS) National Elevation Data (NED, Gesch 2007). Surficial lithology metrics were developed from the USGS terrestrial ecosystems surficial lithology of the conterminous U.S. data layer (Soller and Reheis 2004; Cress et al. 2010). Surficial lithology classes were defined by grouping major categories of substrate size (e.g., coarse and fine). Coarse and fine categories were used to compare streams with a more stable hydrology and potentially higher contribution of base-flow from groundwater inputs versus streams that may be more prone to variable flow regimes, respectively. The base-flow index, a model of hydraulic potential characterizing the percentage of groundwater contribution to stream flow, was modeled by USGS (Wolock 2003; Table 2.1). A range in soil hydrologic groups and soil permeability metrics were developed from the U.S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) State Soil Geographic (STATSGO) Data Base (Schwarz and Alexander 1995). Mean annual air temperature and mean annual precipitation were summarized for the climatological period from 1981 to 2010 by the PRISM Climate Group and attributed to catchments of stream reaches (Daly et al. 2008; PRISM 2013).

Human land uses.—Major categories of human land cover for urban and agriculture classes from the NLCD were used including low, medium, and high intensity developed land; open space developed land; pasture/hay and cultivated crops (Homer et al. 2004). Individual classes for urban and agricultural land uses were summarized into composite metrics to aid in meeting assumptions of statistical tests (described below, Table 2.1). The percentage of impervious surface in the network catchment was developed from the NLCD (Homer et al. 2004). The population density metric was developed from a data layer created by the National Oceanic and Atmospheric Administration (NOAA, NOAA 2010). To consider cumulative effects of catchment-wide barriers on stream fish, variables representing barriers were incorporated for evaluation and analysis (Table 2.1). The density of stream-road crossings, road length and canals and ditches in catchments were developed from the U.S. Census Bureau TIGER/line files data (U.S. Census Bureau 2002). The density of dams was developed from the National Anthropogenic Barrier Dataset (NABD, U.S. Geological Survey 2012).

Fish data.—Data characterizing stream fish assemblages were assembled and referenced to stream reaches in the NHDPlusV1. Assemblages were sampled by state and federal programs using methods determined to be comparable for creeks, small rivers, and medium rivers ≤ 10,000 km^2 in drainage areas, over years from 1990 to 2010 (Esselman et al. 2011; 2013 Wang et al. 2011a). Fish were identified to species, and all scientific naming was standardized to the

Integrated Taxonomic Information System (ITIS,ITIS 2010). Twenty two fish metrics were developed to characterize fish assemblage structure at sites across the study region (Table 2.2), and all metrics were described as being indicators of biological integrity in streams and responsive to human perturbations (Lyons et al. 1996; Wang et al. 1997; Angermeier et al. 2000). Metrics included species and family richness, community diversity, and community evenness (Table 2.2, Shannon 1948; Pielou 1975; Oksanen et al. 2013). Fish assemblages were also characterized by functional metrics describing community structure, trophic grouping, levels of tolerance, and life history characteristics (Table 2.2). Functional metrics were represented as percent of individuals. Assignment of trophic metrics followed Lyons (1992), assignment of tolerance metrics measuring sensitivity of species to perturbation followed Barbour et al. (1999), and assignment of life history characteristics followed Frimpong and Angermeier (2009).

Data analysis

Landscape metric selection.—Fifty two variables describing a range in natural and anthropogenic landscape factors were originally considered for analysis (Table 2.1). All variables were transformed to better meet assumptions of linearity and homoscedasticity. Continuous variables were natural log transformed; percentage and proportional variables were arcsin square root transformed. We ran a Pearson correlation on all fifty two variables to reduce the number of highly correlated metrics (Table C2.1). When a pair of variables was correlated by an absolute value of ≥ 0.7, one of the two was eliminated from further analysis. Network catchment summaries were selected over local catchment summaries of the same factor because they were assumed to characterize a broader and more spatially extensive set of influences from landscape factors on streams, and other highly correlated variables were selected based on ecological interpretability. Principal component analysis (PCA) was then used with twenty two remaining natural and human landscape variables to explore dimensionality in the dataset and to further reduce redundancy (Legendre and Legendre 2012, Table C2.2). Landscape metrics were chosen for additional analyses by their weightings on orthogonal axes to retain unique dimensions of explained variation in the data and based on ecological interpretability. For example, network catchment base-flow was chosen over soil permeability because it was assumed to be a more interpretable measurement even though it had a lower axis weighting in the PCA. Through this process, six natural and eight anthropogenic landscape factors were selected for use in further analysis (Table 2.3).

Fish metric selection.—Pearson correlation was also used to reduce redundancy among the twenty two fish metrics. This analysis showed that fish species richness, family richness, and Shannon's diversity index were highly correlated (Table C2.3), and fish species richness was retained over family richness and diversity because it has been commonly used in development of IBIs (e.g., Karr and Chu 1999). Principal component analysis (PCA) was then used with the remaining fish metrics to characterize dimensionality in the data set (Legendre and Legendre 2012). Based on weightings on orthogonal axes, a final set of seven fish metrics (Table 2.4), were chosen to retain unique dimensions of explained variation in the data and for further analysis (Table C2.4).

Redundancy analysis (RDA). —RDA was used to partition variance in fish metrics into independent (pure) and confounded (inter-correlated) components explained by groupings of natural and human landscape variables following Borcard et al. (1992), and also to characterize how these partitions varied by ecoregion (Borcard et al. 2011; Legendre and Legendre 2012). Six natural landscape factors and six human land use classes were used in RDA, including an urban composite metric comprised of low, medium, and high intensity developed land to ensure a relatively consistent number of variables between groupings (i.e., human, natural, and fish, Table 2.1). A detrended correspondence analysis (DCA) was first used to quantify the gradient length of the dataset to determine the appropriate ordination technique, either canonical correspondence analysis (CCA) or RDA (ter Braak 1995; Esselman and Allan 2010; Pool et al. 2010). The gradient length of species metrics along the first DCA axis indicates if species response to environmental data is closer to linear versus more unimodal. The DCA gradient lengths for our fish metrics was < 2, suggesting a more linear species response and that RDA versus a CCA was more appropriate for further analysis (ter Braak 1995; Esselman and Allan 2010; Pool et al. 2010). We partitioned the total variance in fish metrics explained by natural landscape variables, human land use variables and their corresponding interaction terms for each of the five freshwater ecoregions using CANOCO software (ter Braak and Smilauer 2002).

Developing a composite variable to characterize natural landscape influences.—PCA was used to develop a composite variable from six natural landscape factors across the entire study region (Table 2.1, Figure 2.1). This composite variable was developed for use in multiple wave cascade multivariate regression tree (CMRT) analysis to aid in controlling for natural variability known to influence fish across the five study ecoregions in a consistent and comprehensive manner (Whittier et al. 2007; Whittier and Van Sickle 2010; Van Sickle 2013). Individual site scores from axis 1 of the PCA results were used to create the composite variable (Table 2.5).

Cascade multivariate regression tree (CMRT).—CMRT was performed to quantify regional difference in fish responses to dominant human land uses after controlling for natural landscape influences. A CMRT is based on a tiered analysis of multivariate regression trees (MRT) and does not require that relationships between explanatory and response variables are linear or that residuals be normally distributed (De'ath 2002; Ouellette et al. 2012), making the technique appropriate for large, ecological data sets that do not meet such statistical requirements. The CMRT is conducted in multiple waves where the first wave of data is theorized to have dominant explanatory power over the response data, and a second wave is applied to explain additional variance. The first wave in this CMRT analysis was performed to associate variability in fish metrics with natural landscape influences. Human land use metrics including percent network urban land use, percent network agriculture, and the density of stream-road crossings and dams in the network catchment (Table 2.3) were used in the second wave of analysis to describe additional variation explained in the fish metrics after controlling for the natural landscape variable.

Before analysis, fish metrics were centered and a standardized z-score was calculated for response metrics. To run the CMRT we used the function "CascadeMRT" from the package "mvpart" in R (De'ath 2006; Therneau et al. 2010; Oksanen et al. 2013; Ouellette 2013, R Core Team 2013). This uses a standard recursive greedy splitting algorithm to fit all MRT models (De'ath 2002). We use the "one standard error" rule for the *v*-fold cross-validation to fully grow the MRTs (rule described by De'ath 2002). The one standard error rule suggests using the simplest model within one standard error of the model that minimizes the cross-validated relative error, with the aim of minimizing risk and complexity of the model. This method picks the simplest best model that minimizes both the cross-validated relative error and the number of splits in the MRT (De'ath 2002; Ouellette 2013). The complexity parameter value is the minimum contribution to the R^2 of a MRT tree for a split to be considered for the package "mvpart" in R (Ouellette 2013; R Core Team 2013). In our analyses, we set complexity parameters high enough in both the first and second waves to identify only the main factors determining variation in species composition yet values were still considered conservative, ranging between 0.01-0.05.

The CMRT analysis was used to characterize the hierarchical influences on stream systems with the predominant influence from natural landscape factors followed by influences of human land uses on stream fishes. It allowed us to separate the explanatory power of two data sets on stream fishes, first controlling for natural landscape factors across the entire study area and secondly accounting for anthropogenic landscape variables by ecoregions (Ouellette et al. 2012). Site scores from the natural composite variable were used in the first wave of the CMRT analysis to compute the main partition of explained variance (Table 2.5). Residuals from the first wave of the CMRT analysis were then used in the second wave with the human land use variables to compute human partitions of additional explained variance based on the theorized controls of riverine ecosystems, with a predominant influence on stream systems and biota from natural variables (e.g., catchment area, lithology, etc.) and additional influences from human perturbation in the landscape (e.g., percent catchment urban and agriculture, catchment density of dams, Vannote et al. 1980; Frissell et al. 1986; Benda et al. 2004; Grant et al. 2007). This provides the ability to determine the influence of human land use variables after taking into account the influence of the natural landscape variables, recognizing that one set might change as a function of the other (Ouellette et al. 2012).

Results

Study area.—The five study ecoregions included an area of 2,287,921 km^2 (Figure 2.1). A total of 10,522 fish sampling locations were used in analyses across the study region, with 1083 sampling sites in the Appalachian Piedmont, 807 in the Chesapeake Bay, 3773 in the

Laurentian Great Lakes, 886 in the Middle Missouri, and 3973 in the upper Mississippi ecoregion. Natural landscape factors at study sites are highly diverse across ecoregions (Table 2.3). Mean network catchment area of study sites ranged from 155 km^2 in the Appalachian Piedmont ecoregion to 764 km^2 in the Middle Missouri ecoregion. Fine lithology in the network catchment was lowest in the Upper Mississippi ecoregion (mean of 9%) and highest in the Laurentian Great Lakes ecoregion (mean of 42%). Mean local elevation was lowest at study sites in the Appalachian Piedmont ecoregion at 157 m, and ranged from 20 m to 1166 m across all sites in the study ecoregions, characterized by 10% and 90% exceedance values, respectively (Table 2.3). Mean local elevation was highest at study sites in the Middle Missouri ecoregion at 591 m. Climate varied across sites in the study ecoregions as well, with lowest mean annual air temperatures in the Upper Mississippi (8 °C) and highest mean annual air temperature and precipitation in the Appalachian Piedmont ecoregion (15 °C, 1215 ml, respectively, Table 2.3). The lowest mean annual precipitation was in the Middle Missouri ecoregion at 709 ml.

Study sites across the five ecoregions also exhibited a wide range in human land uses. Mean percentage of urban land use in network catchments of study sites was highest in the Appalachian Piedmont ecoregion at 14% and lowest at study sites in the Middle Missouri at 6% (Table 2.3). There was high variability in mean percentage of agriculture land use in the network catchment across study ecoregions; it was highest in the Upper Mississippi ecoregion at 60%, with 10% and 90% exceedance values of 16% and 90%, respectively. The mean network catchment percent agriculture was lowest in Appalachian Piedmont ecoregion with a value of 21% and 10% and 90% exceedance values of 4% and 41%, respectively (Table 2.3). Density of stream-road crossings in network catchments of study sites was highest in the Chesapeake Bay ecoregion at 54/100 km^2 and was lowest in the network catchment for study sites in the Middle

Missouri ecoregion at 36/100 km^2. Density of dams in the network catchment of study sites was highest in the Appalachian Piedmont ecoregion at 3.91/100 km^2 and lowest in the network catchment of study sites in the Upper Mississippi at 0.71/100 km^2 (Table 2.3)

Variance partitioning with (RDA), differences across study ecoregions.—RDA variance partitioning indicated that natural and human landscape variables contributed to between 28% to 42% of total explained variation in fish metrics across ecoregions (Figure 2.2). The maximum variation explained in fish occurred in the Upper Mississippi ecoregion (42%) and the minimum variation explained occurred in the Laurentian Great Lakes ecoregion (28%, Figure 2.2). Natural landscape variables generally explained the largest proportion of variance in fish metrics as expected, ranging from 12% to 27%, with the exception of the Laurentian Great Lakes freshwater ecoregion, where interactions among the human and natural variables explained the highest percentage of variance in the fish metrics (13%, Figure 2.2). Variation explained by human land uses alone was much less than that explained by natural landscape variables; approximately 2% of the variation in fish was explained by human landscape variables in the Middle Missouri and the Upper Mississippi freshwater ecoregions, ranging to a maximum of 5% in the Chesapeake Bay freshwater ecoregion (Figure 2.2). Interactions between groupings of natural and human landscape factors contributed a large proportion of explained variation in fish metrics from 6% in the Chesapeake Bay and Middle Missouri freshwater ecoregion to 13% in the Appalachian Piedmont, Laurentian Great Lakes, and Upper Mississippi ecoregions (Figure 2.2).

Developing a composite variable to characterize natural landscape influences.—Six natural landscape factors were used in PCA to develop a generalized natural composite variable to account for major natural landscape influences for use as the primary natural landscape variable in the first wave of the CMRT analysis before further analyzing variance described by human metrics (Table 2.5). The PCA of natural landscape variables resulted in two axes explaining 59.70% of the variation across the study sites (Table 2.5). Axis one, explaining 38.89% of the variation in the study sites, was weighted positively by air temperature, average precipitation, and fine lithology and was negatively weighted by mean local elevation and base-flow index (Table 2.5). Axis two, explaining 20.81% of the variation in the study sites, was weighted positively by catchment area and fine lithology, and was negatively weighted by mean annual precipitation in the catchment and base-flow index in the catchment (Table 2.5). The first axis of the PCA described the prominent amount of variance representing natural variation in the data, site scores from axis one were chosen for further analysis, and used as the natural variable for the first wave of the CMRT analysis across all of the five study ecoregions.

Variance partitioning with cascade multivariate regression trees (CMRT).—There were differences in the amount of variance explained in fish metrics between the five ecoregions, but general patterns were similar. The CMRT global variance indicated that natural and human variables combined explained between 7.21% in the Appalachian Piedmont ecoregion to 13.05% in the Chesapeake Bay ecoregion of the total explained variation in fish metrics at sites across the five freshwater ecoregions (Table 2.6). Variance explained from the first wave represented by the natural landscape composite variable (referred to as main natural) ranged from a low of 5.65% in the Upper Mississippi ecoregion to 10.17% in the Appalachian Piedmont ecoregion. The combined variance explained in fish metrics from the dominant two human land uses (i.e. human 1 + human 2) from each drop of the second wave of the CMRT ranged from 2.56% in the Laurentian Great Lakes to 4.91% in the Middle Missouri, across study sites of the five ecoregions (Table 2.6).

Regional influences and differing levels of human land use variables for the second wave of CMRT.— The second wave of the CMRT, constrained by the composite variable of natural landscape factors, identified the two primary human land use variables and at what levels these factors explained variation in fish metrics. Results showed that important metrics differed by ecoregion. For example, the Appalachian Piedmont ecoregion had both a prominent and secondary level of urban land use that described variance in fish assemblage metrics. The Chesapeake Bay ecoregion had urban as the prominent land use and agriculture as a secondary human land use influencing fish assemblage metrics, while the Laurentian Great Lakes, Middle Missouri, and Upper Mississippi ecoregions all had catchment agriculture and density of dams as prominent and/or secondary human land use variables describing variance in fish assemblage metrics.

In those cases when prominent human land use metrics were the same across freshwater ecoregions there were often substantial differences in the levels of the land use that were causing differences in stream fish assemblage metrics across sampling sites (Table 2.6). Percent urban in the network catchment was the primary human land use in the Appalachian Piedmont at two levels; a high level of 38.24%, which was above the 90% exceedance value of 37% and at a level of 10% which is just below the mean level of 14% (Table 2.3 and 2.6). Percent urban in the network catchment was also the primary human land use in the Chesapeake Bay ecoregion at a low level of 1.30%, almost equal to the 10% exceedance value of 1.27% for the ecoregion. Percent agriculture in the network catchment was the primary human land use for the Upper Mississippi and the secondary human land use in Laurentian Great Lakes, Chesapeake Bay, and Middle Missouri ecoregions at levels of 54%, 68%, 0.40% and < 0.01% respectively (Table 2.6). The levels of percent agriculture in the network catchment causing change in fish assemblage metrics across study sites were substantially different for the Upper Mississippi and Laurentian Great Lakes, (i.e., just below the mean and substantially above the mean, respectively) versus in the Chesapeake Bay and Middle Missouri ecoregions (i.e. below the 10% exceedance values, Table 2.2).

A low density of dams in the network catchment was the primary human land use variable describing variation in fish assemblage metrics for Laurentian Great Lakes, Middle Missouri ecoregions, and secondary in the Upper Mississippi ecoregion at levels of 0.05/100 km^2, 0.02/100 km^2, and 0.04/100 km^2, respectively (Table 2.6). The density of road crossings in the network catchment was not found to be one of the two most influential human land use metrics across sites for any one of the five ecoregions we evaluated in this study.

Discussion

This study characterized regional differences in types and levels of human land uses potentially influencing stream fish assemblages across five ecoregions in the eastern portion of the U.S. Fish assemblages were summarized by metrics including species richness; percent intolerant and game individuals; and percent individuals that are invertivores, omnivores, lithophiles, and rheophiles (Lyons 1992; Barbour et al. 1999; Frimpong and Angermeier 2009). We also identified prominent anthropogenic landscape factors within our study regions including percent of urban and agriculture land uses and densities of stream-road crossings and dams in stream catchments. Testing for influences of these factors with CMRT analysis indicated that urban and agricultural land use as well as dam density had regional effects on stream fishes. Urban land use was the prominent factor associated with differences in fish assemblages in the Appalachian Piedmont and Chesapeake Bay ecoregions, while agricultural land use was prominent in the Upper Mississippi ecoregion. Agricultural land use was also identified as a secondary factor influencing fish in the Chesapeake Bay, Laurentian Great Lakes, and Middle Missouri ecoregions. Dam density in catchments was the prominent influence in both the Laurentian Great Lakes and Middle Missouri ecoregions (Table 2.6), underscoring the potential influence of multiple dams within catchments to act as a landscape-scale influence on stream fishes. Besides identifying regional differences in influences, we also identified differences in levels at which fish were associated with landscape disturbances (Table 2.6). For example high percentages of catchment agriculture (i.e., 54% and 68%, respectively) were associated with differences in fish assemblages in the Upper Mississippi and the Laurentian Great Lakes ecoregions, while lower levels (<0.4%) were associated with differences in fish assemblages in the Chesapeake Bay and Middle Missouri ecoregions. Our results suggest that effects of human land uses on stream fishes vary regionally, resulting from complex relationships between landscape factors and mechanisms controlling stream fish assemblages, but explain a low amount of the observed variance.

Variance in fish metrics explained by human and natural landscape factors across five ecoregions.—By partitioning variance explained in stream fish metrics by groupings of natural landscape factors and human land use variables, RDA identified regional differences in landscape controls on stream fishes. Total explained variance in fish metrics ranged from 28% in the Laurentian Great Lakes to 42% in the Upper Mississippi, and of that variance, a majority was attributed to natural landscape factors, which ranged from 12% in the Laurentian Great Lakes to 27% in the Upper Mississippi. Previous work conducted for streams in Louisiana and Mississippi fell within this range; Alford (2014) describes a similar percentage of variance (i.e., 24%) explained in fish species assemblages by catchment variables including catchment area, elevation, and stream density within catchments. The RDA also quantified unique proportions of explained variance in fish metrics by human land uses, underscoring the importance of human land uses on stream fish across large regions and also justifying our evaluation of specific human land uses on fishes with CMRT analysis. An additional insight from the RDA was in the identification of the degree to which natural landscape factors and human land uses were confounded within our study regions. In all five ecoregions, amount of variance explained by covarying natural and anthropogenic landscape factors was greater than that explained by anthropogenic landscape factors alone. This is due in part because natural landscape characteristics may influence the suitability of landscapes for various human land uses (Allan 2004; Scott 2006), and it supported the need to explicitly control for natural landscape factors consistently across the five study ecoregions with development of our natural composite variable in CMRT analyses.

Regionally-specific effects of urban land use on stream fish.—After controlling for the influence of natural landscape factors with our natural composite variable, percent urban land use in the network catchment explained the most variance in fish assemblages in the Appalachian Piedmont and Chesapeake Bay ecoregions at levels of 10% and 2%, respectively. The lower level detected in the Chesapeake Bay ecoregion was similar to levels detected in other studies. Yoder et al. (1999) found that declines in sensitive species in Ohio streams occurred at <5% urban land use in stream catchments, resulting in part from degraded substrate, and Miltner et al. (2004) found changes in fish biotic integrity in Ohio streams at levels as low as 5% urban land use in stream catchments. The higher level of urban land use detected in the Appalachian Piedmont followed studies in Wisconsin. Wang et al. (1997) found decreases in biotic integrity in streams with urban land use occurring at 10%; also, Wang et al. (2000; 2001) showed declines in fish species richness and diversity with levels greater than 10% imperviousness in catchments. In our study regions, percent impervious land cover in catchments was highly correlated with percent urban land use in catchments (R^2 = 0.97, Table C2.1). This is also consistent with studies in Ohio documenting significant declines in fish IBI scores with impervious land use > 15% (Yoder et al. 1999; Miltner et al. 2004). Differences between the Appalachian Piedmont and Chesapeake Bay ecoregions (and differences between these regions from the other three study regions) may be related to different mechanisms from land use and/or differences in fish composition. Variability in fish response by region to the percent of urban in the catchment may be due in part to relationships between natural landscape factors (e.g., lithology) and human land uses between regions (e.g., Utz et al. 2010), or by compositional differences in fish assemblages among regions (e.g., Meador et al 2005). However, the prominence of the urban signal in the Appalachian Piedmont and Chesapeake Bay as opposed to other ecoregions leads us to believe that regional differences may result from landscape characteristics of the ecoregions. For example, percent of agriculture in catchments of study sites was low in both the Appalachian Piedmont and the Chesapeake Bay ecoregion, in comparison to the other three regions, potentially allowing the urban signal to prevail (Paavola et al. 2006).

Two levels of urban land use in Appalachian Piedmont.—In the Appalachian Piedmont ecoregion, we detected a secondary influence from urban land use on fish at 38% catchment urban land. Fish response at this level of urbanization is much higher than typical levels reported in the literature but may be related to low population abundances and/or low fish species diversity resulting from extreme levels of urban land use. Miltner et al. (2004) found an almost complete loss in aquatic life when levels of impervious land cover > 27% for streams in Ohio.

Again, these landscape factors are known to have similar effects on streams and are highly correlated within our study regions.

The influence of urban land use on stream fishes at two levels in the Appalachian Piedmont (again, 10% and 38%), may reflect a series of threshold responses in the grouping of fish metrics, indicating a low and high sensitivity of stream fishes to urban land use (Allan 2004). At a low level of urban land use, fish assemblages may begin to change from those that would exist in the absence of urban land use in catchments, with negative effects on fishes resulting from initial habitat degradation. At the higher level, fish assemblage metrics may stop changing because of a loss of specialist species and some functional groups (e.g., invertivores), then level off and become dominated by a few tolerant species at low to moderate abundances caused from increased sediments, nutrients, toxicity and/or altered thermal regimes (Yoder et al. 1999; Paul and Meyer 2000; Miltner et al. 2004). As described previously, Yoder et al. (1999) showed differences in fish assemblages occurring at levels of <5% urban land use in stream catchments and also at 10% to 15%; they also described responses at levels greater than 15% including severe fish faunal degradation from increased nutrients and toxicity from urbanizations in the catchments.

Regionally-specific effects of agricultural land use on stream fish.—Agriculture was the dominant human land use variable influencing fish assemblages in catchments of the Upper Mississippi ecoregion at a level of 54%. It was also the secondary human land use in the Laurentian Great Lakes, Chesapeake Bay, and Middle Missouri, at levels of 68%, 0.40%, and <0.01%, respectively. These results reflect a high (> 50%) and low level (< 0.40%) agriculture land use affecting fish assemblages across ecoregions. Other studies showed fish assemblage change with high levels of agriculture in the catchment. Fitzpatrick et al. (2001) described a decline in fish IBI scores with percentage of catchment agriculture > 30%, and Wang et al. (1997) found a decline in fish abundance, fish species richness, and fish IBI scores at levels > 50%. Regarding the low levels influencing changes in fish assemblages in the Chesapeake Bay and Middle Missouri ecoregions, these may be due in part to an initial decline in abundances of fishes, but effects can also be species-specific which was documented by Utz et al. (2010). Utz et al. (2010) found that sensitivity of fish species to percent of agriculture in catchments varied by region, with more species having negative responses catchment agriculture in the Highlands region than in the Coastal Plain and Piedmont physiographic region, which may be due to differences in composition of assemblages. Also, fishes sensitive to agriculture may have been reduced in abundances and range in the Coastal Plains and Piedmont regions from previous logging in Maryland (i.e., legacy land use effects), but not to the same degree in the Highlands, leading to compositional differences in fish assemblages and higher sensitivity to agriculture in the Highland region (Harding et al. 1998). Similar factors could be at play leading to differences seen in fish assemblage metrics at low levels of agriculture in the catchment, with potential differences related to natural landscape factors defining the suitability for types of agriculture (e.g., pastoral versus row crop) like the Sandhills area in the Middle Missouri ecoregion (Allan 2004).

Density of dams in the catchment.—Dam density was the prominent human land use influencing fish assemblages in the Laurentian Great Lakes and Middle Missouri ecoregions and secondarily in the Upper Mississippi ecoregion and levels of 0.05/100km^2, 0.02/100km^2, and 0.04/100km^2, respectively. This supports the idea that dams are acting as a landscape influence, and that they may be a dominant human land use causing changes in fish assemblages. In the Laurentian Great Lakes ecoregion, density of dams was the prominent human land use that described differences in groups of study sites based on fish metrics, and these results are supported by work of Wang et al. (2011b) who characterized a unique amount of variation in two groupings of fish indicators explained by a set of dam metrics that included density of dams in the catchment. These dam metrics explained 16% to 19% of unique variation in fish biotic-integrity indicators and fish habitat preference indicators, respectively. Wang et al. (2011b), after selecting for stream reaches with minimal urban and agriculture in their network catchment, found that the majority of fish assemblage metrics tested had negative associations with dam metrics. Our study quantified that even a small proportion of dams in the network catchment, ≤ 0.05/100km^2 can influence fish assemblagesin three out of the five study regions.

Stream–road crossing in the catchment.—Density of stream-road crossings in catchments was not identified as a dominant anthropogenic landscape factor affecting fishes in any of our five study regions. Other studies have shown negative influences on fish movement from stream-road crossings related to types of passage ways at stream-road crossings (e.g., culverts, slab crossings, open-box, and ford, Warren and Pardew 1998; Schaefer et al. 2003) and/or passage way design flaws or failures like perching, slope, or crossing length (Mueller et al. 2008; Bouska and Paukert 2010). Januchowski–Hartley et al. (2013) documented the prevalence that road crossings pose as possible barriers to fishes in the Great Lakes region and described their potential for catchment-wide cumulative effects with in river catchments. The additive effects and the pervasiveness of multiple barriers, including passage ways at stream-road crossings and small and large dams in river catchments, warrants further investigation to quantify their catchment-wide effects on fishes (Perkin and Gido 2012; Cooper et al. In Review). The cumulative effects of stream-road crossing may be important to fish but were just not as important as urban, agriculture and dams in stream catchments on fish assemblage metrics in this study.

Spatial extent of study and number of sampling sites.—The spatial extent of our study region included five freshwater ecoregions encompassing an area greater than two million square kilometers. We tested trends using data from 10,522 study sites on streams and rivers occurring within twenty two states. To our knowledge, this is the only study to date that has conducted a regional comparison that captures the spatial extent and potential variability in fish assemblages; our large data set provided extensive characterizations of species compositions as well as an equally broad ranges in environmental characteristics. The number of sites evaluated in this study likely contributed to our ability to detect differences in groups of study sites related to fish assemblage metrics at multiple levels of influence from agriculture in the catchment, including our detection of fish assemblage response at such low levels of percent catchment agriculture (i.e., <0.40%) that we quantified in the Chesapeake Bay and Middle Missouri ecoregions. The large number of study sites evaluated might have also helped us to distinguish multiple threshold responses in fish assemblage metrics in the Appalachian Piedmont to percent urban land use in the catchment. The trends detected in this study offer a comprehensive baseline for additional evaluation of regional and/or local responses of fish to human land uses.

Management implications and conclusions.—Interregional comparisons into mechanisms controlling regional fish assemblage response to human land uses may be a fruitful area of additional investigation. Some of the potential regional differences causing different fish assemblage response may relate to the buffering capacity of lithology and/or topographic landscape factors as well as natural land covers in a region. The types and proportions of natural versus human land cover and their spatial arrangement in the catchment have been shown to affect the delivery of runoff and other materials to stream ecosystems (Zimmerman et al. 2003; Blann et al. 2009; Carpenter et al. 2011). Intensity of urban classes, specific agricultural practices, and riparian buffers to streams are a few examples of factors that may influence runoff and the delivery of materials to riverine ecosystems (Blann et al. 2009; Carpenter et al. 2011), and such factors can cause heterogeneous responses in stream biota across regions (Meador and Goldstein 2003; Morgan and Cushman 2005; Utz et al. 2010). Our results and methods can be used to assess regional dominance of classes of human land use types that are affecting changes in fish assemblages and can provide insights into levels of human land use that are causing change in fish assemblage metrics.

Our study underscored regional differences in dominant human land uses affecting differences in groups of sites based on fish metrics. If dominant human land uses and their levels of influence on critical management factors have regionally-specific influences, these influences should be accounted for and incorporated into the planning process to develop realistic management priorities. Studies characterizing critical human pressures in one ecoregion may not be directly applicable to a different ecoregion because of these differences. Well-designed regionalized studies could help further characterize regional differences in human land uses effects on stream biota, elucidate important mechanisms of influence on stream systems, and have transferable results or components to help meet management priorities across large spatial extents.

In summary, we quantified unique proportions of variance explained by natural landscape variables versus human land uses in fish assemblage metrics and described how they vary by ecoregion. After controlling for dominant natural landscape factors known to influence fish, we identified that dominant human land uses (i.e., percent urban and agricultural in the catchment and density of dams in the catchment) affecting change in fish assemblage metrics, vary by ecoregions. By looking over a wide spatial extent and evaluating over 10,000 study sites we were able to detect multiple levels of influence seen by fish assemblage response to both urban and agriculture in the catchment across and within study regions. Results from this study highlight that there are regional differences in dominant human land uses influencing changes in fish assemblage structure and that there are regional disparities in the levels of urban and agriculture in the landscape that are affecting fish. This study provides a better understanding of these regional differences which is vital information for establishing realistic management strategies in the hopes of preserving the biodiversity of freshwater ecosystems and to stop their continued degradation. Considering that human populations will continue to grow and land conversion and human development of landscapes will continue to intensity, we need responsible planning and better understanding for future development and land conversion to protect the diversity and complexity of the freshwater resources for future generations.

APPENDICES

APPENDIX 2.A

TABLES

Table 2.1.—List of 52 landscape variables initially evaluated for regional comparison.

Variable code	Landscape variable description
Natural	
Land use (%)	
Water	Water in local catchment
Wetland	Wetland in local catchment
Barren	Barren land in local catchment
Forest	Forest in local catchment
Shrub	Shrub in local catchment
Grassland	Grassland in local catchment
Water_c	Water in network catchment
Wetland_c	Wetland in network catchment
Barren_c	Barren in network catchment
Forest_c	Forest in network catchment
Shrub_c	Shrub in network catchment
Grassland_c	Grassland in network catchment
Catchment area	
AREASQKM	Local catchment area (km^2)
AREASQKMC	Network catchment area (km^2) †*
Slope	
Slope	Mean local catchment slope (degrees)
Elevation	
ELEV_MEAN	Mean local catchment elevation (m) †*
ELEV_MEANC	Mean network catchment elevation (m)
Lithology	
fineC	Fine lithology in the network catchment (%) †*
coarseC	Coarse lithology in the network catchment (%)
Soil hydrology	
Base-flow index	Network catchment groundwater contribution to baseflow (%) †*
SOILHYGRP	Mean local catchment soil hydrologic relative rates * 10 (infiltration rates ranged from high = 1 to very slow = 4)
SOILPERM	Local catchment soil permeability rates (cm/hour * 100)
SOILHYGRPC	Mean network catchment soil hydrologic relative rates * 10 (infiltration rates ranged from high = 1 to very slow = 4)
SOILPERMC	Mean network catchment soil permeability rates (cm/hour * 100)
Climate	
temp	Mean annual air temperature in local catchment (°C) †*
AREAWTMAP	Area weighted average mean annual precipitation in network catchment (ml) †*

† Landscape variables used in the redundancy analysis (RDA)

* Landscape variables used in the cascade multivariate regression tree (CMRT) analysis

Table 2.1.—(cont'd)

Variable code	Landscape variable description
Human	
Land use (%)	
Pasture	Pasture/hay in local catchment
Crops	Cultivated crops in local catchment
Pasture_Crops	Pasture/hay and cultivated crops in local catchment
Developed_open	Open space developed land in local catchment
Developed_low	Low intensity developed land in local catchment
Developed_medium	Medium intensity developed land in local catchment
Developed_high	High intensity developed land in local catchment
Developed_lmh	Low, medium, and high intensity developed land in local catchment
Developed_all	All developed land in local catchment
Pasture_c	Pasture/hay in network catchment †
Crops_c	Cultivated crops in network catchment †
Pasture_Crops_c	Pasture/hay and cultivated crops in network catchment *
Developed_open_c	Open space developed land in network catchment †
Developed_low_c	Low intensity developed land in network catchment
Developed_medium_c	Medium intensity developed land in network catchment
Developed_high_c	High intensity developed land in network catchment
Developed_lmh	Low, medium, and high intensity developed land in network catchment †
Developed_all_c	All developed land in network catchment *
IMPERVC	Impervious surfaces in the network catchment
Population density	
POPDENSCz	Population density in the network catchment (number/km^2)
Roads	
ROAD_CROSS_CTz	Road crossing in local catchment (number/100 km^2)
ROAD_LENz	Road density in local catchment (km/100 km^2)
ROAD_CROSSCz	Road crossing in network catchment (number/100 km^2) †*
ROAD_LENCz	Road density in network catchment (km/100 km^2)
Barriers	
DAM_CTCz	Dam density in network catchment (number/100 km^2) †*
Canal/Ditch	
CANAL_DITCHCz	Canal/ditch in network catchment (m/km^2)

† Landscape variables used in the redundancy analysis (RDA)

* Landscape variables used in the cascade multivariate regression tree (CMRT) analysis

Table 2.2.—Fish metrics calculated and evaluated for a regional landscape comparison.

Fish metric description
Community
Fish family richness
Fish species richness †
Pielou community evenness index (*J* ')
Shannon-Weaver community diversity index (*H* ')
Tolerance
Proportion of individuals that are intolerant †
Proportion of individuals that are tolerant
Threatened or endangered
Proportion of individuals that are threatened or endangered
Game species
Proportion of individuals that are game fish †
Trophic
Proportion of individuals that are generalists
Proportion of individuals that are herbivores
Proportion of individuals that are invertivores †
Proportion of individuals that are omnivores †
Proportion of individuals that are piscivores
Life history
Proportion of individuals that are hiders
Proportion of individuals that are lithophilic †
Proportion of individuals that are migrating (vagile)
Proportion of individuals that are nest gurarders
Proportion of individuals that are rheophilic †
Habitat
Proportion of individuals that prefer benthic
Proportion of individuals that prefer large river
Proportion of individuals that prefer lotic
Proportion of individuals that prefer water column

† Fish metrics used in redundance analysis (RDA) and cascade multivariate regression tree (CMRT) analyses

Table 2.3.—Descriptive statistics of landscape variables for the five freshwater ecoregion with landscape variable descriptions (i.e., mean, minimum, maximum, and the 10th and 90th percentiles).

	Appalachian Piedmont				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	155.16	1.42	8062.60	11.42	180.03
Fine lithology in network catchment (%)	21.76	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	157.30	1.39	937.66	20.42	298.06
Base-flow index, network catchment groundwater contribution to baseflow (%)	45.95	25.23	78.30	30.54	60.35
Mean annual air temperature in local catchment (°C)	15.64	9.53	19.33	14.11	17.52
Area weighted average mean annual precipitation in network catchment (ml)	1215.13	973.82	2372.90	1125.53	1317.59
Human land uses					
Urban (%)					
Developed, open space in network catchment *	8.44	0.00	77.33	2.85	18.88
Developed, low, medium & high intensity in network catchment *	5.76	0.00	77.97	0.09	16.81
Developed, open space, low, medium, & high intensity in network catchment †	14.20	0.00	98.62	3.13	37.22
Agriculture (%)					
Pasture/hay in network catchment *	14.06	0.00	63.49	1.43	32.49
Cultivated crops in network catchment *	7.27	0.00	68.27	0.00	26.55
Pasture/hay & cultivated crops in network catchment †	21.34	0.00	72.63	3.83	40.93
Road crossings					
Road crossings in network catchment (number/100 km^2) *†	48.96	0.00	345.30	15.82	89.03
Dams					
Dam density (number/100 km^2) *†	3.32	0.00	57.56	0.00	9.06

* Used in RDA

† Used in CMRT analysis

Table 2.3.—(cont'd)

Landscape variable description	Chesapeake Bay Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	371.17	0.82	8483.38	3.48	560.87
Fine lithology in network catchment (%)	13.22	0.00	100.00	0.00	99.80
Mean local catchment elevation (m)	288.25	2.52	1050.68	21.71	491.14
Base-flow index, network catchment groundwater contribution to baseflow (%)	46.26	26.99	64.02	38.08	54.74
Mean annual air temperature in local catchment (°C)	9.57	6.35	14.28	7.00	13.25
Area weighted average mean annual precipitation in network catchment (ml)	1027.70	806.87	1239.06	914.37	1108.89
Human land uses					
Urban (%)					
Developed, open space in network catchment *	4.55	0.00	39.90	0.95	8.50
Developed, low, medium & high intensity in network catchment *	3.61	0.00	83.76	0.01	7.09
Developed, open space, low, medium, & high intensity in network catchment †	8.15	0.00	98.44	1.27	14.85
Agriculture (%)					
Pasture/hay in network catchment *	19.55	0.00	69.61	4.84	36.71
Cultivated crops in network catchment *	12.04	0.00	81.75	0.51	27.43
Pasture/hay & cultivated crops in network catchment †	31.59	0.00	94.91	7.72	63.49
Road crossings					
Road crossings in network catchment (number/100 km^2) *†	53.99	0.00	588.24	9.40	96.04
Dams					
Dam density (number/100 km^2) *†	1.10	0.00	30.53	0.00	3.04

* Used in RDA

† Used in CMRT analysis

Table 2.3.—(cont'd)

	Laurentian Great Lakes				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	354.81	0.23	9533.74	10.27	758.72
Fine lithology in network catchment (%)	41.97	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	277.15	74.56	680.78	180.28	430.92
Base-flow index, network catchment groundwater contribution to baseflow (%)	45.04	18.69	87.95	21.99	68.45
Mean annual air temperature in local catchment (°C)	7.74	2.12	10.56	4.69	9.68
Area weighted average mean annual precipitation in network catchment (ml)	929.80	641.04	1566.84	764.17	1123.50
Human land uses					
Urban (%)					
Developed, open space in network catchment *	5.92	0.00	58.15	0.88	12.08
Developed, low, medium & high intensity in network catchment *	5.13	0.00	93.37	0.06	12.57
Developed, open space, low, medium, & high intensity in network catchment †	11.05	0.00	99.92	1.15	26.31
Agriculture (%)					
Pasture/hay in network catchment *	10.61	0.00	62.63	0.01	26.51
Cultivated crops in network catchment *	29.24	0.00	94.26	0.06	79.76
Pasture/hay & cultivated crops in network catchment †	39.85	0.00	94.26	0.47	83.07
Road crossings					
Road crossings in network catchment (number/100 km^2) *†	48.49	0.00	413.37	8.35	91.15
Dams					
Dam density (number/100 km^2) *†	1.13	0.00	73.69	0.00	2.84

* Used in RDA

† Used in CMRT analysis

Table 2.3.—(cont'd)

Landscape variable description	Middle Missouri Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	764.33	1.57	9984.84	15.36	2196.10
Fine lithology in network catchment (%)	32.01	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	591.36	195.32	3134.90	288.62	1165.51
Base-flow index, network catchment groundwater contribution to baseflow (%)	38.90	12.20	84.20	19.19	69.00
Mean annual air temperature in local catchment (°C)	10.22	0.19	12.92	8.11	12.29
Area weighted average mean annual precipitation in network catchment (ml)	708.96	344.53	1113.56	441.07	929.31
Human land uses					
Urban (%)					
Developed, open space in network catchment *	3.88	0.00	34.60	1.75	5.48
Developed, low, medium & high intensity in network catchment *	2.06	0.00	82.72	0.04	2.45
Developed, open space, low, medium, & high intensity in network catchment †	5.93	0.00	92.22	1.99	7.65
Agriculture (%)					
Pasture/hay in network catchment *	9.92	0.00	80.99	0.00	39.88
Cultivated crops in network catchment *	41.58	0.00	93.56	2.05	82.94
Pasture/hay & cultivated crops in network catchment †	51.50	0.00	94.88	4.00	87.86
Road crossings					
Road crossings in network catchment (number/100 km^2) *†	35.90	0.00	254.61	3.63	70.55
Dams					
Dam density (number/100 km^2) *†	3.91	0.00	73.31	0.00	11.60

* Used in RDA

† Used in CMRT analysis

Table 2.3.—(cont'd)

	Upper Mississippi				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	356.01	0.23	9964.22	9.65	740.40
Fine lithology in network catchment (%)	9.49	0.00	100.00	0.00	27.43
Mean local catchment elevation (m)	288.86	114.85	589.09	184.87	382.03
Base-flow index, network catchment groundwater contribution to baseflow (%)	49.85	7.84	74.87	31.21	66.29
Mean annual air temperature in local catchment (°C)	7.56	3.07	13.60	5.48	10.61
Area weighted average mean annual precipitation in network catchment (ml)	823.55	556.81	1190.27	704.84	949.22
Human land uses					
Urban (%)					
Developed, open space in network catchment *	4.56	0.00	30.15	2.32	6.81
Developed, low, medium & high intensity in network catchment *	4.09	0.00	92.83	0.10	7.25
Developed, open space, low, medium, & high intensity in network catchment †	8.65	0.00	99.46	3.24	13.05
Agriculture (%)					
Pasture/hay in network catchment *	12.34	0.00	68.33	0.39	27.99
Cultivated crops in network catchment *	47.87	0.00	98.06	5.14	87.11
Pasture/hay & cultivated crops in network catchment †	60.21	0.00	98.06	15.54	89.80
Road crossings					
Road crossings in network catchment (number/100 km^2) *†	39.58	0.00	643.09	8.88	69.17
Dams					
Dam density (number/100 km^2) *†	0.77	0.00	39.03	0.00	1.88

* Used in RDA

† Used in CMRT analysis

Table 2.4.—Descriptive statistics (i.e., mean, range, 10th and 90th percentiles) of fish metrics in five freshwater ecoregions with number of sample sites per region.

Freshwater ecoregion (# of sites)		Fish richness count	Intolerant % individual	Game fish % individual	Invertivore % individual	Omnivore % individual	Lithophilic % individual	Rheophilic % individual
Appalachian Piedmont (1083)	Mean	15	1.27	28.46	65.38	23.90	49.85	20.25
	Range	1—34	0—95.81	0—100.00	0—100.00	0—93.44	0—100.00	0—97.13
	10%	8	0.00	3.11	40.00	3.71	4.86	0.00
	90%	22	2.59	67.26	88.31	45.74	86.65	48.83
Chesapeake Bay (807)	Mean	10	12.67	22.15	35.09	14.12	45.41	19.80
	Range	1—31	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00
	10%	2	0.00	0.00	0.00	0.00	0.00	0.00
	90%	19	37.15	68.91	69.67	38.54	83.00	53.44
Laurentian Great Lakes (3773)	Mean	11	12.53	20.63	38.90	18.10	27.76	29.01
	Range	1—37	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00
	10%	4	0.00	0.00	4.87	0.00	0.00	0.00
	90%	19	43.80	72.48	76.54	45.97	65.08	69.95
Middle Missouri (886)	Mean	10	2.60	9.42	35.78	37.79	10.71	42.68
	Range	1—29	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00
	10%	4	0.00	0.00	4.29	2.79	0.00	0.29
	90%	17	3.23	26.51	70.80	81.00	35.31	83.68
Upper Mississippi (3973)	Mean	13	11.75	15.07	42.75	25.97	23.65	24.19
	Range	1—48	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00	0—100.00
	10%	3	0.00	0.00	3.45	0.93	0.00	0.00
	90%	24	37.05	55.25	78.70	60.33	57.96	66.34

Table 2.5.—Principle component analysis (PCA) results for six natural landscape variables for all study sites across the entire study area. Variable descriptions and axes weightings are provided. Total amount of variation explained was 59.91%.

	Axis 1	Axis 2
Variance explained (%)	39.10	20.81
Natural landscape variable description		
Mean annual air temperature in local catchemnt	0.83	-0.01
Area weighted average mean annual percipitation in network catchment	0.68	-0.54
Fine lithology in network catchment	0.53	0.55
Network catchment area	-0.02	0.64
Base-flow index, network catchment groundwater contribution to baseflow	-0.58	-0.44
Mean local catchment elevation	-0.77	0.21

Table 2.6.—Variable, value and percent variance explained from the main (natural) and (human) influences on fish assemblage metrics across five freshwater ecoregions from cascade multivariate regression tree analysis (CMRT).

Freshwater ecoregion (# of sites)		Main natural	Human 1	Human 2	Total variance explained
All data (10522)	Variable	Natural	Agriculture	Agriculture	
	Value	0.12	53.46%	64.17%	
	% Variance explained	3.66%	2.01%	1.54%	7.21%
Appalachian Piedmont (1083)	Variable	Natural	Urban	Urban	
	Value	1.40	9.93%	38.24%	
	% Variance explained	10.17%	1.83%	1.05%	13.05%
Chesapeake Bay (807)	Variable	Natural	Urban	Agriculture	
	Value	0.08	1.30%	0.40%	
	% Variance explained	5.91%	4.35%	0.55%	10.81%
Laurentian Great Lakes (3773)	Variable	Natural	Dams	Agriculture	
	Value	0.08	0.05/100 km^2	67.67%	
	% Variance explained	7.04%	1.46%	1.10%	9.60%
Middle Missouri (886)	Variable	Natural	Dams	Agriculture	
	Value	-1.55	0.02/100 km^2	<0.01%	
	% Variance explained	7.45%	2.95%	1.96%	12.36%
Upper Mississippi (3973)	Variable	Natural	Agriculture	Dams	
	Value	-0.25	53.64%	0.04/100 km^2	
	% Variance explained	5.65%	2.78%	0.34%	8.77%

APPENDIX 2.B

FIGURES

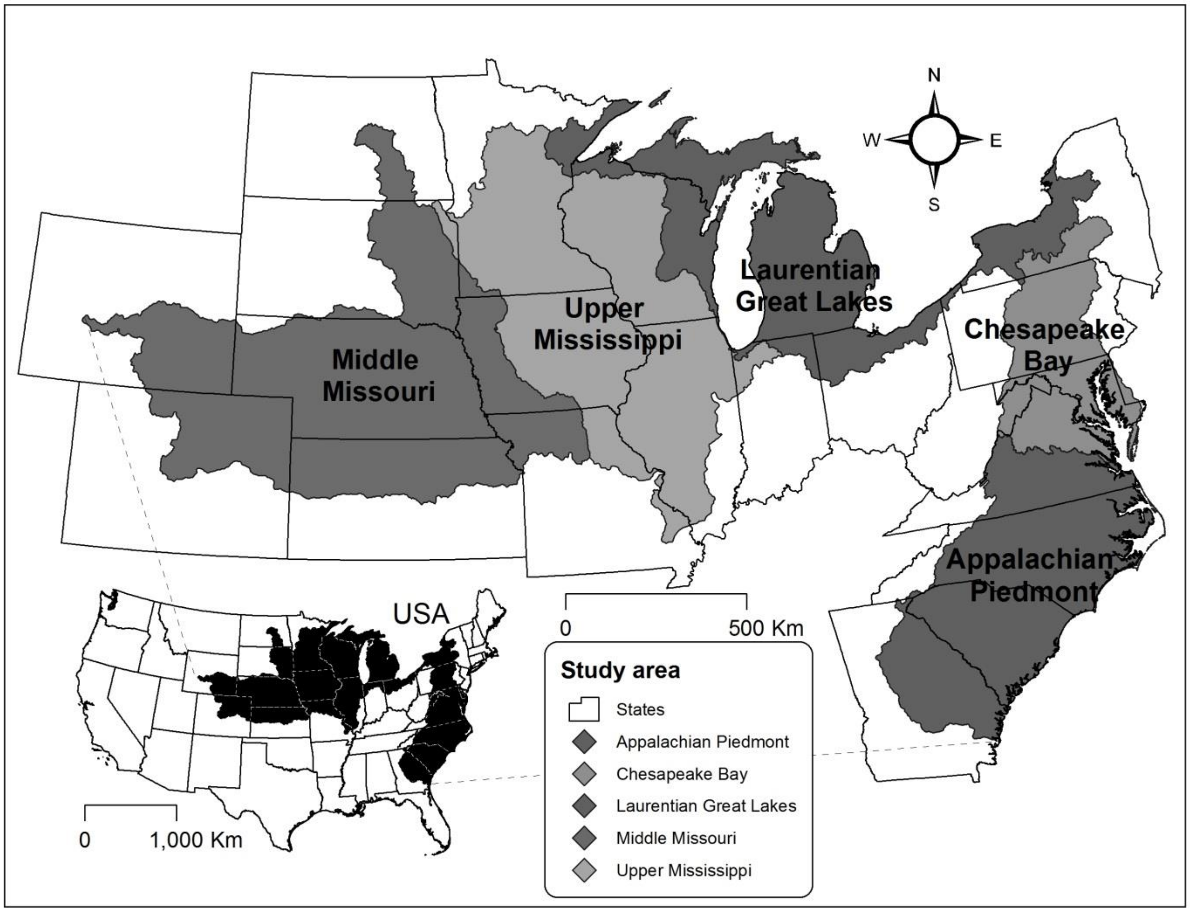

Figure 2.1.—Five freshwater ecoregions of the United States that comprised the study area (Abell et al. 2008)

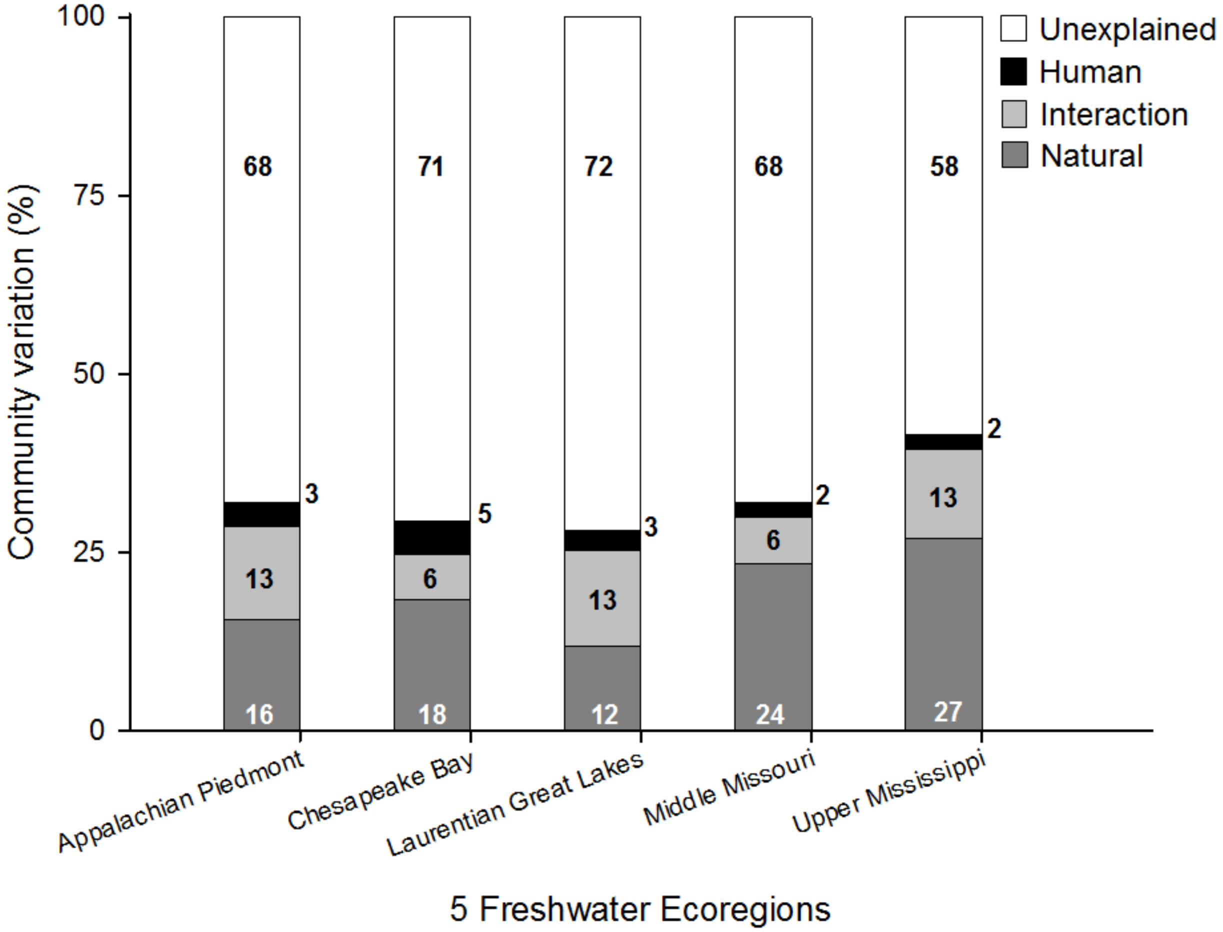

Figure 2.2.—Results from RDA partitioned variation explained in fish community metrics by natural and human variables across the five freshwater ecoregions in our study area.

APPENDIX 2.C

SUPPLEMENTAL TABLES

Table C2.1.—Results of Pearson correlation among landscape metrics; only results with *r* values ≥.0.70 or ≤ -0.70 are displayed.

Landscape variables	Wetland	Forest	Shrub	Grassland	Forest_c	Developed_open	Developed_low	Developed_med	Developed_high	Developed_lmh	Developed_all	Pasture	Crops	Pasture_Crops	Developed_openc	Developed_lowc	Developed_medc	Developed_highc	Developed_lmhc	Developed_allc	Crop_c	ELEV_MEAN	SOILHYGRP	SOILPERM	POPDENSC	IMPERVC
Wetland_c	0.75																									
Forest_c		0.82																								
Shrub_c			0.81																							
Grassland_c				0.85																						
Developed_med							0.82																			
Developed_high								0.88																		
Developed_lmh							0.97	0.92	0.82																	
Developed_all						0.79	0.90	0.86	0.77	0.93																
Pasture_Crops													0.90													
Developed_lowc							0.73			0.73	0.71				0.74											
Developed_medc								0.70		0.71						0.90										
Developed_highc																0.83	0.95									
Developed_lmhc							0.71			0.74	0.72				0.72	0.98	0.96	0.90								
Developed_allc											0.74				0.87	0.94	0.91	0.86	0.96							
Pasture_c												0.76														
Crop_c					-0.77								0.85	0.75												
Pasture_Crops_c					-0.74								0.79	0.82							0.92					
ELEV_MEANC																						0.96				
SOILHYGRPC																							0.79			
SOILPERMC																								0.83		
POPDENSC																0.81	0.78	0.73	0.81	0.79						
IMPERVC										0.73	0.72				0.75	0.96	0.97	0.93	0.99	0.97					0.81	
ROAD_LENCz															0.74	0.75	0.71		0.74	0.78					0.76	0.76

Table C2.2.—PCA results for landscape variables including variance explained by each axis and axis interpretation.

Variance explained	28.12	12.73	10.08	9.59	7.88	6.99
Cumulative variance explained	28.12	40.85	50.93	60.52	68.39	75.39
Axis interpretation	Urban	Groundwater index	Agriculture	Temperature precipitation	Road crossing	Dams
Landscape variable description	**axis 1**	**axis 2**	**axis 3**	**axis 4**	**axis 5**	**axis 6**
All developed land in network catchment (%)	0.98	0.09	-0.06	0.05	-0.08	-0.02
Low, medium, and high intensity developed land in network catchment (%)	0.97	0.06	-0.05	0.05	-0.01	-0.06
Low intensity developed land in network catchment (%)	0.95	0.07	-0.02	0.06	-0.02	-0.03
Medium intensity developed land in network catchment (%)	0.94	0.06	-0.09	0.04	0.05	-0.08
High intensity developed land in network catchment (%)	0.90	0.05	-0.11	0.02	0.09	-0.09
Road density in network catchment (km/100 km^2)	0.82	0.02	0.13	0.23	-0.12	0.15
Open space in network catchment (%)	0.81	0.11	0.04	0.10	-0.12	0.10
Road crossing in network catchment (number/100 km^2)	0.41	0.21	0.11	0.07	-0.70	0.03
Mean annual air temperature in local catchment (°C)	0.25	0.24	0.14	0.74	0.02	0.25
Fine lithology in the network catchment (%)	0.19	0.49	0.17	0.28	0.02	-0.49
Dam density in network catchment (number/100 km^2)	0.17	0.27	-0.24	0.00	0.13	0.56
Mean network catchment soil hydrologic relative rates * 10 (infiltration rates ranged from high = 1 to very slow = 4)	0.09	0.77	0.00	-0.03	0.05	-0.30
Canal/ditch in network catchement (m/km^2)	0.09	0.12	0.32	-0.03	0.46	-0.33
Coarse lithology in the network catchment (%)	0.03	-0.53	-0.14	-0.15	0.35	-0.22
Mean network catchment area (km^2)	0.03	0.01	0.08	0.00	0.87	0.06
Area weighted average mean annual precipitation in network catchment (ml)	0.02	0.17	-0.35	0.72	-0.15	0.16
Cultivated crops in network catchment (%)	-0.06	0.19	0.91	-0.06	0.07	-0.15
Pasture/hay in network catchment (%)	-0.07	-0.07	0.15	0.20	-0.15	0.71
Pasture/hay & cultivated crops in network catchment (%)	-0.09	0.19	0.95	0.02	0.01	0.12
Network catchment soil permeability rates (cm/hour * 100)	-0.09	-0.85	-0.17	-0.02	0.15	-0.21
Base-flow index, network catchment groundwater contribution to baseflow (%)	-0.10	-0.80	-0.14	-0.19	-0.10	-0.02
Mean local catchment elevation (m)	-0.12	0.02	-0.04	-0.89	-0.01	0.13

Table C2.3.—Pearson Correlation of fish metrics, only results with *r* values ≥.0.70 or ≤ -0.70 are displayed.

	Shannon's diversity index (*H'*)	Fish species richness
Fish species richness	0.86	
Fish family richness	0.73	0.80

Table C2.4.—PCA results for fish metrics.

variance explained	16.74	15.45	10.19	10.06	9.76	7.09
cumulative variance explained	16.74	32.20	42.39	52.45	62.21	69.31
Axis interpretation	fish richness	intolerant	rheophilic /water column	lithophilic	river / game	omnivore / invertivore
Fish metric	axis 1	axis 2	axis 3	axis 4	axis 5	axis 6
Fish species richness	0.91	-0.14	0.18	0.10	0.07	0.02
Invertivore individual (%)	0.46	-0.25	0.00	-0.27	0.07	-0.62
Lithophilic individual (%)	0.30	-0.23	-0.02	0.60	-0.11	-0.19
Lotic individual (%)	0.29	-0.34	0.34	0.57	-0.22	-0.04
Large river individual (%)	0.28	-0.33	0.20	-0.18	0.69	0.29
Omnivore individual (%)	0.23	-0.29	-0.02	-0.23	0.06	0.75
Herbivore individual (%)	0.07	-0.15	0.70	0.14	-0.20	-0.02
Rheophilic individual (%)	0.03	0.13	0.75	0.12	0.33	0.04
Tolerant individual (%)	-0.02	-0.41	-0.21	0.33	-0.37	0.51
Nest gurarder individual (%)	-0.05	-0.18	-0.21	-0.66	-0.21	-0.07
Threatened or endangered individual (%)	-0.06	0.79	0.21	-0.06	-0.07	0.11
Migrating (vagile) individual (%)	-0.09	0.81	-0.32	-0.06	0.01	-0.12
Intolerant individual (%)	-0.13	0.81	0.05	0.11	-0.06	-0.19
Hiders individual (%)	-0.21	0.46	-0.01	0.65	-0.06	0.11
Game fish individual (%)	-0.23	0.00	-0.14	0.20	0.68	-0.13
Generalist individual (%)	-0.24	-0.19	-0.04	0.52	-0.66	0.06
Carnivore individual (%)	-0.27	0.70	-0.18	0.07	0.50	-0.07
Benthic individual (%)	-0.32	0.08	0.39	0.05	-0.32	0.25
Water column individual (%)	-0.39	0.03	-0.70	0.04	0.02	0.16
Pielou's evenness index (*J'*)	-0.58	0.04	-0.25	0.03	0.09	-0.20

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CHAPTER THREE

REGIONAL TRENDS OF BIODIVERSITY INDICES: NATURAL LANDSCAPE AND HUMAN LAND USE CONTROLS ON STREAM FISH ASSEMBLAGES

Abstract

Biodiversity of fluvial freshwater fishes is critically threatened globally, and a major factor leading to loss of biodiversity is anthropogenic disturbances in landscapes drained by fluvial ecosystems. Declines in biodiversity of freshwater fish are often identified by loss of species or fewer individuals comprising assemblages, but biological degradation can also occur with increases in non-native species and/or spread of fish tolerant to human disturbances, suggesting the importance of accounting for distinctness of assemblages along with richness and diversity to best characterize response of stream fishes to human stressors. We summarized stream fish assemblages by multiple biodiversity indices and then quantified their responsiveness to landscape factors in stream catchments across five large ecoregions of the eastern U.S. Indices included species richness, Shannon’s diversity, Pielou’s evenness, taxonomic diversity, and taxonomic distinctness. We first tested for correlations among indices across regions and found that while species richness and Shannon’s diversity were always highly correlated, taxonomic distinctiveness was not highly correlated with these factors. We then used multiple linear regressions to predict indices in each of the five ecoregions to identify significant factors from natural landscape and human land uses. Indices were consistently predicted by catchment area and elevation, emphasizing the importance of these factors on biodiversity. In contrast, taxonomic distinctness was consistently predicted by the amount of urban in the catchment, but

the direction of the relationship varied. Agriculture in the catchment was a better predictor of species richness and Shannon's diversity. These results indicate complex influences of natural and anthropogenic landscape factors on unique elements of biodiversity and offers insights from our large regional study that may enhance conservation of stream fishes now and into the future.

Introduction

Habitat degradation and loss caused by anthropogenic disturbances is a dominant reason for global declines in biological diversity of freshwater fishes (Sala et al. 2000; Helfman 2007; Jelks et al. 2008; Burkhead 2012). Reduced biodiversity in freshwater systems may be related to lost species and/or fewer individuals within a species, but researchers recognize that increases in non-native species and/or spread of fishes tolerant to human disturbance may also be indicators of biological degradation (Rahel 2000; Scott and Helfman 2001; Olden and Poff 2004; Scott 2006). For example, anthropogenic disturbances can encourage extirpations of endemic fishes intolerant to human disturbance in altered habitats, while more tolerant fish species to human stressors may thrive because of modified abiotic conditions or from suppression of predators or competitors that do not persist in altered habitats (Olden and Poff 2004; Scott 2006; Helfman 2007). Such changes may be reflected by increased faunal similarity across regions. Because of this, measures of species richness, diversity, and characterizations of regional distinctiveness should be used together to more fully account for changes in biodiversity that may result from anthropogenic disturbances, and such understanding is critical for protecting and preserving biodiversity from current and future human stressors.

Many indices representing biological diversity in fish assemblages are based on counts of species and abundances of individuals. Species richness measures numbers of species found, and it has been shown to be responsive to anthropogenic disturbances in the landscape (Hughes et al. 1998; Pont et al. 2006). However species richness can vary widely across regions due to biogeographic history, stream size, and other natural landscape-scale factors that may influence suitability of habitats for different species (Schlosser 1991; Goldstein and Meador 2004). Species richness also does not account for differences in rare species versus common species, and richness is recommended to be used in concert with other measures that account for abundances of individual species (Stirling and Wilsey 2001; Magurran 2004). Measures of evenness account for abundances, with high measures indicating more equal numbers of individuals per species in assemblages and low measures reflecting dominance in abundances of fewer species (Magurran 2004). Shannon's diversity index weights all species proportionately to their abundances; high values for Shannon's diversity indicate more equitable distributions of individuals present in a sample, while low values may indicate dominance of a few species comprising an assemblage (Magurran 2004). Together, these biodiversity measures can effectively indicate changes in diversity driven by loss of species or individuals, yet not necessarily for non-natives or species tolerant of human disturbance (Magurran and Phillip 2001).

Taxonomic distinctness measures can indicate changes in biodiversity that do not necessarily result in changes to species richness or diversity (Warwick and Clarke 1995). Taxonomic diversity and taxonomic distinctness indices depend on the composition of assemblages found throughout an entire study region; they include a hierarchical measure of relatedness between fish species within a single sample based on their taxonomy to the pool of species found throughout a study region (Clarke and Warwick 1998; 2001). In relatively pristine streams, fish assemblage composition may be comprised of more distinct species and an assemblage that covers a wider breadth in taxonomic diversity and distinctness (Hughes et al. 1990; Angermeier and Winston 1999). These can include endemic habitat specialists, species with specialized feeding preferences, or species with unique life history traits. Under anthropogenic disturbance, a loss in endemic specialist species and/or a spread of tolerant species may result in a smaller number of taxonomic groups and a decline in fish assemblage distinctness. The loss of fish assemblage distinctness can happen through loss of endemic specialists, losing unique genera distinctness, or loss of whole intolerant family groups (e.g. percidae), or expansion in similarity of genera or family groups from emigration and loss of unique fish genera or family groups. Because of this, taxonomic distinctness measures can indicate unique changes in assemblages resulting from anthropogenic land uses and urbanization.

A better understanding of how different biodiversity indices respond to anthropogenic disturbances, to natural factors that influence regional species pools, and habitat factors that constrain species distributions could help to improve understanding of biological changes in streams. Further, such a study conducted over large regions that considers anthropogenic landscape factors as a source of disturbance to stream habitats and evaluates response of multiple indices could yield new insights into broad patterns of biodiversity changes occurring with large-scale disturbances, like human land uses. To help meet these needs, the goal of this study is to characterize regionally-specific landscape controls affecting multiple fish biodiversity indices in streams across five regions of eastern United States (U.S.) We have three objectives. First, we characterized major patterns in multiple fish biodiversity indices across study regions, including interrelationships among the various indices. Indices evaluated included species richness, assemblage diversity, and taxonomic distinctiveness. Second, we identified dominant natural landscape factors and human lands uses important in predicting each of the indices. Finally, we quantified how influences of natural landscape factors and human lands on biodiversity indices vary by study ecoregion. Addressing these objectives yielded new insights into influences on stream fish assemblages across large regions and provided opportunities to enhance conservation efforts to protect stream fishes from current and future landscape changes.

Methods

Study area.—This study was conducted within five large freshwater ecoregions located in the eastern U.S. These freshwater ecoregions, referred to throughout as “ecoregions,” were delineated by the World Wildlife Fund and included: the Appalachian Piedmont, Chesapeake Bay, Laurentian Great Lakes, Middle Missouri, and the Upper Mississippi (Abell et al. 2008; Figure 3.1). Freshwater ecoregions are defined as areas with similar biogeographic history in fish faunas encompassing major river basins and matching large basin boundaries; they represent ecologically-relevant units for groupings of fishes based on evolutionary patterns across large landscapes (Maxwell et al. 1995; Matthews 1998; Abell et al. 2000; 2008; Esselman et al. 2011). Freshwater ecoregions were chosen as the spatial units to evaluate in this study because they encompass a wide range in fish assemblage composition, and as such have the potential for a wide range in richness, biodiversity, and taxonomic distinctness. This ensures that these regions will be effective test areas to evaluate the performance of biodiversity indices in showing responsiveness to human land uses because of the diverse range in natural and human landscape variables across regions.

The study area extends from the western Great Plains to the east coastal plains of the U.S. (Figure 3.1). Natural landscape factors within the study area are highly diverse; study ecoregions include previously glaciated landscapes in the Chesapeake Bay and Laurentian Great Lakes and regions that have not been glaciated including the coastal plains and highlands of the Appalachian Piedmont ecoregion. In the eastern and central portion of the study area, the Middle Missouri and Upper Mississippi ecoregions include areas of intensive agriculture, while high percentages of grasslands occur within the western Middle Missouri ecoregion. High percentage of forested areas are located within the Laurentian Great Lakes, and the Appalachian Piedmont and the Chesapeake Bay ecoregion include areas of high urban land use.

Stream layer.—The 1:100,000-scale National Hydrography Dataset Plus Version 1 (NHDPlusV1) national streams layer was used as a base layer for geographic representation of streams reaches and their catchments (USEPA and USGS 2005). We defined a stream reach as a section of river in the NHDPlusV1 that extends: 1) from the stream origin to the first downstream confluence or junction with a lake or reservoir, 2) from an upstream confluence or lake/reservoir outflow to the next downstream confluence or lake/reservoir junction, or 3) from an upstream confluence or lake/reservoir outflow to the river mouth where it meets with a lake or estuary (Brenden et al. 2006; Esselman et al. 2011; Wang et al. 2011). Catchments summarizing information over two spatial extents were used in this analysis based on the NHDPlusV1. "Local catchments" include all land that drains directly into an individual stream reach without being transported via other fluvial pathways represented in the NHDPlusV1, and "network catchments" include all land upstream of and draining into a given reach via fluvial pathways and including the local catchment.

Natural landscape variables.—Six natural landscape variables were evaluated in this study, including network catchment area, percent of fine lithology in the network catchment, mean local catchment elevation, base-flow index in the network catchment, mean annual air temperature in the local catchment, and mean annual precipitation in the network catchment.

These factors were selected in a previous analysis (Thornbrugh this volume b) as explaining major patterns of variation in natural landscape factors across the five study regions. A variety of nationally-available landscape datasets were used to derive these factors. Catchment areas were calculated using a GIS. Elevation was developed from the U.S. Geological Survey (USGS) National Elevation Data (NED, Gesch 2007). Fine surficial lithology was developed from the USGS terrestrial ecosystems surficial lithology of the conterminous U.S. data layer (Soller and Reheis 2004; Cress et al. 2010). The fine surficial lithology category was defined by grouping major classes of fine substrate size from surficial lithology for use in analysis. The fine lithology category was used to indicate the potential of streams to have variable flow regimes as opposed to more stable hydrology and potentially higher contribution of base-flow from groundwater inputs. The base-flow index, a model of hydraulic potential characterizing the percentage of groundwater contribution to stream flow, was modeled by USGS (Wolock 2003). Mean annual air temperature and mean annual precipitation were summarized for the climatological period from 1981 to 2010 by the PRISM Climate Group (Daly et al. 2008; PRISM 2013).

Human land uses.—Four human land use variables were evaluated in this study. They include percent of urban and agricultural land use in network catchments and the density of stream-road crossings and dams in network catchments. These factors describe major variability in human land uses across the five study ecoregions (Thornbrugh this volume b). Also, percent agricultural land use, percent urban land use, and density of dams in network catchments were shown to be important influences on stream fish assemblage metrics including taxonomic measures, trophic preferences, tolerance to stressors, and life history traits in the study region (Thornbrugh this volume b). Stream road crossings are theorized to be a secondary influence on fish (Bouska and Paukert 2010, Januchowski–Hartley et al. 2013), and we tested for the cumulative effects of these potential barriers to fish passage throughout stream catchments in this study. Major categories of human land cover for urban and agriculture were developed from the 2001 National Land Cover Dataset (2001 NLCD, Homer et al. 2004, USEPA 2008). Urban land use included low, medium, and high intensity developed land along with open space developed land cover classes. Agricultural land use included pasture/hay and cultivated crops land cover classes. The density of dams was developed from the National Anthropogenic Barrier Dataset (NABD, U.S. Geological Survey 2012), and the density of stream-road crossings was developed from the U. S. Census Bureau TIGER/line files data (U.S. Census Bureau 2002).

Fish data.—Data characterizing stream fish assemblages were assembled and referenced to stream reaches in the NHDPlusV1. Assemblages were sampled with electrofishing by state and federal programs using methods determined to be comparable for creeks, small rivers and medium rivers $\leq 10{,}000$ km^2 between years from 1990 to 2010 (Wang et al. 2011; Esselman et al. 2011; 2013). Fish data used in analysis were identified to species, and all scientific naming was standardized to the Integrated Taxonomic Information System (ITIS; ITIS 2010).

Biodiversity indices.—Five measures of fish assemblage biodiversity were derived from site specific data characterizing number of species and their abundances. Three of these indices included species richness, diversity, and evenness: (i) the number of species included in a sample, species richness (S); (ii) species diversity based on Shannon's diversity index (H'), where pi is the proportional of individuals belonging to the ith species and S is the number of species at a sample site (Shannon 1948); and (iii) Pielou's evenness (J') based on Shannon's index and on richness: where the H' is the Shannon's index and S is the number of species (Pielou 1975). Evenness measures relative similarity in abundances of fish species present at a site, relativizing the overall Shannon's index based on number of species found at sites.

Shannon's index and Pielou's evenness indices were calculated using the function "diversity" from the package "vegan" in R (Oksanen et al. 2013; R Core Team. 2013).

(ii) $$H' = -\sum_{i}^{S} pi \log pi$$

(iii) $$J' = H'/\log S$$

The two additional indices that describe taxonomic diversity and taxonomic distinctness of fish assemblages were used. They were derived from abundance data and were based on relationships in composition of stream fish assemblages at individual study sites evaluated against taxonomic relatedness from the regional species pool across all sites in our study region (Clarke and Warwick 1998; 2001). This is in contrast to species richness, Shannon's diversity, and Pielou's evenness, which are calculated from information on assemblages from a single study site. Taxonomic relatedness is derived in part from cladistics classification of all organisms that account for taxonomic levels at which species are related (species, genus, family, order, and class). A numeric weighting of branch lengths of the hierarchical cladistics classification tree accounts for interrelationships among all species in the regional species pool (Table C3.1). A hypothetical cladogram is shown in Figure 3.2 to highlight differences in relatedness weighting among individuals. Sites are considered to be more taxonomically related when most assemblage membership is comprised of species of similar genera with maximal family, order, or class relatedness, while sites are considered to be more distinct in taxonomic assemblage when membership is comprised of species of a variety of genera, multiple families, orders, and classes.

These indices were derived as follows: (iv) taxonomic diversity (Δ): where x_i denotes the abundance of ith species (i =, ..., S), n is the total number of individuals in a sample, and the w_{ij} is the “distinctness weight,” a taxonomic distance measure that links species *i* and *j* in a taxonomy (Clarke and Warwick 2001): and (v) taxonomic distinctness (Δ^*) is defined as (Δ) divided by the value it takes when the taxonomic hierarchical tree has the simplest possible structure, that of all species belonging to the same genus (Warwick and Clarke 1995; Clarke and Warwick 1998; 2001).

(iv) $$\Delta = \left[\sum\sum_{i<j} \omega_{ij}\, x_i\, x_j\right]/[n(n-1)/2]$$

(v) $$\Delta^* = \left[\sum\sum_{i<j} \omega_{ij}\, x_i\, x_j\right]/\left[\sum\sum_{i<j} x_i\, x_j\right]$$

Five taxonomic levels were used, species, genus, family, order, and class, to calculate the distinctness weight (w_{ij}) from the master fish species list for the study region (Table C3.1). The distinctness weight was calculated using function “taxa2dist” and taxonomic diversity and taxonomic distinctness indices were calculated using the function “taxondive” from the package “vegan” in R (Oksanen et al. 2013; R Core Team 2013).

Data analysis

Pearson correlation among fish biodiversity indices.—A Pearson correlation was run to compare co-variability among fish biodiversity indices within regions and to characterize how these interrelationships varied across the five study ecoregions. All variables were transformed to better meet assumptions of linearity and homoscedasticity. Species richness was square-root transformed; all other indices were natural log transformed. Correlations were judged to be high when R^2 values were ≥ 0.65; moderate at 0.35 to 0.65 and low when values were < 0.35.

Regression analysis.—Multiple linear regression models were developed to identify the most important natural landscape variables and human land uses predicting each of the five fish biodiversity indices and to evaluate the variability in best models across the five study ecoregions. All variables were transformed before regression analysis. The best linear regression models were developed utilizing an exhaustive search with a branch-and-bound algorithm for the best subset of five or fewer natural landscape variables and/or human land use variables (from a total of 10 possible predictors, Table 3.1) predicting each of five fish biodiversity indices in all five study ecoregions (Little et al. 1963; Miller 2002; Lumley 2009). Best models were selected using Bayesian Information Criterion (BIC). A standardized regression coefficient (β) value was calculated to evaluate the importance of variables selected for inclusion in the models predicting biodiversity indices. To identify collinearity among explanatory variables, a variance inflation factor (VIF) was calculated. Multiple linear regression models were calculated using the function "regsubsets" from the package "leaps" in R (Lumley 2009; R Core Team 2013). The standardized regression coefficient (β) was calculated using the function "lm.beta" from the package "QuantPsyc" in R (Fletcher 2012; R Core Team 2013).

Results

Study area.—The five study ecoregions included an area greater than 2,000,000 km^2 (Figure 3.1), and data from more than 10,500 fish sampling locations were used in analyses. Natural landscape factors across the study regions are highly diverse (Table 3.1). Mean network catchment area of study sites ranged from 155 km^2 in the Appalachian Piedmont ecoregion to 764 km^2 in the Middle Missouri ecoregion. Fine lithology in the network catchment was lowest in the Upper Mississippi ecoregion (mean of 9%) and highest in the Laurentian Great Lakes ecoregion (mean of 42%). Mean local elevation was lowest at study sites in the Appalachian Piedmont ecoregion at 157 m, and ranged from 20 m to 1166 m across all sites in the study ecoregions, characterized by 10% and 90% exceedance values, respectively (Table 3.1). Mean local elevation was highest at study sites in the Middle Missouri ecoregion at 591 m. Climate varied across sites in the study ecoregions, with lowest mean annual air temperatures in the Upper Mississippi (8 °C) and highest mean annual air temperature and precipitation in the Appalachian Piedmont ecoregion (15 °C, 1215 ml, respectively Table 3.1). The lowest mean annual precipitation was in the Middle Missouri ecoregion at 709 ml.

There was also wide variability in study sites across ecoregions in the four human land uses. Mean percentage of urban land use in network catchments of study sites was highest in the Chesapeake Bay ecoregion at 32% and lowest at study sites in the Middle Missouri at 6% (Table 3.1). There was a high variability in levels of mean percentage of agriculture land use in the network catchment across study ecoregions; it was highest in the Upper Mississippi ecoregion at 60%, with 10% and 90% exceedance values of 16% and 90%, respectively. The mean network catchment percent agriculture was lowest in Appalachian Piedmont ecoregion with a value of 21%, and with 10% and 90% exceedance values of 4% and 41%, respectively. Density of stream-road crossings in network catchments of study sites was highest in the Chesapeake Bay ecoregion at 54/100 km^2 and was lowest in the network catchment for study sites in Middle Missouri ecoregion at 36/100 km^2. Density of dams in the network catchment of study sites was highest in the Appalachian Piedmont ecoregion at 3.91/100 km^2 and lowest in the network catchment of study sites in the Upper Mississippi at 0.71/100 km^2.

Regional patterns in biodiversity indices.— Study regions supported 312 species of fish, comprising 98 genera, 34 families, 21 orders, and two classes (Table C3.1). Patterns in biodiversity indices varied across study ecoregions. Species richness across all sites ranged from one in every ecoregion to a maximum of 48 in the Upper Mississippi. While mean species richness was highest in the Appalachian (15 species), it ranged to a low of 10 in both the Chesapeake and Middle Missouri ecoregions (Table 3.2). Differences across study regions were also shown when considering the 10% exceedance values for species richness. In the Chesapeake Bay ecoregion, the 10% exceedance value for species richness was two, while in the Appalachian Piedmont, it was eight, indicating a substantial number of sites with low species richness in the Chesapeake (Table 3.2).

Shannon's diversity and Pielou's evenness values were also variable. Similar to species richness, mean Shannon's diversity was highest in the Appalachian (1.89, Table 3.2), while evenness was highest in the Chesapeake Bay (0.61, Table 3.2). This likely reflects the fact that while sites in the Chesapeake support fewer species on average compared to other regions, the species comprising assemblages are more even in numbers. Mean diversity and mean evenness across sites were lowest in the Middle Missouri. Finally, the highest value for Shannon's diversity was found in the Appalachian Piedmont at 2.77 (Table 3.2).

Patterns in taxonomic diversity varied from patterns expressed by species richness and Shannon's diversity across study ecoregions. For example, mean taxonomic diversity and distinctness were highest in the Appalachian Piedmont (54.05 and 69.68, respectively, Table 3.2), following highest values for species richness and Shannon's diversity in the Appalachian Piedmont ecoregion. In contrast, the second highest mean taxonomic diversity and distinctness value were in the Middle Missouri ecoregion (41.89 and 66.40, respectively). While mean species richness and Shannon's diversity were low here, this result emphasizes that even in regions with lower species richness or Shannon's diversity; sites may still support assemblages with a high degree of taxonomic diversity and taxonomic distinctness.

Regional patterns in correlation of biodiversity indices.—Patterns in correlation among biological indices were similar across study regions (Table 3.3). Species richness and Shannon's diversity highly correlated in each of the five study regions and ranged in strength from a high of $R^2 = 0.86$ in the Chesapeake Bay ecoregion to a low of $R^2 = 0.69$ in the Middle Missouri ecoregion. Shannon's diversity also had a high correlation with taxonomic diversity across all regions; the highest value was $R^2 = 0.87$ in the Upper Mississippi ecoregion and the low was $R^2 = 0.77$ in the Laurentian Great Lakes (Table 3.3). Taxonomic diversity was highly correlated with taxonomic distinctness across study regions (high of $R^2 = 0.77$ to a low of $R^2 = 0.59$ in both the Chesapeake Bay and Laurentian Great Lakes ecoregions). Interestingly, while taxonomic diversity was moderately correlated with species richness and highly correlated Shannon's diversity, taxonomic distinctness was never highly correlated with these factors (highest $R^2 = 0.46$ in the Upper Mississippi), emphasizing that this metric captures a different biodiversity component (Table 3.3). Evenness was not strongly correlated with any other metrics with the exception of species richness; it was moderately correlated with richness in all regions (Table 3.3).

Predicting biodiversity indices from landscape factors with linear regression models.—All biodiversity indices were identified as being significantly predicted by at least two landscape factors. Adjusted R^2 ranged from 0.52 for species richness in the Upper Mississippi ecoregion to 0.04 for Pielou's evenness in the Appalachian. All natural landscape factors and human land use variables selected for inclusion into models were significant ($p \leq 0.01$). Variance inflation factors (VIF) were low (i.e., maximum VIF = 5.2) for all natural landscape factors and human land uses that were selected as predictor variables in the best models across all five study ecoregions. The low VIF values below 5.2 for all selected predictor variables indicated that there was low collinearity between variables selected in the best models predicting biodiversity indices (Legendre and Legendre 2012).

Trends in predicting biodiversity indices from landscape factors.— Biodiversity indices were variably predicted across regions, but the best predicted index in all ecoregions was species richness with a mean adjusted $R^2 = 0.37$ (Figure 3.3). The second best predicted index across ecoregions was taxonomic distinctness (mean adjusted $R^2 = 0.25$), while the worst predicted biodiversity index was Pielou's evenness across study ecoregions with a mean adjusted $R^2 = 0.13$ (Figure 3.3). The most important predictor of biodiversity indices was catchment area. Catchment area was the strongest or second strongest predictor in 24 of the 25 best models predicting all biodiversity indices across the five study ecoregions (Table 3.4). Local catchment elevation was also important at predicting taxonomic diversity and taxonomic distinctness indices in four of the five ecoregions (Table 3.4). Catchment agriculture was an important human land use predicting species richness and Shannon's diversity in three of the five ecoregions, and it also significantly predicted species richness in Middle Missouri and Shannon's diversity in the Laurentian Great Lakes ecoregions. Agriculture, however, was never a predictor for taxonomic distinctness (Table 3.4). Catchment urban land use was a consistent predictor of taxonomic distinctness in four of the five ecoregions, but the direction of that influence varied by region (Table 3.4). Both local air temperature and catchment precipitation were important predictors of indices across all ecoregions, yet no consistent patterns could be discerned in their ability to predict specific indices or in regional trends.

Regional differences in predicting biodiversity indices from landscape factors.— Biodiversity indices were strongly influenced by catchment fine lithology in the Laurentian Greats Lakes (all indices except distinctiveness) and Middle Missouri ecoregions (richness, Shannon’s diversity, and distinctiveness), and metrics in both regions had no influence from catchment base-flow index. While fine lithology and base-flow index occasionally predicted indices in other regions, there was never an occasion where both catchment fine lithology and catchment base-flow index occurred together as predictors in a model. Regression models showed regional differences in the influences of catchment urban and agricultural land use on biodiversity indices. Catchment urban was a good predictor for taxonomic distinctness in all ecoregions but the direction of the influence varied across ecoregions. Catchment urban had a positive influence on taxonomic distinctness in the Appalachian Piedmont and the Chesapeake Bay ecoregions and a negative influence on taxonomic distinctness in the Laurentian Great Lakes, Middle Missouri, and Upper Mississippi ecoregions. Although they had comparatively less predictive capacity than other metrics, density of stream road crossing and dams in the catchment were significant predictors of species richness and Shannon’s diversity in the Chesapeake Bay ecoregion. Density of stream-road crossing in catchments was a significant predictor of species richness in the Middle Missouri ecoregions and the density of dams in the catchment was also and significant predictor of Shannon’s diversity in the Laurentian Great Lakes ecoregion (Table 3.4).

Discussion

This study characterized trends in stream fish assemblages across five ecoregions in the eastern portion of the U.S. using biodiversity indices including species richness, Shannon’s diversity, Pielou’s evenness, taxonomic diversity, and taxonomic distinctness (Shannon 1948; Pielou 1975; Clarke and Warwick 1998; 2001). General patterns in correlations among individual indices were variable, but relationships among indices were similar across ecoregions. For example, species richness and Shannon’s diversity were always highly correlated in each of the five study ecoregions, yet taxonomic distinctiveness was never highly correlated with these factors, emphasizing the independence of distinctness from richness and Shannon's diversity. Results of multiple linear regression models suggested differences in landscape influences on groups of metrics. Natural landscape factors including stream size and elevation were important and consistent predictors of biodiversity indices, while climatological factors and factors indicating groundwater delivery to streams had more variable influences. Percent of agriculture and urban in the catchment were important predictors of biodiversity across all regions. Catchment agriculture had a fairly consistent response on richness and diversity, while catchment urban land use most consistently predicted taxonomic distinctness, yet that response varied by region. High amounts of catchment urban land use could negatively affect taxonomic distinctness causing shifting fish assemblage composition from endemic faunas to more tolerant fish fauna promoting fish assemblages with more regional similarity (McKinney and Lockwood 1999; Rahel 2002). Together, these results suggest that multiple measures of fish biodiversity should be used to characterize response of stream fish assemblages to landscape influences, not only because they capture unique attributes of the fish assemblage, but also because indices are being influenced by land uses differently.

Correlation among biodiversity indices.— Measures of biodiversity were variably intercorrelated, but showed similar trends in correlations across ecoregions. Species richness and Shannon's diversity were always highly correlated, Shannon's diversity and taxonomic diversity were always highly correlated, and taxonomic diversity and taxonomic distinctness were moderately to highly correlated in each of the five study ecoregions. In contrast, taxonomic distinctness was never strongly correlated with species richness, Shannon's diversity, or Pielou's evenness. Similar relationships between biodiversity indices were seen in macroinvertebrate communities from stream sites in western and central Finland (Heino et al. 2007); they found that taxonomic distinctness of macroinvertebrate assemblages was not correlated with Shannon's diversity or Pielou's evenness (Heino et al. 2007). In a similar study, Heino et al. (2005) found that fish species richness and taxonomic distinctness were moderately to weakly correlated for lake fish assemblages in northeastern Finland. Results of these studies, along with ours, emphasize that these biodiversity indices represent unique attributes of stream fish assemblages, and that commonly used metrics such as richness, Shannon's diversity, and Pielou's evenness may not be fully effective at capturing differences in regional distinctiveness of freshwater assemblages, including differences resulting from anthropogenic landscape factors.

Natural landscape factors predicting biodiversity indices.—Of the major natural and anthropogenic gradients analyzed, biodiversity indices were most strongly influenced by catchment area, it was a significant predictor of every biodiversity index in all ecoregions. This result follows from species-area relationships in fish faunas (Eadie et al. 1986; Angermeier and Schlosser 1989; Thornbrugh and Gido 2010); with increasing stream size, there is an increase in stream productivity, habitat heterogeneity, and habitat area, promoting fish assemblage diversity (Sheldon 1968; Vannote et al. 1980; Marsh-Matthews and Matthews 2000). Local elevation was also an important natural landscape predictor of taxonomic diversity and taxonomic distinctness indices with negative effects in four of the five ecoregions (Table 3.4). This may be due to an increase in assemblage taxonomic complexity at lower elevations where increased stability in flow and temperature regimes and spatial connectivity in fluvial systems contribute to increased taxonomic diversity with additions of unique genus and family groups (Angermeier and Winston 1998; Jackson et al. 2011). Together, these findings underscore the role of natural landscape factors on biodiversity indices and the sensitivity of indices to catchment area as a control of habitat heterogeneity and influence on biodiversity in fish assemblages of fluvial ecosystems.

Catchment fine lithology was also found to be influential in biodiversity indices for the Laurentian Great Lakes ecoregion, positively influencing species richness, Shannon's diversity and taxonomic diversity in the ecoregion. Percent of fine lithology in the catchment has been shown to have a landscape-scale influence directly controlling fish assemblage structure by distinguishing streams with different thermal and hydrologic conditions, and it also acts as a surrogate measure for groundwater potential to base-flow (Zorn et al. 2002; Wehrly et al. 2003). Fine catchment lithology has also been shown to mediate fish assemblages by controlling specific aspects of stream thermal regimes like maximums and variability in stream summer temperatures in Michigan (Thornbrugh this volume a).

Both mean annual air temperature and precipitation were important predictors of biodiversity indices across all ecoregions, yet no consistent patterns could be interpreted in their ability to predict specific indices or in regional trends. For example, species richness and Shannon's diversity were positively associated with air temperature in the Chesapeake Bay and Laurentian Great Lakes ecoregions, but were negatively associated with temperature in the Appalachian Piedmont. Also, catchment precipitation had a positive influence on species richness, Shannon's diversity and both taxonomic indices in the Upper Mississippi, yet catchment precipitation was not a good predictor for any biodiversity indices in the Appalachian Piedmont ecoregion. Despite the lack of consistent trends across indices or regions, the variable associations between air temperature and precipitation on indices does suggest their importance in controlling stream fish assemblages. Further, it underscores the fact that fish biodiversity has the potential to be influenced by future climate changes (Dudgeon et al. 2006; Buisson et al.

2008; Olden et al. 2010), and that a better understanding of regional influences of climate on stream fish assemblages is warranted.

Human land uses predicting biodiversity indices.— Percent of catchment agriculture and urban land use were important predictors of biodiversity across all regions; however associations of these land uses with indices were variable. Catchment agriculture was shown to generally have a positive effect on fish species richness and Shannon's diversity across ecoregions, except for a negative influence on species richness in the Middle Missouri ecoregion. Wang et al. (2001) also found that species richness and diversity of stream fishes from 47 sites in southeastern Wisconsin, U.S., were positively associated with catchment agriculture. Their study sites also had a wide range in human land use in their catchments, including some with high levels of urban and agricultural lands. They surmised that, if impervious surfaces associated with urban land uses were low in catchments, sites with high levels of agriculture still had the potential for high species richness and diversity. However, Wang et al. (1997) showed that with high levels of agriculture (>50% in catchments), fish IBI scores from streams decreased across study sites that had moderate levels of agriculture in their catchments. This suggests that agriculture may have negative effects on stream fish assemblages that are not necessarily reflected in changes in species richness and diversity. Such changes could include losses of intolerant fishes and co-occurring increases in tolerant fish or nonnatives, and it emphasizes the importance of using multiple metrics to best characterize changes in biodiversity that may result in streams from human land uses. Our findings, along with those of the studies referenced above, could also result from differences in types of agriculture occurring on the landscape and/or specific mechanisms by which agriculture could influence streams, and investigations that accounted for specific changes in stream habitat that occurred with agriculture (e.g., increased nutrient loadings, and/or changes in sediment, thermal or flow regimes), would likely yield more specific insights into how fish respond to agriculture.

Catchment urban land use was a consistent predictor of taxonomic distinctness in four of the five ecoregions, although its influence on taxonomic distinctness was positive in the Appalachian Piedmont and negative in the Laurentian Great Lakes, Middle Missouri, and Upper Mississippi ecoregions. These varying influences on taxonomic distinctness may be due in part to regional influences related to the specific proportion or intensity of urban land use in the ecoregion or the interaction between natural landscape factor like lithology and topography and their control on the delivery of runoff and other materials to stream systems (Utz et al. 2010, Thornbrugh this volume b). More significantly, these results suggest that high amounts of catchment urban land use negatively affecting taxonomic distinctness, that may reflect the loss of endemic or sensitive fish taxa and increases in more tolerant taxa, leading to homogenization of assemblages across study regions (Scott 2006; Helfman 2007). These results emphasize how taxonomic distinctness measures can indicate unique changes occurring in stream fish assemblages resulting from anthropogenic land uses, and that taxonomic distinctness may also be an effective metric for bioassessment of streams along with richness and diversity (Stoddard et al. 2008).

The density of road crossings and dams in the catchment were also significant predictors of species richness and Shannon’s diversity. However their influence was always positive on these indices in the three ecoregions where they were significant predictors. Studies have emphasized how these landscape factors may have the potential to influence stream fishes (e.g., Januchowski–Hartley et al. 2013; Perkin and Gido 2012), and our results support this. However, they also suggest that greater numbers of dams and/or stream road crossings may potentially make stream habitats more favorable for more species than could be negatively affected by barriers. In a study of dam influences on stream fishes in Michigan and Wisconsin, Wang et al. (2011) showed increases in IBI scores with more upstream dams. They attributed their finding to potential modifications in habitat that benefited species including reduced sediment loads and potentially more stable stream flow regimes in streams downstream of dams.

Spatial extent of study and scope of natural and human environmental gradients captured.— The spatial extent over which this study was conducted offers important insights into the response of stream fish assemblages to natural landscape factors and human land uses. Our study area included five freshwater ecoregions encompassing an area greater than two million square km, and we tested associations between stream fishes and landscape factors using data from over 10,500 study sites on streams and rivers occurring within twenty two states. This has provided a unique opportunity for conducting regional comparisons based on extensive variability in fish assemblages and characterizations of species compositions that were vital in summarizing patterns in biodiversity. Also, our large data set allowed us the ability to capture equally broad ranges in environmental characteristics to associate with biodiversity indices. While the amount of variance predicted in the biodiversity indices were moderately low, given the spatial extent of the study, species richness and taxonomic distinctness indices were relatively well predicted across ecoregions (i.e., mean adjusted R^2 = 0.37 and 0.25, respectively, Figure 3.3). For Shannon’s diversity, Pielou’s evenness, and taxonomic diversity we were likely unable to capture regionally-specific mechanisms that may be most strongly influencing these indices.

Management implications.—This study emphasized that, across large regions, biodiversity indices for stream fish assemblages are significantly influenced by both natural landscape factors and human land uses. Catchment area was a strong predictor of all biodiversity indices across study regions, and should be controlled for when utilizing biodiversity indices as response metrics in assessments of stream integrity. Taxonomic distinctiveness, found to represent a unique attribute of stream fish assemblages compared to diversity and richness, was also predicted by local elevation, which should similarly be accounted for when using this index for assessment.

This study also showed the importance of human land uses in predicting biodiversity indices, underscoring their value in identifying broad changes in stream fish assemblages resulting from anthropogenic stressors. Taxonomic distinctness was consistently predicted by catchment urban land use, while catchment agriculture was a better predictor of species richness and Shannon's diversity across ecoregions. These findings reflect how unique attributes of fish assemblages are influenced by human land uses differently, and that those changes are likely due in part to shifting species membership, and not always due to the loss of species or individuals (Scott and Helfman 2001; Scott 2006), Based on our results, we recommend using multiple biodiversity measures to capture unique attributes of stream fish assemblages when testing for effects of human stressors. This has important implications for development of multimetric indices of biotic integrity to assess streams, and it highlights the importance of identifying species-specific targets when implementing actions to conserve or protect biodiversity in stream systems.

APPENDICES

APPENDIX 3.A

TABLES

Table 3.1.—Descriptive statistics of landscape variables for the five freshwater ecoregion with landscape variable descriptions (i.e., mean, minimum, maximum, and the 10th and 90th percentiles).

	Appalachian Piedmont				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	155.16	1.42	8062.60	11.42	180.03
Fine lithology in network catchment (%)	21.76	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	157.30	1.39	937.66	20.42	298.06
Base-flow index, network catchment groundwater contribution to baseflow (%)	45.95	25.23	78.30	30.54	60.35
Mean annual air temperature in local catchment (°C)	15.64	9.53	19.33	14.11	17.52
Area weighted average mean annual precipitation in network catchment (ml)	1215.13	973.82	2372.90	1125.53	1317.59
Human land uses					
Urban (%)					
Developed, open space, low, medium, & high intensity in network catchment	14.20	0.00	98.62	3.13	37.22
Agriculture (%)					
Pasture/hay & cultivated crops in network catchment	21.34	0.00	72.63	3.83	40.93
Road crossings					
Density of road crossings in network catchment (number/100 km^2)	48.96	0.00	345.30	15.82	89.03
Dams					
Dam density (number/100 km^2)	3.32	0.00	57.56	0.00	9.06

Table 3.1.—(cont'd)

	Chesapeake Bay				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	371.17	0.82	8483.38	3.48	560.87
Fine lithology in network catchment (%)	13.22	0.00	100.00	0.00	99.80
Mean local catchment elevation (m)	288.25	2.52	1050.68	21.71	491.14
Base-flow index, network catchment groundwater contribution to baseflow (%)	46.26	26.99	64.02	38.08	54.74
Mean annual air temperature in local catchment (°C)	9.57	6.35	14.28	7.00	13.25
Area weighted average mean annual precipitation in network catchment (ml)	1027.70	806.87	1239.06	914.37	1108.89
Human land uses					
Urban (%)					
Developed, open space, low, medium, & high intensity in network catchment	8.15	0.00	98.44	1.27	14.85
Agriculture (%)					
Pasture/hay & cultivated crops in network catchment	31.59	0.00	94.91	7.72	63.49
Road crossings					
Density of road crossings in network catchment (number/100 km^2)	53.99	0.00	588.24	9.40	96.04
Dams					
Dam density (number/100 km^2)	1.10	0.00	30.53	0.00	3.04

Table 3.1.—(cont'd)

	Laurentian Great Lakes				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	354.81	0.23	9533.74	10.27	758.72
Fine lithology in network catchment (%)	41.97	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	277.15	74.56	680.78	180.28	430.92
Base-flow index, network catchment groundwater contribution to baseflow (%)	45.04	18.69	87.95	21.99	68.45
Mean annual air temperature in local catchment (°C)	7.74	2.12	10.56	4.69	9.68
Area weighted average mean annual precipitation in network catchment (ml)	929.80	641.04	1566.84	764.17	1123.50
Human land uses					
Urban (%)					
Developed, open space, low, medium, & high intensity in network catchment	11.05	0.00	99.92	1.15	26.31
Agriculture (%)					
Pasture/hay & cultivated crops in network catchment	39.85	0.00	94.26	0.47	83.07
Road crossings					
Density of road crossings in network catchment (number/100 km^2)	48.49	0.00	413.37	8.35	91.15
Dams					
Dam density (number/100 km^2)	1.13	0.00	73.69	0.00	2.84

Table 3.1.—(cont'd)

	Middle Missouri				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	764.33	1.57	9984.84	15.36	2196.10
Fine lithology in network catchment (%)	32.01	0.00	100.00	0.00	100.00
Mean local catchment elevation (m)	591.36	195.32	3134.90	288.62	1165.51
Base-flow index, network catchment groundwater contribution to baseflow (%)	38.90	12.20	84.20	19.19	69.00
Mean annual air temperature in local catchment (°C)	10.22	0.19	12.92	8.11	12.29
Area weighted average mean annual precipitation in network catchment (ml)	708.96	344.53	1113.56	441.07	929.31
Human land uses					
Urban (%)					
Developed, open space, low, medium, & high intensity in network catchment	5.93	0.00	92.22	1.99	7.65
Agriculture (%)					
Pasture/hay & cultivated crops in network catchment	51.50	0.00	94.88	4.00	87.86
Road crossings					
Density of road crossings in network catchment (number/100 km^2)	35.90	0.00	254.61	3.63	70.55
Dams					
Dam density (number/100 km^2)	3.91	0.00	73.31	0.00	11.60

Table 3.1.—(cont'd)

	Upper Mississippi				
Landscape variable description	Mean	Min	Max	10%	90%
Natural					
Network catchment area (km^2)	356.01	0.23	9964.22	9.65	740.40
Fine lithology in network catchment (%)	9.49	0.00	100.00	0.00	27.43
Mean local catchment elevation (m)	288.86	114.85	589.09	184.87	382.03
Base-flow index, network catchment groundwater contribution to baseflow (%)	49.85	7.84	74.87	31.21	66.29
Mean annual air temperature in local catchment (°C)	7.56	3.07	13.60	5.48	10.61
Area weighted average mean annual precipitation in network catchment (ml)	823.55	556.81	1190.27	704.84	949.22
Human land uses					
Urban (%)					
Developed, open space, low, medium, & high intensity in network catchment	8.65	0.00	99.46	3.24	13.05
Agriculture (%)					
Pasture/hay & cultivated crops in network catchment	60.21	0.00	98.06	15.54	89.80
Road crossings					
Density of road crossings in network catchment (number/100 km^2)	39.58	0.00	643.09	8.88	69.17
Dams					
Dam density (number/100 km^2)	0.77	0.00	39.03	0.00	1.88

Table 3.2.—Descriptive statistics (i.e., mean, range, 10th and 90th percentiles) of fish biodiversity indices in five freshwater ecoregions.

Freshwater ecoregion		Species richness (S)	Shannon's diversity (H')	Pielou's evenness (J')	Taxonomic diversity (Δ)	Taxonomic distinctness (Δ^*)
Appalachian Piedmont						
	Mean	15	1.89	0.51	54.05	69.98
	Range	1–34	0–2.77	0.11–1.00	0–76.62	21.94–96.17
	10%	8	1.28	0.33	38.79	58.57
	90%	22	2.37	0.69	66.62	79.73
Chesapeake Bay						
	Mean	10	1.46	0.61	38.51	58.35
	Range	1–31	0–2.94	0.14–1.00	0–84.01	21.94–100.00
	10%	2	0.36	0.37	6.55	38.80
	90%	19	2.29	0.95	62.48	80.15
Laurentian Great Lakes						
	Mean	11	1.56	0.55	37.31	54.08
	Range	1–37	0–2.87	0.10–1.00	0–84.01	21.94–95.65
	10%	4	0.74	0.33	18.62	38.26
	90%	19	2.23	0.82	56.98	74.39
Middle Missouri						
	Mean	10	1.38	0.50	41.89	66.40
	Range	1–29	0–2.69	0.12–1.00	0–70.06	21.94–84.01
	10%	4	0.63	0.25	16.05	42.83
	90%	17	2.03	0.76	59.91	82.05
Upper Mississippi						
	Mean	13	1.61	0.54	38.35	54.95
	Range	1–48	0–3.11	0.07–1.00	0–84.01	21.94–100.00
	10%	3	0.62	0.33	15.25	39.10
	90%	24	2.38	0.78	60.74	74.21

Table 3.3.—Pearson's correlations between the five biodiversity indices for the five study freshwater ecoregions.

Freshwater ecoregion Variable	S	H'	J'	Δ	Δ^*
Appalachian Piedmont					
Species richness (S)	.				
Shannon's diversity (H')	0.73**	.			
Pielou's evenness (J')	-0.38	0.25**	.		
Taxonomic diversity (Δ)	0.50**	0.80**	0.33**	.	
Taxonomic distinctness (Δ^*)	0.24**	0.25**	-0.01	0.72**	.
Chesapeake Bay					
Species richness (S)	.				
Shannon's diversity (H')	0.84**	.			
Pielou's evenness (J')	-0.44	-0.06	.		
Taxonomic diversity (Δ)	0.57**	0.74**	0.09*	.	
Taxonomic distinctness (Δ^*)	0.26**	0.28**	-0.01	0.79**	.
Laurentian Great Lakes					
Species richness (S)	.				
Shannon's diversity (H')	0.77**	.			
Pielou's evenness (J')	-0.49	0.02	.		
Taxonomic diversity (Δ)	0.47**	0.71**	0.22**	.	
Taxonomic distinctness (Δ^*)	0.15**	0.13**	0.05**	0.70**	.
Middle Missouri					
Species richness (S)	.				
Shannon's diversity (H')	0.66**	.			
Pielou's evenness (J')	-0.52	0.17**	.		
Taxonomic diversity (Δ)	0.53**	0.80**	0.10**	.	
Taxonomic distinctness (Δ^*)	0.33**	0.16**	-0.31	0.62**	.
Upper Mississippi					
Species richness (S)	.				
Shannon's diversity (H')	0.81**	.			
Pielou's evenness (J')	-0.47	-0.05	.		
Taxonomic diversity (Δ)	0.69**	0.83**	0.01	.	
Taxonomic distinctness (Δ^*)	0.46**	0.38**	-0.16	0.76**	.

*P <0.05; **P <0.01.

Table 3.4.—Results of multiple linear regression models for relationships of the biodiversity indices to natural landscape variables and human land use variables, with degrees of freedom, adjusted R^2, and standardized regression coefficient (β) describing the variable strength in the model and direction of influence on biodiversity indices. All variables selected for inclusion in best models as predictors for biodiversity indices were significant at p-value ≤ 0.01.

Freshwater ecoregion Variable	d. f.	Adj R^2	Area_c	Elev	Fine_c	Baseflow_c	Temp_air	Precip_c	Urban_c	Ag_c	Rd_dc	Dam_dc
Appalachian Piedmont												
Species richness (S)	1077	0.25	+0.42	–	–	-0.14	-0.14	–	-0.10	+0.10	–	–
Shannon's diversity (H')	1077	0.16	+0.32	–	–	-0.14	-0.11	–	-0.11	+0.09	–	–
Pielou's evenness (J')	1080	0.04	-0.18	–	+0.14	–	–	–	–	–	–	–
Taxonomic diversity (Δ)	1078	0.09	+0.25	-0.12	–	–	–	–	–	–	–	–
Taxonomic distinctness (Δ^*)	1073	0.14	+0.22	-0.26	–	–	–	–	+0.12	–	–	–
Chesapeake Bay												
Species richness (S)	801	0.33	+0.59	–	–	–	+0.19	–	–	+0.16	+0.13	+0.12
Shannon's diversity (H')	801	0.24	+0.50	–	–	–	+0.16	–	–	+0.14	+0.13	+0.11
Pielou's evenness (J')	803	0.11	-0.31	–	–	–	–	-0.09	–	-0.15	–	–
Taxonomic diversity (Δ)	795	0.23	+0.42	-0.19	–	–	–	–	+0.13	+0.16	–	–
Taxonomic distinctness (Δ^*)	737	0.33	+0.42	-0.45	–	+0.16	–	–	–	–	–	–
Laurentian Great Lakes												
Species richness (S)	3767	0.35	+0.42	+0.16	+0.29	–	+0.31	-0.13	–	–	–	–
Shannon's diversity (H')	3767	0.17	+0.31	–	+0.16	–	+0.07	–	–	+0.09	–	+0.05
Pielou's evenness (J')	3767	0.16	-0.17	-0.08	-0.25	–	-0.18	+0.16	–	–	–	–
Taxonomic diversity (Δ)	3753	0.15	+0.30	-0.13	+0.13	–	–	–	-0.06	–	–	–
Taxonomic distinctness (Δ^*)	3652	0.22	+0.39	-0.13	–	–	+0.11	–	-0.15	-0.12	–	–
Middle Missouri												
Species richness (S)	880	0.40	+0.47	-0.65	-0.20	–	–	–	–	-0.20	+0.10	–
Shannon's diversity (H')	882	0.21	+0.24	-0.44	-0.15	–	–	–	–	–	–	–
Pielou's evenness (J')	881	0.22	-0.39	–	–	–	-0.22	-0.31	–	+0.13	–	–
Taxonomic diversity (Δ)	879	0.23	+0.28	-0.45	–	–	–	–	–	–	–	–
Taxonomic distinctness (Δ^*)	857	0.24	+0.26	-0.28	+0.12	–	–	+0.19	-0.16	–	–	–
Upper Mississippi												
Species richness (S)	3967	0.52	+0.63	–	–	-0.20	-0.18	+0.22	–	+0.15	–	–
Shannon's diversity (H')	3967	0.34	+0.50	+0.22	–	-0.23	–	+0.22	–	+0.09	–	–
Pielou's evenness (J')	3970	0.14	-0.36	–	–	–	–	–	–	-0.06	–	–
Taxonomic diversity (Δ)	3947	0.25	+0.42	+0.14	–	-0.17	–	+0.20	–	+0.08	–	–
Taxonomic distinctness (Δ^*)	3843	0.34	+0.43	–	+0.07	–	+0.15	+0.19	-0.07	–	–	–

APPENDIX 3.B

FIGURES

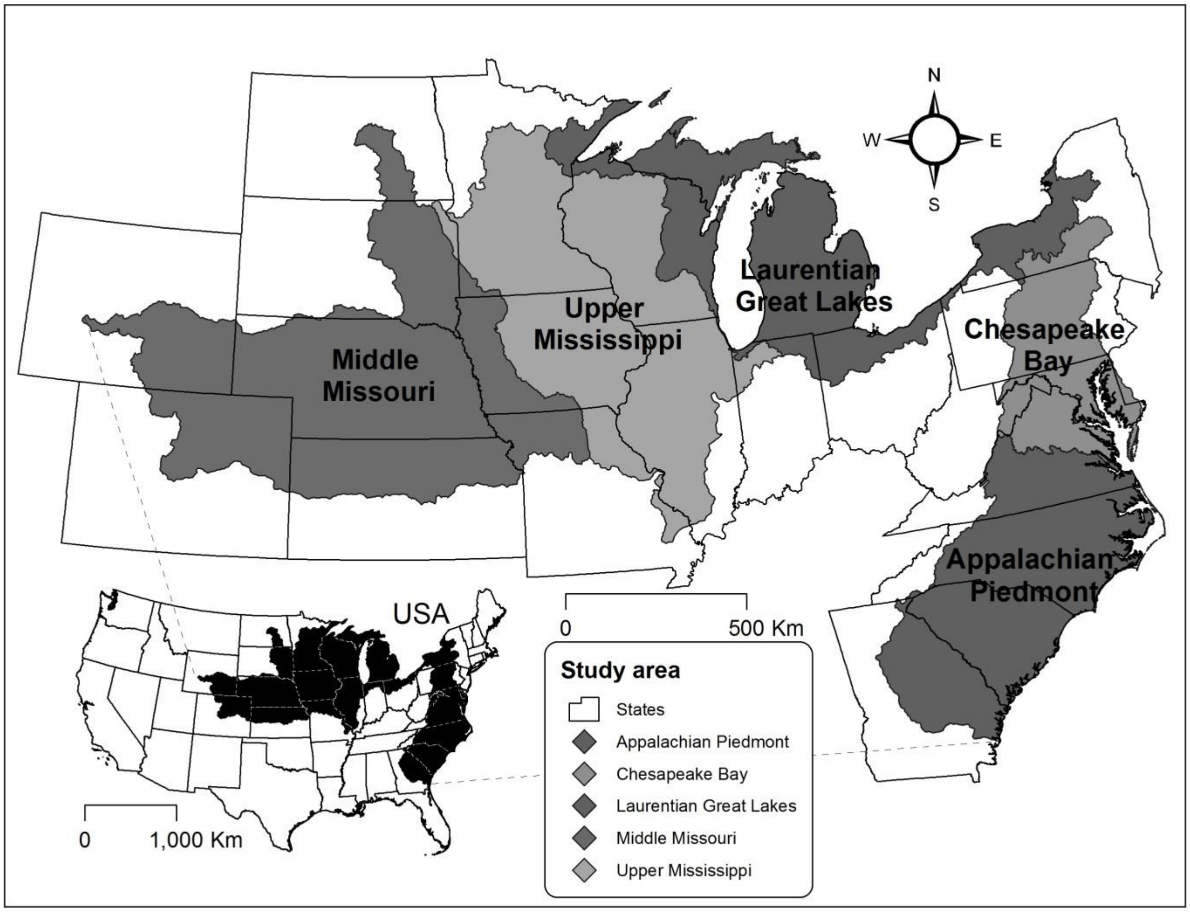

Figure 3.1.—Five freshwater ecoregions of the United States that comprised the study area (Abell et al. 2008).

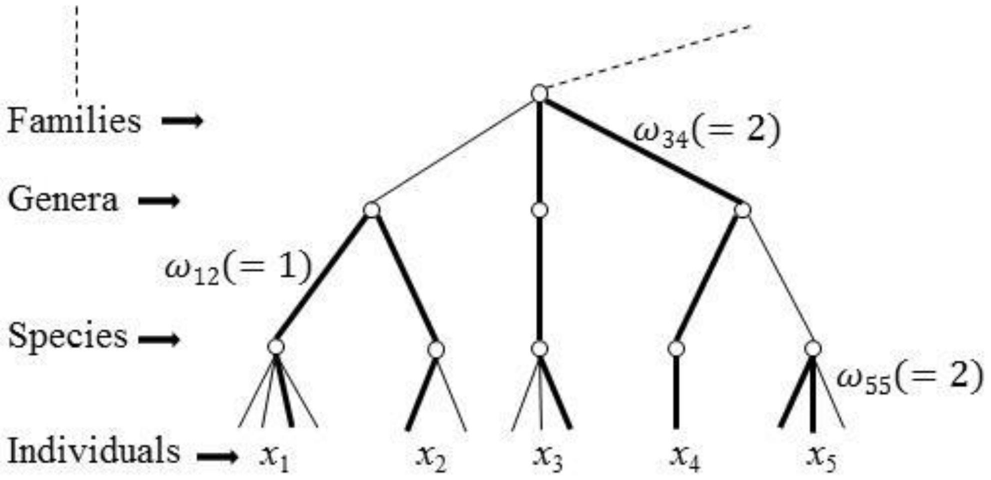

Figure 3.2.—Part of a taxonomic cladogram, showing examples of path length weights $\{w_{ij}\}$ used to define taxonomic diversity and taxonomic distinctness (example from Clark and Warwick 1998)

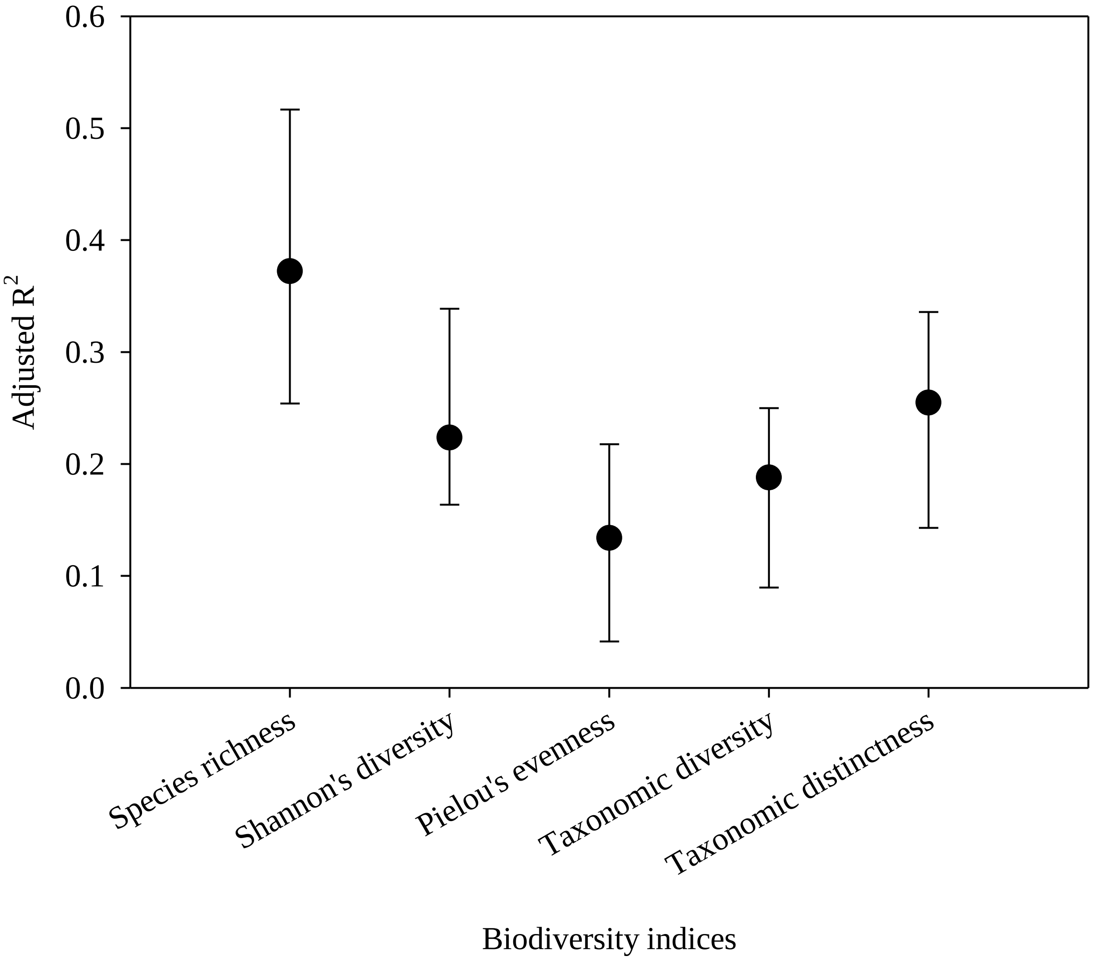

Figure 3.3.—Range in Adjusted R^2 values in biodiversity indices across five study ecoregions from the multiple linear regressions. The dots are mean values with the whiskers maximum and minimum values.

APPENDIX 3.C

SUPPLEMENTAL TABLES

Table C3.1.—List of species use in biodiversity calculations. (n=312)

Common name	Scientific name	Family	Order	Class
Least brook lamprey	*Lampetra aepyptera*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
American brook Lamprey	*Lethenteron appendix*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Sea lamprey	*Petromyzon marinus*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Chestnut lamprey	*Ichthyomyzon castaneus*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Northern brook lamprey	*Ichthyomyzon fossor*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Southern brook lamprey	*Ichthyomyzon gagei*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Silver lamprey	*Ichthyomyzon unicuspis*	Petromyzontidae	Petromyzontiformes	Cephalaspidomorphi
Lake sturgeon	*Acipenser fulvescens*	Acipenseridae	Acipenseriformes	Actinopterygii
Shovelnose sturgeon	*Scaphirhynchus platorynchus*	Acipenseridae	Acipenseriformes	Actinopterygii
Paddlefish	*Polyodon spathula*	Polyodontidae	Acipenseriformes	Actinopterygii
Longnose gar	*Lepisosteus osseus*	Lepisosteidae	Semionotiformes	Actinopterygii
Spotted gar	*Lepisosteus oculatus*	Lepisosteidae	Semionotiformes	Actinopterygii
Shortnose gar	*Lepisosteus platostomus*	Lepisosteidae	Semionotiformes	Actinopterygii
Florida gar	*Lepisosteus platyrhincus*	Lepisosteidae	Semionotiformes	Actinopterygii
Bowfin	*Amia calva*	Amiidae	Amiiformes	Actinopterygii
American eel	*Anguilla rostrata*	Anguillidae	Anguilliformes	Actinopterygii
American Shad	*Alosa sapidissima*	Clupeidae	Clupeiformes	Actinopterygii
Blueback herring	*Alosa aestivalis*	Clupeidae	Clupeiformes	Actinopterygii
Alewife	*Alosa pseudoharengus*	Clupeidae	Clupeiformes	Actinopterygii
Skipjack herring	*Alosa chrysochloris*	Clupeidae	Clupeiformes	Actinopterygii
Gizzard shad	*Dorosoma cepedianum*	Clupeidae	Clupeiformes	Actinopterygii
Threadfin shad	*Dorosoma petenense*	Clupeidae	Clupeiformes	Actinopterygii
Goldeye	*Hiodon alosoides*	Hiodontidae	Osteoglossiformes	Actinopterygii
Mooneye	*Hiodon tergisus*	Hiodontidae	Osteoglossiformes	Actinopterygii
Pink salmon	*Oncorhynchus gorbuscha*	Salmonidae	Salmoniformes	Actinopterygii
Coho salmon	*Oncorhynchus kisutch*	Salmonidae	Salmoniformes	Actinopterygii
Chinook salmon	*Oncorhynchus tshawytscha*	Salmonidae	Salmoniformes	Actinopterygii
Cutthroat trout	*Oncorhynchus clarkii*	Salmonidae	Salmoniformes	Actinopterygii
Rainbow trout	*Oncorhynchus mykiss*	Salmonidae	Salmoniformes	Actinopterygii
Atlantic salmon	*Salmo salar*	Salmonidae	Salmoniformes	Actinopterygii
Brown trout	*Salmo trutta*	Salmonidae	Salmoniformes	Actinopterygii
Brook trout	*Salvelinus fontinalis*	Salmonidae	Salmoniformes	Actinopterygii
Round whitefish	*Prosopium cylindraceum*	Salmonidae	Salmoniformes	Actinopterygii
Rainbow smelt	*Osmerus mordax*	Osmeridae	Osmeriformes	Actinopterygii
Northern pike	*Esox lucius*	Esocidae	Esociformes	Actinopterygii
Redfin pickerel	*Esox americanus*	Esocidae	Esociformes	Actinopterygii
Chain pickerel	*Esox niger*	Esocidae	Esociformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
Muskellunge	*Esox masquinongy*	Esocidae	Esociformes	Actinopterygii
Eastern mudminnow	*Umbra pygmaea*	Umbridae	Esociformes	Actinopterygii
Central mudminnow	*Umbra limi*	Umbridae	Esociformes	Actinopterygii
Common carp	*Cyprinus carpio*	Cyprinidae	Cypriniformes	Actinopterygii
Goldfish	*Carassius auratus*	Cyprinidae	Cypriniformes	Actinopterygii
Cutlips minnow	*Exoglossum maxillingua*	Cyprinidae	Cypriniformes	Actinopterygii
Tonguetied minnow	*Exoglossum laurae*	Cyprinidae	Cypriniformes	Actinopterygii
Eastern silvery minnow	*Hybognathus regius*	Cyprinidae	Cypriniformes	Actinopterygii
Mississippi silvery minnow	*Hybognathus nuchalis*	Cyprinidae	Cypriniformes	Actinopterygii
Plains minnow	*Hybognathus placitus*	Cyprinidae	Cypriniformes	Actinopterygii
Western silvery minnow	*Hybognathus argyritis*	Cyprinidae	Cypriniformes	Actinopterygii
Brassy minnow	*Hybognathus hankinsoni*	Cyprinidae	Cypriniformes	Actinopterygii
Golden shiner	*Notemigonus crysoleucas*	Cyprinidae	Cypriniformes	Actinopterygii
Rosyside dace	*Clinostomus funduloides*	Cyprinidae	Cypriniformes	Actinopterygii
Redside dace	*Clinostomus elongatus*	Cyprinidae	Cypriniformes	Actinopterygii
Fallfish	*Semotilus corporalis*	Cyprinidae	Cypriniformes	Actinopterygii
Creek chub	*Semotilus atromaculatus*	Cyprinidae	Cypriniformes	Actinopterygii
Sandhills chub	*Semotilus lumbee*	Cyprinidae	Cypriniformes	Actinopterygii
Eastern blacknose dace	*Rhinichthys atratulus*	Cyprinidae	Cypriniformes	Actinopterygii
Longnose dace	*Rhinichthys cataractae*	Cyprinidae	Cypriniformes	Actinopterygii
River chub	*Nocomis micropogon*	Cyprinidae	Cypriniformes	Actinopterygii
Bluehead chub	*Nocomis leptocephalus*	Cyprinidae	Cypriniformes	Actinopterygii
Hornyhead chub	*Nocomis biguttatus*	Cyprinidae	Cypriniformes	Actinopterygii
Bull chub	*Nocomis raneyi*	Cyprinidae	Cypriniformes	Actinopterygii
Comely shiner	*Notropis amoenus*	Cyprinidae	Cypriniformes	Actinopterygii
Bridle shiner	*Notropis bifrenatus*	Cyprinidae	Cypriniformes	Actinopterygii
Ironcolor shiner	*Notropis chalybaeus*	Cyprinidae	Cypriniformes	Actinopterygii
Spottail shiner	*Notropis hudsonius*	Cyprinidae	Cypriniformes	Actinopterygii
Swallowtail shiner	*Notropis procne*	Cyprinidae	Cypriniformes	Actinopterygii
Rosyface shiner	*Notropis rubellus*	Cyprinidae	Cypriniformes	Actinopterygii
Emerald shiner	*Notropis atherinoides*	Cyprinidae	Cypriniformes	Actinopterygii
Ghost shiner	*Notropis buchanani*	Cyprinidae	Cypriniformes	Actinopterygii
Sand shiner	*Notropis stramineus*	Cyprinidae	Cypriniformes	Actinopterygii
Weed shiner	*Notropis texanus*	Cyprinidae	Cypriniformes	Actinopterygii
Mimic shiner	*Notropis volucellus*	Cyprinidae	Cypriniformes	Actinopterygii
Whitemouth shiner	*Notropis alborus*	Cyprinidae	Cypriniformes	Actinopterygii
Highfin shiner	*Notropis altipinnis*	Cyprinidae	Cypriniformes	Actinopterygii
Pugnose shiner	*Notropis anogenus*	Cyprinidae	Cypriniformes	Actinopterygii
River shiner	*Notropis blennius*	Cyprinidae	Cypriniformes	Actinopterygii
Bigeye shiner	*Notropis boops*	Cyprinidae	Cypriniformes	Actinopterygii
Redlip shiner	*Notropis chiliticus*	Cyprinidae	Cypriniformes	Actinopterygii
Greenhead shiner	*Notropis chlorocephalus*	Cyprinidae	Cypriniformes	Actinopterygii
Dusky shiner	*Notropis cummingsae*	Cyprinidae	Cypriniformes	Actinopterygii
Wedgespot shiner	*Notropis greenei*	Cyprinidae	Cypriniformes	Actinopterygii
Blackchin shiner	*Notropis heterodon*	Cyprinidae	Cypriniformes	Actinopterygii
Blacknose shiner	*Notropis heterolepis*	Cyprinidae	Cypriniformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
Longnose shiner	*Notropis longirostris*	Cyprinidae	Cypriniformes	Actinopterygii
Yellowfin shiner	*Notropis lutipinnis*	Cyprinidae	Cypriniformes	Actinopterygii
Taillight shiner	*Notropis maculatus*	Cyprinidae	Cypriniformes	Actinopterygii
Cape Fear shiner	*Notropis mekistocholas*	Cyprinidae	Cypriniformes	Actinopterygii
Ozark minnow	*Notropis nubilus*	Cyprinidae	Cypriniformes	Actinopterygii
Coastal shiner	*Notropis petersoni*	Cyprinidae	Cypriniformes	Actinopterygii
Silver shiner	*Notropis photogenis*	Cyprinidae	Cypriniformes	Actinopterygii
Sandbar shiner	*Notropis scepticus*	Cyprinidae	Cypriniformes	Actinopterygii
Mirror shiner	*Notropis spectrunculus*	Cyprinidae	Cypriniformes	Actinopterygii
Telescope shiner	*Notropis telescopus*	Cyprinidae	Cypriniformes	Actinopterygii
Topeka shiner	*Notropis topeka*	Cyprinidae	Cypriniformes	Actinopterygii
Bigeye chub	*Hybopsis amblops*	Cyprinidae	Cypriniformes	Actinopterygii
Silverjaw minnow	*Notropis buccatus*	Cyprinidae	Cypriniformes	Actinopterygii
Highback chub	*Hybopsis hypsinotus*	Cyprinidae	Cypriniformes	Actinopterygii
Rosyface chub	*Hybopsis rubrifrons*	Cyprinidae	Cypriniformes	Actinopterygii
Channel shiner	*notropis wickliffi*	Cyprinidae	Cypriniformes	Actinopterygii
Suckermouth minnow	*Phenacobius mirabilis*	Cyprinidae	Cypriniformes	Actinopterygii
Central stoneroller	*Campostoma anomalum*	Cyprinidae	Cypriniformes	Actinopterygii
Largescale stoneroller	*Campostoma oligolepis*	Cyprinidae	Cypriniformes	Actinopterygii
Bluefin stoneroller	*Campostoma pauciradii*	Cyprinidae	Cypriniformes	Actinopterygii
Bluntnose minnow	*Pimephales notatus*	Cyprinidae	Cypriniformes	Actinopterygii
Fathead minnow	*Pimephales promelas*	Cyprinidae	Cypriniformes	Actinopterygii
Bullhead minnow	*Pimephales vigilax*	Cyprinidae	Cypriniformes	Actinopterygii
Lake chub	*Couesius plumbeus*	Cyprinidae	Cypriniformes	Actinopterygii
Grass carp	*Ctenopharyngodon idella*	Cyprinidae	Cypriniformes	Actinopterygii
Northern redbelly dace	*Phoxinus eos*	Cyprinidae	Cypriniformes	Actinopterygii
Southern redbelly dace	*Phoxinus erythrogaster*	Cyprinidae	Cypriniformes	Actinopterygii
Finescale dace	*Phoxinus neogaeus*	Cyprinidae	Cypriniformes	Actinopterygii
Mountain redbelly dace	*Phoxinus oreas*	Cyprinidae	Cypriniformes	Actinopterygii
Rudd	*Scardinius erythrophthalmus*	Cyprinidae	Cypriniformes	Actinopterygii
Silver carp	*Hypophthalmichthys molitrix*	Cyprinidae	Cypriniformes	Actinopterygii
Bighead carp	*Hypophthalmichthys nobilis*	Cyprinidae	Cypriniformes	Actinopterygii
Satinfin shiner	*Cyprinella analostana*	Cyprinidae	Cypriniformes	Actinopterygii
Ocmulgee shiner	*Cyprinella callisema*	Cyprinidae	Cypriniformes	Actinopterygii
Greenfin shiner	*Cyprinella chloristia*	Cyprinidae	Cypriniformes	Actinopterygii
Whitetail shiner	*Cyprinella galactura*	Cyprinidae	Cypriniformes	Actinopterygii
Thicklip chub	*Cyprinella labrosa*	Cyprinidae	Cypriniformes	Actinopterygii
Bannerfin shiner	*Cyprinella leedsi*	Cyprinidae	Cypriniformes	Actinopterygii
Red shiner	*Cyprinella lutrensis*	Cyprinidae	Cypriniformes	Actinopterygii
Whitefin shiner	*Cyprinella nivea*	Cyprinidae	Cypriniformes	Actinopterygii
Fieryblack shiner	*Cyprinella pyrrhomelas*	Cyprinidae	Cypriniformes	Actinopterygii
Spotfin shiner	*Cyprinella spiloptera*	Cyprinidae	Cypriniformes	Actinopterygii
Blacktail shiner	*Cyprinella venusta*	Cyprinidae	Cypriniformes	Actinopterygii
Steelcolor shiner	*Cyprinella whipplei*	Cyprinidae	Cypriniformes	Actinopterygii
Altamaha shiner	*Cyprinella xaenura*	Cyprinidae	Cypriniformes	Actinopterygii
Santee chub	*Hybopsis zanema*	Cyprinidae	Cypriniformes	Actinopterygii
Gravel chub	*Erimystax x-punctatus*	Cyprinidae	Cypriniformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
White shiner	*Luxilus albeolus*	Cyprinidae	Cypriniformes	Actinopterygii
Crescent shiner	*Luxilus cerasinus*	Cyprinidae	Cypriniformes	Actinopterygii
Striped shiner	*Luxilus chrysocephalus*	Cyprinidae	Cypriniformes	Actinopterygii
Warpaint shiner	*Luxilus coccogenis*	Cyprinidae	Cypriniformes	Actinopterygii
Common shiner	*Luxilus cornutus*	Cyprinidae	Cypriniformes	Actinopterygii
Bleeding shiner	*Luxilus zonatus*	Cyprinidae	Cypriniformes	Actinopterygii
Bandfin shiner	*Luxilus zonistius*	Cyprinidae	Cypriniformes	Actinopterygii
Rosefin shiner	*Lythrurus ardens*	Cyprinidae	Cypriniformes	Actinopterygii
Ribbon shiner	*Lythrurus fumeus*	Cyprinidae	Cypriniformes	Actinopterygii
Redfin shiner	*Lythrurus umbratilis*	Cyprinidae	Cypriniformes	Actinopterygii
Speckled chub	*Macrhybopsis aestivalis*	Cyprinidae	Cypriniformes	Actinopterygii
Silver chub	*Macrhybopsis storeriana*	Cyprinidae	Cypriniformes	Actinopterygii
Pearl dace	*Margariscus margarita*	Cyprinidae	Cypriniformes	Actinopterygii
Pugnose minnow	*Opsopoeodus emiliae*	Cyprinidae	Cypriniformes	Actinopterygii
Flathead chub	*Platygobio gracilis*	Cyprinidae	Cypriniformes	Actinopterygii
Longnose sucker	*Catostomus catostomus*	Catostomidae	Cypriniformes	Actinopterygii
Mountain sucker	*Catostomus platyrhynchus*	Catostomidae	Cypriniformes	Actinopterygii
Quillback	*Carpiodes cyprinus*	Catostomidae	Cypriniformes	Actinopterygii
River carpsucker	*Carpiodes carpio*	Catostomidae	Cypriniformes	Actinopterygii
Highfin carpsucker	*Carpiodes velifer*	Catostomidae	Cypriniformes	Actinopterygii
Lake chubsucker	*Erimyzon sucetta*	Catostomidae	Cypriniformes	Actinopterygii
Creek chubsucker	*Erimyzon oblongus*	Catostomidae	Cypriniformes	Actinopterygii
Shorthead redhorse	*Moxostoma macrolepidotum*	Catostomidae	Cypriniformes	Actinopterygii
Silver redhorse	*Moxostoma anisurum*	Catostomidae	Cypriniformes	Actinopterygii
Bigeye jumprock	*Moxostoma ariommum*	Catostomidae	Cypriniformes	Actinopterygii
River redhorse	*Moxostoma carinatum*	Catostomidae	Cypriniformes	Actinopterygii
Blacktip jumprock	*Moxostoma cervinum*	Catostomidae	Cypriniformes	Actinopterygii
Golden redhorse	*Moxostoma erythrurum*	Catostomidae	Cypriniformes	Actinopterygii
V-lip redhorse	*Moxostoma pappillosum*	Catostomidae	Cypriniformes	Actinopterygii
Striped jumprock	*Moxostoma rupiscartes*	Catostomidae	Cypriniformes	Actinopterygii
Greater redhorse	*Moxostoma valenciennesi*	Catostomidae	Cypriniformes	Actinopterygii
Northern hog sucker	*Hypentelium nigricans*	Catostomidae	Cypriniformes	Actinopterygii
Roanoke Hogsucker	*Hypentelium roanokense*	Catostomidae	Cypriniformes	Actinopterygii
Blue sucker	*Cycleptus elongatus*	Catostomidae	Cypriniformes	Actinopterygii
Smallmouth buffalo	*Ictiobus bubalus*	Catostomidae	Cypriniformes	Actinopterygii
Bigmouth buffalo	*Ictiobus cyprinellus*	Catostomidae	Cypriniformes	Actinopterygii
Black buffalo	*Ictiobus niger*	Catostomidae	Cypriniformes	Actinopterygii
Spotted sucker	*Minytrema melanops*	Catostomidae	Cypriniformes	Actinopterygii
Oriental weatherfish	*Misgurnus anguillicaudatus*	Cobitidae	Cypriniformes	Actinopterygii
Blue catfish	*Ictalurus furcatus*	Ictaluridae	Siluriformes	Actinopterygii
Channel catfish	*Ictalurus punctatus*	Ictaluridae	Siluriformes	Actinopterygii
Tadpole madtom	*Noturus gyrinus*	Ictaluridae	Siluriformes	Actinopterygii
Margined madtom	*Noturus insignis*	Ictaluridae	Siluriformes	Actinopterygii
Freckled madtom	*Noturus nocturnus*	Ictaluridae	Siluriformes	Actinopterygii
Slender madtom	*Noturus exilis*	Ictaluridae	Siluriformes	Actinopterygii
Stonecat	*Noturus flavus*	Ictaluridae	Siluriformes	Actinopterygii
Carolina madtom	*Noturus furiosus*	Ictaluridae	Siluriformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
Speckled madtom	*Noturus leptacanthus*	Ictaluridae	Siluriformes	Actinopterygii
Brindled madtom	*Noturus miurus*	Ictaluridae	Siluriformes	Actinopterygii
Northern madtom	*Noturus stigmosus*	Ictaluridae	Siluriformes	Actinopterygii
Flathead catfish	*Pylodictis olivaris*	Ictaluridae	Siluriformes	Actinopterygii
Snail bullhead	*Ameiurus brunneus*	Ictaluridae	Siluriformes	Actinopterygii
White catfish	*Ameiurus catus*	Ictaluridae	Siluriformes	Actinopterygii
Black bullhead	*Ameiurus melas*	Ictaluridae	Siluriformes	Actinopterygii
Yellow bullhead	*Ameiurus natalis*	Ictaluridae	Siluriformes	Actinopterygii
Brown bullhead	*Ameiurus nebulosus*	Ictaluridae	Siluriformes	Actinopterygii
Flat bullhead	*Ameiurus platycephalus*	Ictaluridae	Siluriformes	Actinopterygii
Spotted bullhead	*Ameiurus serracanthus*	Ictaluridae	Siluriformes	Actinopterygii
Swampfish	*Chologaster cornuta*	Amblyopsidae	Percopsiformes	Actinopterygii
Pirate perch	*Aphredoderus sayanus*	Aphredoderidae	Percopsiformes	Actinopterygii
Trout-perch	*Percopsis omiscomaycus*	Percopsidae	Percopsiformes	Actinopterygii
Burbot	*Lota lota*	Gadidae	Gadiformes	Actinopterygii
Banded killifish	*Fundulus diaphanus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Mummichog	*Fundulus heteroclitus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Golden topminnow	*Fundulus chrysotus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Northern plains killifish	*Fundulus kansae*	Fundulidae	Cyprinodontiformes	Actinopterygii
Blackspotted topminnow	*Fundulus olivaceus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Plains killifish	*Fundulus zebrinus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Northern studfish	*Fundulus catenatus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Lined topminnow	*Fundulus lineolatus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Blackstripe topminnow	*Fundulus notatus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Speckled killifish	*Fundulus rathbuni*	Fundulidae	Cyprinodontiformes	Actinopterygii
Plains topminnow	*Fundulus sciadicus*	Fundulidae	Cyprinodontiformes	Actinopterygii
Starhead topminnow	*Fundulus dispar*	Fundulidae	Cyprinodontiformes	Actinopterygii
Bluefin killifish	*Lucania goodei*	Fundulidae	Cyprinodontiformes	Actinopterygii
Mosquitofish	*Gambusia affinis*	Poeciliidae	Cyprinodontiformes	Actinopterygii
Least killifish	*Heterandria formosa*	Poeciliidae	Cyprinodontiformes	Actinopterygii
Inland silverside	*Menidia beryllina*	Atherinopsidae	Atheriniformes	Actinopterygii
Brook silverside	*Labidesthes sicculus*	Atherinopsidae	Atheriniformes	Actinopterygii
Threespine stickleback	*Gasterosteus aculeatus*	Gasterosteidae	Gasterosteiformes	Actinopterygii
Ninespine stickleback	*Pungitius pungitius*	Gasterosteidae	Gasterosteiformes	Actinopterygii
Fourspine stickleback	*Apeltes quadracus*	Gasterosteidae	Gasterosteiformes	Actinopterygii
Brook stickleback	*Culaea inconstans*	Gasterosteidae	Gasterosteiformes	Actinopterygii
Slimy sculpin	*Cottus cognatus*	Cottidae	Scorpaeniformes	Actinopterygii
Mottled sculpin	*Cottus bairdii*	Cottidae	Scorpaeniformes	Actinopterygii
Banded sculpin	*Cottus carolinae*	Cottidae	Scorpaeniformes	Actinopterygii
Potomac sculpin	*Cottus girardi*	Cottidae	Scorpaeniformes	Actinopterygii
White perch	*Morone americana*	Moronidae	Perciformes	Actinopterygii
Striped bass	*Morone saxatilis*	Moronidae	Perciformes	Actinopterygii
White bass	*Morone chrysops*	Moronidae	Perciformes	Actinopterygii
Yellow bass	*Morone mississippiensis*	Moronidae	Perciformes	Actinopterygii
Mud sunfish	*Acantharchus pomotis*	Centrarchidae	Perciformes	Actinopterygii
Rock bass	*Ambloplites rupestris*	Centrarchidae	Perciformes	Actinopterygii
Roanoke bass	*Ambloplites cavifrons*	Centrarchidae	Perciformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
Shadow bass	*Ambloplites ariommus*	Centrarchidae	Perciformes	Actinopterygii
Flier	*Centrarchus macropterus*	Centrarchidae	Perciformes	Actinopterygii
Blackbanded sunfish	*Enneacanthus chaetodon*	Centrarchidae	Perciformes	Actinopterygii
Bluespotted sunfish	*Enneacanthus gloriosus*	Centrarchidae	Perciformes	Actinopterygii
Banded sunfish	*Enneacanthus obesus*	Centrarchidae	Perciformes	Actinopterygii
Redbreast sunfish	*Lepomis auritus*	Centrarchidae	Perciformes	Actinopterygii
Green sunfish	*Lepomis cyanellus*	Centrarchidae	Perciformes	Actinopterygii
Warmouth	*Chaenobryttus gulosus*	Centrarchidae	Perciformes	Actinopterygii
Bluegill	*Lepomis macrochirus*	Centrarchidae	Perciformes	Actinopterygii
Pumpkinseed	*Lepomis gibbosus*	Centrarchidae	Perciformes	Actinopterygii
Orangespotted sunfish	*Lepomis humilis*	Centrarchidae	Perciformes	Actinopterygii
Dollar sunfish	*Lepomis marginatus*	Centrarchidae	Perciformes	Actinopterygii
Longear sunfish	*Lepomis megalotis*	Centrarchidae	Perciformes	Actinopterygii
Redear sunfish	*Lepomis microlophus*	Centrarchidae	Perciformes	Actinopterygii
Spotted sunfish	*Lepomis punctatus*	Centrarchidae	Perciformes	Actinopterygii
Largemouth bass	*Micropterus salmoides*	Centrarchidae	Perciformes	Actinopterygii
Spotted bass	*Micropterus punctulatus*	Centrarchidae	Perciformes	Actinopterygii
Redeye bass	*Micropterus coosae*	Centrarchidae	Perciformes	Actinopterygii
White crappie	*Pomoxis annularis*	Centrarchidae	Perciformes	Actinopterygii
Black crappie	*Pomoxis nigromaculatus*	Centrarchidae	Perciformes	Actinopterygii
Everglades pygmy sunfish	*Elassoma evergladei*	Elassomatidae	Perciformes	Actinopterygii
Banded pygmy sunfish	*Elassoma zonatum*	Elassomatidae	Perciformes	Actinopterygii
Swamp darter	*Etheostoma fusiforme*	Percidae	Perciformes	Actinopterygii
Tessellated darter	*Etheostoma olmstedi*	Percidae	Perciformes	Actinopterygii
Sawcheek darter	*Etheostoma serrifer*	Percidae	Perciformes	Actinopterygii
Glassy darter	*Etheostoma vitreum*	Percidae	Perciformes	Actinopterygii
Bluntnose darter	*Etheostoma chlorosoma*	Percidae	Perciformes	Actinopterygii
Slough darter	*Etheostoma gracile*	Percidae	Perciformes	Actinopterygii
Orangethroat darter	*Etheostoma spectabile*	Percidae	Perciformes	Actinopterygii
Johnny darter	*Etheostoma nigrum*	Percidae	Perciformes	Actinopterygii
Mud darter	*Etheostoma asprigene*	Percidae	Perciformes	Actinopterygii
Greenside darter	*Etheostoma blennioides*	Percidae	Perciformes	Actinopterygii
Rainbow darter	*Etheostoma caeruleum*	Percidae	Perciformes	Actinopterygii
Carolina darter	*Etheostoma collis*	Percidae	Perciformes	Actinopterygii
Saluda darter	*Etheostoma saludae*	Percidae	Perciformes	Actinopterygii
Iowa darter	*Etheostoma exile*	Percidae	Perciformes	Actinopterygii
Fantail darter	*Etheostoma flabellare*	Percidae	Perciformes	Actinopterygii
Savannah darter	*Etheostoma fricksium*	Percidae	Perciformes	Actinopterygii
Christmas darter	*Etheostoma hopkinsi*	Percidae	Perciformes	Actinopterygii
Turquoise darter	*Etheostoma inscriptum*	Percidae	Perciformes	Actinopterygii
Longfin darter	*Etheostoma longimanum*	Percidae	Perciformes	Actinopterygii
Spotted darter	*Etheostoma maculatum*	Percidae	Perciformes	Actinopterygii
Pinewoods darter	*Etheostoma mariae*	Percidae	Perciformes	Actinopterygii
Least darter	*Etheostoma microperca*	Percidae	Perciformes	Actinopterygii
Goldstripe darter	*Etheostoma parvipinne*	Percidae	Perciformes	Actinopterygii
Riverweed darter	*Etheostoma podostemone*	Percidae	Perciformes	Actinopterygii
Seagreen darter	*Etheostoma thalassinum*	Percidae	Perciformes	Actinopterygii

Table C3.1.—(cont'd)

Common name	Scientific name	Family	Order	Class
Banded darter	*Etheostoma zonale*	Percidae	Perciformes	Actinopterygii
Yellow perch	*Perca flavescens*	Percidae	Perciformes	Actinopterygii
Logperch	*Percina caprodes*	Percidae	Perciformes	Actinopterygii
Stripeback darter	*Percina notogramma*	Percidae	Perciformes	Actinopterygii
Shield darter	*Percina peltata*	Percidae	Perciformes	Actinopterygii
Dusky darter	*Percina sciera*	Percidae	Perciformes	Actinopterygii
Channel darter	*Percina copelandi*	Percidae	Perciformes	Actinopterygii
Piedmont darter	*Percina crassa*	Percidae	Perciformes	Actinopterygii
Gilt darter	*Percina evides*	Percidae	Perciformes	Actinopterygii
Blackside darter	*Percina maculata*	Percidae	Perciformes	Actinopterygii
Blackbanded darter	*Percina nigrofasciata*	Percidae	Perciformes	Actinopterygii
Slenderhead darter	*Percina phoxocephala*	Percidae	Perciformes	Actinopterygii
Roanoke darter	*Percina roanoka*	Percidae	Perciformes	Actinopterygii
River darter	*Percina shumardi*	Percidae	Perciformes	Actinopterygii
Western sand darter	*Ammocrypta clara*	Percidae	Perciformes	Actinopterygii
Eastern sand darter	*Ammocrypta pellucida*	Percidae	Perciformes	Actinopterygii
Freshwater drum	*Aplodinotus grunniens*	Sciaenidae	Perciformes	Actinopterygii
Striped mullet	*Mugil cephalus*	Mugilidae	Mugiliformes	Actinopterygii
Round goby	*Neogobius melanostomus*	Gobiidae	Perciformes	Actinopterygii
Southern flounder	*Paralichthys lethostigma*	Paralichthyidae	Pleuronectiformes	Actinopterygii
Hogchoker	*Trinectes maculatus*	Achiridae	Pleuronectiformes	Actinopterygii
Pallid shiner	*Hybopsis amnis*	Cyprinidae	Cypriniformes	Actinopterygii
Clear chub	*Hybopsis winchelli*	Cyprinidae	Cypriniformes	Actinopterygii
Pinewoods shiner	*Lythrurus matutinus*	Cyprinidae	Cypriniformes	Actinopterygii
Scarlet shiner	*Lythrurus fasciolaris*	Cyprinidae	Cypriniformes	Actinopterygii
Sailfin shiner	*Pteronotropis hypselopterus*	Cyprinidae	Cypriniformes	Actinopterygii
Notchlip redhorse	*Moxostoma collapsum*	Catostomidae	Cypriniformes	Actinopterygii
Crystal darter	*Crystallaria asprella*	Percidae	Perciformes	Actinopterygii
Holiday darter	*Etheostoma brevirostrum*	Percidae	Perciformes	Actinopterygii
Smallmouth bass	*Micropterus dolomieu*	Centrarchidae	Perciformes	Actinopterygii
White sucker	*Catostomus commersonii*	Catostomidae	Cypriniformes	Actinopterygii
Black redhorse	*Moxostoma duquesnii*	Catostomidae	Cypriniformes	Actinopterygii
Torrent sucker	*Thoburnia rhothoeca*	Catostomidae	Cypriniformes	Actinopterygii
Shoal chub	*Macrhybopsis hyostoma*	Cyprinidae	Cypriniformes	Actinopterygii
Blue Ridge sculpin	*Cottus caeruleomentum*	Cottidae	Scorpaeniformes	Actinopterygii
Bayou topminnow	*Fundulus notti*	Fundulidae	Cyprinodontiformes	Actinopterygii
Sauger	*Sander canadensis*	Percidae	Perciformes	Actinopterygii
Walleye	*Sander vitreus*	Percidae	Perciformes	Actinopterygii
Bigmouth shiner	*Hybopsis dorsalis*	Cyprinidae	Cypriniformes	Actinopterygii
Carmine shiner	*Notropis percobromus*	Cyprinidae	Cypriniformes	Actinopterygii
Western blacknose dace	*rhinichthys obtusus*	Cyprinidae	Cypriniformes	Actinopterygii

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CHAPTER FOUR

CONCLUSIONS: REGIONAL INFLUENCES ON FISH ASSEMBLAGES – SUMMARY OF FINDINGS AND IMPLICATIONS FOR MANAGEMENT

In the concluding chapter, I provide a brief overview of the principle findings of my dissertation, Further I will highlight some implications for management opportunities that presented themselves through results and research findings of these studies.

Principle Findings

Chapter one: multiple facets of a streams thermal regime: effects of stream temperature on Michigan's fluvial fish assemblages.—In this study, we summarized stream water temperature data collected from 233 stream reaches located throughout three ecoregions within the state of Michigan into multiple thermal metrics and identified major patterns in thermal regimes of streams representative of temperature magnitudes, variability of ranges in temperatures, and the timing of both summer maximums in temperature and variability of temperatures. We then showed how various thermal metrics were influential to species of fishes common to the state of Michigan. Thermal preferences of fishes were shown to vary across ecoregions, but dominant temperature metrics influencing fishes in Michigan were those describing maximums in stream summer temperatures and variability in stream summer temperature. This chapter provides additional insight into which fluvial fish species in Michigan are being affected by different thermal characteristic and highlights some of the regional variability in influences across the state.

Results from this chapter also showed that abundances of some fish species in Michigan are being indirectly influenced by landscape-level factors through their mediating effects on stream temperature. This highlights that specific facets of stream temperature (including summer thermal maximums and variability in summer stream temperatures) may be vulnerable to different changes in landscapes drained by Michigan streams. Maximum summer stream temperatures are potentially most heavily influenced by changes in land cover (e.g. % forest land cover), while the variability in summer stream temperatures may be most vulnerable to climate change (e.g. mean July air temperature, Table 1.9) across Michigan streams. This adds critical new insight into the mediating effects that landscape-scale influences like forest land cover and watershed July air temperature may have on controlling abundances and distribution of stream fishes in Michigan, and points to two different sources of environmental risk (i.e., land use change and climate change) that may be future sources influencing changes if fish assemblages in Michigan streams.

Chapter two: landscape effects on fluvial fish assemblage structure: regional responses to human land uses.—In this study, we evaluated influences of human land uses on stream fish assemblages from more than 10,500 locations across five large regions of the eastern United States. Natural landscape factors (i.e., catchment area, percent catchment fine lithology, mean local elevation, catchment base-flow index, local mean annual air temperature, and catchment mean annual precipitation) and human land uses (i.e., percent urban and agricultural in the catchment and density of dams in the catchment) were identified as describing major patterns of variation in landscape factors of the study regions. Fish assemblages were summarized by metrics including species richness; percent intolerant and game individuals; and percent individuals that are invertivores, omnivores, lithophiles, and rheophiles (Lyons 1992; Barbour et al. 1999; Frimpong and Angermeier 2009). These metrics have been used in many investigations for assessing stream integrity, and they describe variability in assemblages across the study regions. After controlling for dominant natural landscape factors, we identified that dominant human land uses (i.e., percent urban and agricultural in the catchment and density of dams in the catchment) were associated with change in fish assemblage metrics occurring across study sites, and that these influences varied by study regions.

Results highlighted that there are regional differences in dominant human land uses influencing changes in fish assemblage metrics and that levels of catchment urban and agriculture land use affecting stream fishes varied by study regions. Findings from this study add new depth to our understanding of regional influences on streams fishes and highlights that location can play a big part in dictating which and at what levels human stressors are influencing stream fish assemblages.

Chapter three: regional trends of biodiversity indices: natural landscape and human land use controls on stream fish assemblages.—In this chapter, characterized trends in stream fish assemblages from more than 10,500 locations across five ecoregions in the eastern portion of the United States using biodiversity indices including species richness, Shannon’s diversity, Pielou’s evenness, taxonomic diversity, and taxonomic distinctness (Shannon 1948; Pielou 1975; Clarke and Warwick 1998; Clarke and Warwick 2001). General patterns in correlations among individual indices were variable, but relationships among indices were similar across ecoregions. For example, species richness and Shannon’s diversity were always highly correlated in each of the five study ecoregions, yet taxonomic distinctiveness was never highly correlated with these factors, emphasizing the independence of distinctness from richness and Shannon’s diversity. Results of multiple linear regression models suggest differences in landscape influences on groups of metrics. Natural landscape factors including stream size and elevation were important and consistent predictors of biodiversity indices, while climatological factors and factors indicating groundwater delivery to streams had more variable influences. Percent of agriculture and urban lands in catchments were important predictors of biodiversity across all regions. Catchment agriculture had a fairly consistent response on richness and diversity, while catchment urban land use most consistently predicted taxonomic distinctness, yet that response varied by region. High amounts of catchment urban land use could negatively affect taxonomic distinctness causing shifting fish assemblage composition from endemic faunas to more tolerant fish fauna promoting fish assemblages with more regional similarity (McKinney and Lockwood 1999; Rahel 2000). Together, these results suggest that multiple measures of fish biodiversity should be used to characterize response of stream fish assemblages to landscape influences, not only because they capture unique attributes of the fish assemblage, but also because indices are being influenced by land uses differently.

Management Implication

Chapter one: management implications.— Our results emphasized that thermal maximums in the summer months are important to fish assemblage structure, but the variability in monthly and daily range in stream temperatures also influences fish assemblage structure in Michigan. These results have important implications for thermal habitat availability and their suitability for specific game fish species and species of greatest conservation need (SGCN). Under predicted land use change and climate changes, there may be substantial effects on prey fish availability for game species and SGCN species related to stream temperature changes in Michigan. Environmental changes may also cause changes in interactions among competing species or in predator–prey relationships due in part to changes in the thermal regime in Michigan streams (Taniguchi and Nakano 2000).

While this study was conducted with comprehensive datasets of community fish assemblages with corresponding stream temperature data from throughout Michigan, the seasonality of our dataset was not complete enough to fully explore all of the seasonal effects that streams thermal regimes may also have in structuring fish assemblages. Other seasons are known to be energy expensive times for fishes, including spring and fall due to spawning and/or migration as well as winter, during which fish may be limited by cold temperatures and/or feeding opportunities (Carter 2005). Understanding the full annual variability in a stream's thermal regime is vital for developing management strategies that maximize the suitability of conditions for stream fishes of interest. This requires additional research and underscores the importance of sampling programs that capture stream thermal characteristics throughout the year. Also, to the degree that our results showed the importance of multiple unique characteristics of thermal regimes in Michigan, management efforts targeting the collection of continuous temperature data (vs., for example, maximum and minimum temperatures only) would be beneficial for understanding the complex set of responses of stream fishes to thermal regimes, including fish response to variability, timing, and frequency of key thermal events. Together, such information would ensure better understanding or relationships between stream fishes and thermal regimes of streams, and would encourage development of more effective management strategies in the face of current and future changes to stream temperatures.

Chapter two: management implications.— Our results and the approaches taken can be used to assess regional influences of human land uses that are affecting changes in fish assemblages and can provide insights into what levels of human land use by regions will be expected to cause change in assemblages. This study underscored regional differences in dominant human land uses like catchment urban and agriculture and density of dams in the catchment and quantified that different levels of human land uses like percent of urban and agriculture in the catchment are effecting change in fish assemblage metrics, but that these levels can be regionally specific. If dominant human land uses and their levels of influence on critical management factors have regionally-specific influences, these influences should be accounted for and incorporated into the planning process to develop realistic management priorities. Studies characterizing critical human pressures in one ecoregion may not be directly applicable to a different ecoregion because of these differences. Well-designed regionalized studies could help further characterize regional differences in human land uses effects on stream biota, elucidate important mechanisms of influence on stream systems, and have transferable results or components to help meet management priorities across large spatial extents.

Results elucidate that interregional comparison into mechanisms controlling regional fish assemblage response to human land uses may be a fruitful area of additional investigation. Some of the potential regional differences causing different fish assemblage response may relate to the buffering capacity of lithology and/or topographic landscape factors as well as natural land covers in a region. The types and proportions of natural versus human land cover and their spatial arrangement in the catchment have been shown to affect the delivery of runoff and other materials to stream systems (Zimmerman et al. 2003; Blann et al. 2009; Carpenter et al. 2011). Intensity of urban classes, specific agricultural practices, and riparian buffers to streams are a few examples of factors that may influence runoff and the delivery of materials to riverine ecosystems (Blann et al. 2009; Carpenter et al. 2011), and such factors can cause heterogeneous responses in stream biota across regions (Meador and Goldstein 2003; Morgan and Cushman

2005; Utz et al. 2010). Specific methods from in this study can be used to assess regional dominance of classes of human land use types and at what levels these of human land uses might be expected to cause changes in fish assemblages.

Chapter three: management implications.—This study showed that, across large regions, biodiversity indices for stream fish assemblages are strongly influenced by both natural landscape factors. Catchment area was a strong predictor of all biodiversity indices across study regions, and should be controlled for when utilizing biodiversity indices as response metrics in assessments of stream integrity. Taxonomic distinctiveness, found to represent a unique attribute of stream fish assemblages compared to diversity and richness, was also predicted by local elevation, which should similarly be accounted for when using this index for assessment.

This study also showed the importance of human land uses in predicting indices, underscoring their value in identifying broad changes in stream fish assemblages resulting from anthropogenic stressors. Taxonomic distinctness was consistently predicted by catchment urban land use, while catchment agriculture was a better predictor of species richness and Shannon’s diversity across ecoregions. These findings reflect how unique attributes of fish assemblages are influenced by human land uses differently, and that those changes are likely due in part to shifting species membership, and not always loss of species or individuals (Scott and Helfman 2001; Scott 2006). Based on our results, we recommend using multiple biodiversity measures to capture unique attributes of stream fish assemblages when testing for effects of human stressors. This has important implications for development of multimetic indices of biotic integrity to assess streams, and it highlights the importance of identifying species-specific targets when implementing actions to conserve or protect biodiversity in stream systems.

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