Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Modeling and mapping fish abundance across wadeable streams of Illinois, USA based on landscape-level environmental variables

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0343.R2
Manuscript Type:	Article
Date Submitted by the Author:	19-Nov-2015
Complete List of Authors:	Cao, Yong; Illinois Natural History Survey Hinz, Leon; University of Illinois, Illinois Natural History Survey Metzke, Brian; University of Illinois, Illinois Natural History Survey Stein, Jeffrey; University of Illinois, Illinois Natural History Survey Holtrop, Ann; IL Department of Natural Resources,
Keyword:	MODELS < General, STREAMS < Environment/Habitat, ABUNDANCE < General, FRESHWATER FISHES < General, HABITAT < General

SCHOLARONE™
Manuscripts

Modeling and mapping fish abundance across Wadeable streams of Illinois, USA based on landscape-level environmental variables

Yong Cao^{1*}, Leon Hinz¹, Brian Metzke¹, Jeffrey Stein¹, Ann Holtrop²

¹ Illinois Natural History Survey, Prairie Research Institute, University of Illinois

² Illinois Department of Natural Resources

Draft

* correspondence author, email: yongcao@illinois.edu; phone: 217 244 6847.

Abstract: To effectively conserve and restore stream ecosystems, we need to better understand the distribution and abundance of individual fish species in relation to natural environments and anthropological stressors. In this study, we modeled the abundance of 97 fish species in small wadeable streams of Illinois, USA, based on random-forests regression and landscape-level environmental variables. Model R^2 -values for intermediately-common species were higher than for common species, but highly variable among rare ones. Models for 50 species reached R^2 of 0.2 – 0.70 and were tested with a separate set of samples and applied to unsampled wadeable reaches to show the population hotspots of each species across the state. Furthermore, we evaluated the importance of individual environmental variables to a given fish species as well as the directional responses of each species to top 10 key predictors. Climate and land-use were the best predictors for most species, followed by topography, geology, and soil permeability. Spatial connection of a stream also was associated with a large number of species. These findings improved our understanding of the relationships between fish species and landscape environments. The distribution maps could guide resource management, restoration, and monitoring of stream fish assemblages.

Key words: species abundance model, freshwater biodiversity, random forests, fish-environment relationship, prairie streams.

Introduction

How individual species and species diversity are distributed across space in relation to both natural and anthropological factors has been a central question in ecology for a long time (Forbes 1908; Andrewartha and Birch 1954; Royle et al. 2007). This knowledge is of great importance for addressing a wide range of basic and applied issues, particularly for effective biodiversity conservation and environmental management (Oberdorff et al. 2001; Royle et al. 2007). Species modeling is the main avenue to quantify the relationships between species and their environments based on limited sampling data, and to predict the presence or abundance of species at unsampled locations, or to predict potential changes in the future (Peterson et al. 2011). In the past decade, a great deal of research effort has been directed toward species modeling (Elith and Leatherwick 2009; Peterson et al. 2011), but mainly in terrestrial ecosystems (Soininen and Luoto 2014).

In freshwater ecosystems, fish species modeling (Oberdorff et al. 2001; Oakes et al. 2005; Steen et al. 2008; Lyons et al. 2010) has led to better understanding of fish-environment relationships and provided valuable information for effective resource management (Wenger et al. 2008; Esselman and Allan 2010). Based on our review of 70 peer-reviewed publications on stream/lake fish species modeling found for 2000-15 via Web of Science and Google Scholar (Appendix 1), we identified a number of trends and knowledge gaps. First, most studies (81%) modeled the presence-absence of species. The occurrence probability of a species at a location provides a basic description of the potential species range and potential shifts under changing climate and landuse (Wenger and Freeman 2008; Lyons et al. 2010). However, this information may not be adequate for many other purposes, such as the management of sportfish or common fish species, identification of most viable populations, or the estimation of ecosystem functions. Information on species abundance is required for these needs, yet species abundance was modeled in only approximately 20% of the studies, and was often restricted to one or a few species, such as salmon and trout (Wenger and Freeman 2008; McKenna and Johnson 2011). Modeling of common and non-sport species has been rare, in spite of their critical roles in ecosystem processes (e.g., productivity and nutrient cycles), and sometime high sensitivity to landuse changes (Utz 2014). A second trend is that about half of fish species models examined were at least partly based on local habitat variables, such as substrate type and water depth. Those models can offer insights into how local habitats affect fish species, but such models are difficult to apply to the great number of unsampled locations (i.e., no habitat data available), an issue that constrains the utilities of the models. For example, we would need species distributions across the whole study region to prioritize streams for conservation and restoration (Merovich et al. 2013; Stoll et al. 2013, 2014). A last trend is that most

studies were restricted to a single river basin or a region defined for the specific purpose of a project. However, many conservation, restoration, and environmental programs are established and managed by a jurisdictional entity, such as a state in the US. For many of these programs there is a clear benefit to use the boundaries of a state or province as the spatial extent in modeling.

In the present study, we attempted to fill some of the knowledge gaps by developing and applying abundance models for a large number of fish species, including most common ones in wadeable streams in Illinois, USA. Based on a wide range of landscape-level variables summarized at stream reach level and a robust machine learning approach, the models provide valuable information on species distribution at a relevant spatial scale in resource management. We further asked three specific questions: 1) how stream fish species are generally associated with natural environmental environments (climate, geology, watershed topography, etc.) versus human alternations in land use and spatial connections in a agriculturally-dominated region, 2) what environmental variables were most strongly associated with each individual fish species modeled, and how, and 3) how the strength of fish–environment associations, as measured with model R^2 -value, varied with species rarity, and why. The answers to these questions will improve our understanding of fish –environment relationships and help us to assess the future impacts of broad-scale human disturbances (e.g., urbanization and climate changes) on stream ecosystems.

Data and Methods

Fish Sampling Data

Illinois Department of Natural Resources (IL-DNR) and Environmental Protection Agency (IL-EPA) jointly initialed a statewide stream monitoring program (the Intensive Basin Survey) for the state (149,998 km²) in 1981. Thirty-six major river basins were established as a framework of survey design for the state monitoring programs of fish, aquatic macroinvertebrates, stream habitat, and basic water quality. State and local fisheries biologists selected sampling sites to be representative of each basin in terms of stream size, type, known diversity hotspots, point sources of pollution, and to include sites that were sampled in the past (IL-EPA 1996).

At each sampling site in a wadeable stream, a stream segment of 20 channel-widths (no less than 100m and no more than 300m) was selected for sampling with one-pass electro-seining (9.14m), a highly effective method developed and used in Illinois since the 1960s (Bayley et al. 1989), or backpack electrofisher in small streams (IL-DNR 2010). For streams wider than approximately 9m, one pass for each half was carried out. On average, this sampling effort captures >70% of all species in a sampled

reach (Holtrop et al. 2010). To better characterize the current state of fish populations and diversity, we only included those samples collected between 1995 and 2010. Streams of Midwest US, including Illinois, are generally productive and specious (Smith et al. 2010), 10-30 fish species per site (Moyle and Herbold 1987). All samples containing fewer than 20 fish individuals and fewer than five species were thus likely resulted from unsuccessful field operation and removed. Because electric seine could not cover the whole channel in a wide stream, we further excluded those sites where wet-channel width greater was than 18m. As a result samples of 701 wadeable small stream sites were retained (Fig. 1). The width of wet channel at the sites ranged from 0.76 to 18m (average 8m, standard deviation or SD = 3.1m), and the sampling areas from 64 to 5523m²(average 1112m², SD = 1450m²) These sites were not randomly selected, however they are well spread across the state, presumably represent all major basins and capture key environmental gradients in the study region. When multiple yearly samples were collected from a site, we averaged the abundance of each species and standardized it as the number of individual per 1000m². Understanding that catchability of individuals in any species is rarely, if ever, perfect in field sampling, we took the standardized abundance as an index of the true abundance.

A second dataset was derived from a separate project in Kaskaskia River Basin, IL, a major tributary of Mississippi River (Fig. 1). Samples were collected from 109 reaches (0.75 – 10m wide) using the same field protocol during the summers of 2013-15. Based on the same sample selection criteria described above, samples from 104 reaches were retained for model validation.

Spatial Framework and GIS-based environmental data

Our species modeling was based on a spatial framework and the associated environmental database developed by the Great Lakes Regional Aquatic Gap Analysis Project (Brenden et al. 2006; Steen et al. 2008; McKenna et al. 2013; Cao et al. 2015). The basic spatial unit of a stream network is a reach, defined as a stream section from the confluence of an upper-stream tributary to the confluence of a down-stream tributary (based on a 1:100,000 map of US National Hydrology Dataset). Environmental variables on climate, geology, and others were summarized at four spatial levels: 1) the total watershed (WT), the drainage above the downstream confluence of the reach; 2) the local watershed (W), the area that directly drains into a reach; 3) the 30-m riparian zone in the total watershed (RT); and 4) the 30-m riparian zone in the local watershed (R).

More than 300 environmental variables originally compiled at the four spatial scales include detailed geological and land-use categories (e.g., different types of urban lands and moraines) for multiple states in the Great Lakes region of the US. The data sources, spatial resolutions and time periods used varied

with types of variables and were detailed in Brenden et al. (2006). Steen et al. (2008) and Seelbach et al. (2010) combined similar categories (e.g., different types of urban lands) into a major group (e.g., urban land). We adopted their grouping in this study to reduce the number of predictor variables, assuming that the majority of information was retained by the major groups. We further removed those variables that have few non-zero values in Illinois (e.g., certain types of geology), and ended with 110 variables. Strong correlations, negative or positive, mean data redundancy for modeling. The absolute value of Pearson r ($|r|$) was greater than 0.8 for 90 pairs of variables. To reduce variable co-linearity, we conducted cluster analysis based on $|r|$ and unweighted-group-mean algorithm. Twenty-one highly-compacted groups were identified (2-9 per group, within-group $|r| \geq 0.9$) (Supplementary 1). While keeping all other variables, we chose the variable that seemed most biologically meaningful from each group (e.g., growing-degree-days in a temperature-related group), or selected one at random if no such a judgment could be made. As a result, 65 variables were retained with average $|r|$ of 0.13 and $|r|$ slightly great than 0.8 only in 7 pairs (2145 pairs in total). We kept the 7 pairs because they did not appear environmentally redundant (e.g., slope and forest land) and the modeling method we used for this study is much more resistant to co-linearity than parametric regression methods. These variables were classified into seven categories: stream size, climate, connection, geology, landuse, soil, and topography (Appendix 2). All these types of environmental variables were shown to be important at least for some species (e.g., Wang et al. 2000; Alan 2004; Smith et al. 2010; Stoll et al. 2014).

Model calibrations

Abundance of a species is often associated with high sampling variability and this variability increases with the mean (Gaston and McArdle 1994). To reduce the effects of sampling variability, we transformed the raw data with $\log(x+1)$ for all species. We examined the number of sites where a species was recorded, and excluded species occurring at ≤ 10 sites for modeling.

Random forest regression (RF) (Breiman 2001) is advantageous over many conventional regression methods when used to model the complex responses (linear, non-linear, or threshold) of species to a large number of inter-correlated and potentially interacting environmental variables (Cutler et al. 2007). This method also appears robust to overfitting (Breiman 2001) and the effects of autocorrelation (Karpievitch et al. 2009; Stuart-Smith et al. 2013), a major concern in modeling (Dormann et al. 2007). A test on one basin (Upper Illinois River) showed the waterway distance for 99.3% of site pairs ≥ 10 km, a likely upper limit of dispersals by most stream fish species (Stoll et al. 2013; Radinger and Wolter 2014). Therefore, spatial autocorrelation in our dataset should be weak if present.

RF is a bootstrapping version of classification tree. A tree model recursively splits a group of samples based on a selected predictor to minimize the variance (Breiman 1984). In RF modeling, one randomly draws a small number (i.e., `mtry` in R-package `randomForest`) of predictors to build a tree using 2/3 of the sample and then applies the tree to predict the other 1/3 (out-of-bag sample). One can repeat this process many times (5000 in our case) and average the predictions from each tree model. We built a series of RF models by progressively increasing the number of predictors used for splitting a sample group until the pseudo- R^2 stabilized. The number of variables needed for a stable R^2 is often far smaller than 1/3 of number of predictors, a factor that can further reduce potential overfitting.

RF uses a unique way to assess the importance of a given predictor. After the order of a predictor in the out-of-bag samples is randomized, the original site-environment matches no longer exist. If the predictor is important, mean standard error (MSE) of the predictions will then increase substantially, and *vice versa*. Many predictor variables may be important in a model, but the top 10 predictors are typically presented and analyzed (Kuhn and Johnson 2013; Cao et al. 2015). The overall importance of a given variable was measured as the number of models that ranked it within the top 10 predictors, and the average and maximum % increase of MSE across all models. To evaluate the relative importance of different variables for a given species, we counted the number of variables in a category (e.g., climate) that were ranked in the top 10 predictors and identified the highest rank. The response of species abundance to a given predictor was examined with a partial-dependence plot, which averages out the effects of other predictors. The directions of responses were classified into three types, positive, negative, and multimodal. For the top 10 predictors we counted the number of species whose responses to a given variable fell into each of these three categories. We measured how well a model performed with R^2 -value and related the performance to the number of sites where a species was recorded (prevalence).

It is important to assess the uncertainty of predictions by a model (Beale and Lennon 2012). A number of factors may contribute to the uncertainty, including replicate variability, seasonal/inter-annual variation, estimation errors in environmental variables, and modeling errors. In this study, we were only able to evaluate the last one, i.e., modeling error. For conventional methods, one can estimate the confidence limits of each model parameter and the 95% confidence limits of predictions. However, RF regression is non-parametric and the uncertainty cannot be assessed in the same way. We created 10 replicate models for six selected species that differed in model performance (Table 1), by using different random seeds (i.e., different sets of random tree models). We then calculated the

coefficient of variation (CV) for the 10 predictions of each species in each reach and correlated it with latitude and longitude of a reach, with which climate and many other variables co-vary.

Model validation and application

Although RF modeling always uses out-of-bag samples to calculate R^2 (internal validation), an external validation was also conducted. We calculated the Pearson correlations between the observed values at 108 validation reaches and their predictions by individual species models. These comparisons included only those species that were modeled with $R^2 \geq 0.20$, and recorded at ≥ 5 validation reaches. We assessed model performance using Spearman rank correlations between the predictions and observations (Pineda and Lobo 2009). A strong correlation would be sufficient to identify similar sets of reaches as population hotspots of a given species in a region and put a given stream in a similar rank for conservation.

We took two step to identify small Wadeable streams to which our models can be applied. First, we used the maximum watershed size and the highest number of the 1st–order stream reaches (links) in the total watershed among 701 sampling sites to identify stream reaches across the state as high-likely Wadeable. Second, we built a random-forests classification model based on the same set of environmental variables used for species modeling to predict whether a stream was $\leq 18\text{m}$ wide. The model reached an error rate of 5% and identified 46443 Wadeable reaches that were likely $\leq 18\text{m}$ wide. The models that explain meaningful amounts of variance ($R^2 > 0.2$ in our case) were applied to all unsampled small Wadeable stream reaches. The predictions were then transformed back to abundance per 1000m² stream wet channel.

Species-specific abundance classes, four for abundant species and three for less abundant ones, were established for mapping to best show the spatial variation of abundance, which are associated with potentially high prediction errors. To illustrate the detailed spatial patterns of species abundance predicted, we also mapped the local watershed of a reach (as defined earlier), rather than the reach *per se* (also see Cao et al. 2015), recognizing the local watershed size is not always proportional to the length of a reach.

Results

We recorded 130 species at the 701 small Wadeable sites with 97 recorded at >10 sites (Table 1). Across the state, bluntnose minnow and green sunfish (see Table 1 for species scientific names) are most common, occurring at $\geq 89\%$ of sites, followed by bluegill and white sucker, at $>77\%$ sites. Central

stoneroller, bluntnose minnow, and sand shiner are most abundant (on average 50-87 individuals per 1000m²). More widely distributed species tended to be more locally abundant ($r = 0.68$, $p < 0.01$), however, some species occur widely in relatively low numbers, such as yellow bullhead, largemouth bass, and blackside darter. The number of species captured in a reach varied greatly (5-40), 18.7 on average (SD = 5.6), indicating substantial variation in across streams.

We built RF abundance models for 97 species recorded at ≥ 10 sites based on 2-8 environmental variables (median = 4) for a split. R^2 -value for the model varied substantially among species ($0.0 \leq R^2 \leq 0.70$), and was strongly and nonlinearly related to species prevalence (Fig. 2). R^2 for species of intermediate prevalence were generally high, but low for common species. The performance of models for rare species was highly variable. Fifty species models achieved R^2 -values ≥ 0.20 , a minimum performance with which we considered a model to be useful in this study.

We applied the RF models of the 50 species to all wadeable stream reaches across the state. After the predicted abundance was transformed back to the number of individuals in a standard sample, we then mapped estimates of abundance of each species in the state (see Figs. 3 and Supplementary Data 2 for 10 more examples). The population hotspots of most species were evident, such as the Kankakee River in the northeastern of the state for smallmouth bass (dark green areas in Fig. 3b), and Central-eastern Illinois for greenside darter (Supplementary Data 2).

The CV of abundance predictions across 10 replicate models for the six example species were all low, 0.04-0.05 on average with CV < 0.1 at $\geq 99\%$ of the reaches, indicating low modeling uncertainty in general. The correlations between CV and latitude or longitude were all weak in the six species ($-0.22 \leq r \leq 0.33$, $-0.11 \leq r \leq 0.11$, respectively), indicating no clear spatial trends in modeling uncertainty. In model validation, out of 50 species recorded from the 103 validation reaches in Kaskaskia River Basin, 27 recorded at ≥ 2 reaches were tested. The Spearman rank correlation between the predicted and observed abundance varied substantially among the species ($0.0 \leq r \leq 0.57$, on average 0.37) (Table 2), indicating somewhat high prediction errors.

The overall importance of individual environmental variables for fish species abundance were first assessed based on variable ranks for % MSE Increase and the average (Supplementary data 3). Three climate variables at the total-watershed level, growing-degree-days (WT_GDD), July-minimum temperature (WT_JMin), and annual precipitation (WT_Precip) were the most important predictors, being ranked in the top 10 predictors by 46-49 species, and yielded high average % MSE Increase (23.4 – 23.8). They were followed by three of the other total-watershed variables, soil permeability (WT_Perm) and % of forest lands (WT_Perm), and % of agricultural land (WT_Agri) ranked as the top 10 predictors

by 33 and 36 species, respectively (17-18.4% MSE increase on average). Other key predictors included the total-watershed slope (WT_Slope), % of WT with bedrock depth <15m (50 feet) (WT_BR50). Noticeably, some other variables were greatly important for one or a few species in spite of their low average importance, such as channel gradient (CH_Grad), and % of bedrock of Shale at the total-watershed level (WT_Shale), for instance, six species were closely associated with high channel gradient, including central stoneroller, orangethroat darter, and fantail darter.

We then grouped the top 10 environmental predictors into 7 major categories and assessed the overall effects of each category on specific species (Table 1) based on the number of species that ranked any variables in a given category in the top 3 predictors. Multimodal species responses to an environmental variable likely resulted from its interactions with other variables, and such responses are difficult to interpret. We thus focused on clearly defined responses, i.e., positive or negative below, starting with the most important category.

1) *Climate*. RF models ranked climate in the top three predictors for 43 of 50 species and in the top 10 for 49 species (Table 1). We observed more negative responses than positive ones to temperature and precipitation (Appendix 3). For example, 26 species decreased with increasing growing-degree-days (WT_GDD) (e.g., smallmouth bass, horneyhead chub, and common shiner), but 12 increased (e.g., longear sunfish) (Fig. 4a). Similarly, 23 species negatively responded to annual precipitation in the total watershed (WT_Precip) while 19 responded positively.

2) *Land use*. Ten species ranked land use in the top three predictors, and all 50 species in the top 10, showing its broad significance (Table 1). Among 10 land-use variables, % of forest lands (WT_Forest) and % of agricultural land (WT_Agri) in the total watershed were most important. Fifteen species decreased with WT_Forest, and 11 species increased. In comparison, 25 species increased with WT_Agri, but only 5 species decreased (Fig. 4b, Appendix 3). Only five species ranked % of urban land in the total watershed (WT_Urban) in the top 10 predictors, and none in the top three. The other land uses (e.g., grassland and water) were related to fewer species negatively or positively.

3) *Stream and watershed topography*. Channel gradient (CH_Grad) and watershed slope (WT_Slope) were ranked in the top 3 predictors by 10 species, and in the top 10 by 35 species (Table 1). Slightly more species preferred high-slope than low-slope streams. For example, 13 species were positively related to WT_Slope (e.g., shorthead redhorse), but 12 negatively (e.g., striped shiner, golden shiner, and longear sunfish, see Fig. 4c, Appendix 3).

4) *Geology*. Seven and 42 species ranked geology in the top 3 and 10 predictors, respectively (Table 1). The most commonly ranked variable was % of the total watershed with bedrock depth <15m

(WT_BR50). Eight species (e.g., pirate perch) increased with WT_BR50, but 16 species decreased (e.g., northern hogsucker, redbelly darter, and striped shiner) (Fig. 4d, Appendix 3). Percent watershed with bedrock deeper than approximately 50m (100 Feet) (WT_BRG100) was also important, being positively or negatively associated with 11 and 4 species, respectively. Smaller numbers of species were associated with other types of geology.

5) *Soil permeability*. Seven species ranked this category of variables in the top 3 predictors, and 39 in the top 10 (Table 1), including 20 species positively associated and 8 species negatively with soil permeability in the total watershed (WT_Perm) (Appendix 3). As expected, those species that prefer lentic habitats, such as green sunfish and pirate perch tended to decrease with increasing soil permeability while typical lotic species, such as smallmouth bass and fantail darter tended to increase (Fig. 4e).

6). *Stream size*. Seven species ranked one or more variables of this category as a top 3 predictor, and 17 species as a top 10 (Table 1). Eleven species increased with Link (e.g., shorhead redhorse, channel catfish), and 5 three decreased, including creek chub and white sucker, typical smaller stream species in Illinois. Fourteen species ranked the total-watershed size as the top 10 predictor, half positively associated and half negatively.

7) *Spatial connection*. This group of variables seems least important, yet were ranked in the top 3 predictors by six species, and in the top 10 by 25 species (Table 1). Distance to downstream dam (Damdn_L) was most important, with which 13 species increased (e.g., northern hogsucker, shorhead redhorse, smallmouth bass), and two species decreased (e.g., spotfin shiner and blackspotted topminnow) (Fig. 4f, Appendix 3). Nine species increased with the distance to downstream ponds/impoundments, but one decreased.

In summary, climate appeared to be the most important for stream fish species in the study area, followed by land-use, stream topography, geology, and soil permeability. Spatial connection also was associated with a considerable number of species.

Discussion

Freshwater ecosystems have been deteriorating across the world and contain the greatest proportion of species classified as extinct, endangered and threatened of the major ecosystem types (Dudgeon et al. 2006; Strayer and Dudgeon 2010; Burkhead 2012). Species distribution models (SDM) as valuable tools to assist protection and restoration of fish biodiversity have attracted substantial research efforts (Peterson et al. 2011). However, fish species modeling is typically restricted to presence-absence,

small numbers of species or small spatial scales (Appendix 1), inadequate for general biodiversity conservation and management at the broad spatial scale. In the present study, we developed SDMs for the abundance of 97 species occurring in Wadeable streams of Illinois, USA, probably representing one of the largest modeling efforts for freshwater fish to date. Because all predictors were derived at the landscape level, the species models could be applied to all >46000 stream reaches in the study region for 50 species, and provide a valuable tool for management and data for future research.

Our predictions and mapping of species abundance across all small Wadeable streams in the study region can help fish management and restoration in several ways. First, resource managers can readily use the maps to identify the reaches that are likely to be highly populated by a given species. However, the observation-prediction correlation was not strong in validation (Table 2), and therefore clustered population hotspots would be more reliable than isolated ones. Among other potential applications of the maps are 1) identifying what forms of protection these areas are under (e.g., state parks, National Forests, conservation easements, and wildlife refuges) (see Lawrence et al. 2011), and 2) which species are most vulnerable to planned land-use changes (i.e., urbanization) and overall human disturbances. Based on the spatial patterns of species abundance, resource managers also may adjust their monitoring and restoration programs accordingly (Merovich et al. 2013; Stoll et al. 2014). For example, they can maximize the benefits of Conservation Reserve Program (Allen and Vandever 2012) by focusing on those streams that are in poor condition, but with good access to populated streams.

How fish species are distributed in relation to their environment has been a central theme in aquatic ecology for a long time, particularly in the State of Illinois (Forbes 1908; Larimore 1963; Smith 1979). Our modeling provided rich information on species-environment relationships at the landscape scale (Table 1), which helps data synthesis of fish-environment relationship and may lead to development of new hypotheses regarding the response of a species to a specific environmental variable. The associations of individual fish species with most natural factors, climate, channel/watershed slopes, and geology were highly variable (Table 1, Appendix 6), suggesting niche partitioning of species along these natural environmental gradients. Fish-climate relationships are particularly important and complex. More species were associated with low WT_GDD and WT_Precip than with the high, suggesting broad effects of climate changes. Any specific association, however, may suggest the response of a species to climate, or may simply be the result of co-variation (Olden et al. 2002). For example, Ozark minnow occurs in the hilly northwestern corner of the state (Driftless Area), where substrates are largely pebble/gravels, and water is relatively clear. It also widely occurs in similar habitats in the Ozark Plateau in the South and Wisconsin and Minnesota in the North. Thus, climate is unlikely to be the limiting factor. However, the

climate in the driftless area happens to be cold and dry, compared with the rest of the state. The co-variation appears to lead the RF model to ranking WT_GDD, WT_Precip, and WT_JMin high. One may avoid this type of compounding effect by developing a model for a species based on data from its whole range (or most of it), something that is particularly important to predict the impact of climate change (Barbert-Massin et al. 2010). If required data are unavailable, one at least should carefully review the ecology of a species, particularly its known range before including climate variables into a regional species model for predicting climate-change impacts. For cool-water species, such as smallmouth bass, common shiner, mottled sculpin in IL (Hinz et al. 2011), our RF models should be useful to assess potential future changes under changing climate.

Although natural environmental variables, particularly climate, remained to be best predictors of abundances in most species (Table 1, Supplementary Data 3), land-use in the total watershed, and to a lesser extent the dams/impoundments also were strongly associated with a large number of species. This result is expectable as the landscapes of Illinois have been greatly altered over past 100 years with once-dominated wet prairie and marshes replaced by farmlands and urban areas (Iverson 1988). Interestingly, many fish species tended to increase with % of agricultural land in the total watershed, but decreased with % of forest land, something that does not seem intuitive. However, in our study region, most forests are located in the southern and western parts of the state near the Mississippi and Illinois Rivers, where flows are unstable and habitats relatively poor. Furthermore, the third major land-use, urban land, is highly detrimental to aquatic ecosystems (Paul and Meyer 2001; Allan 2004). As a result, it is not surprising to see streams in agriculture-dominated landscapes supporting large fish populations in the state. Similar findings were reported for Wisconsin fishes (Wang et al. 2000) and Illinois mussel species (Cao et al. 2015). In comparison, the negative effects of impoundments and dams on abundance of most species are consistent with many previous studies (Wang et al. 2011; Nislow et al. 2011).

For either resource management or inferences of fish-environment relationships, the utilities of species models depend on model performance. R^2 -values were low for many rare species (Fig. 2). Most of those species typically occur in large rivers/streams, only sporadically in small wadeable streams (e.g., river shiner, yellow bass, and black buffalo), and a weak association with stream environment variables is thus expected. In comparison, those well-fitted rare species often occur in wadeable streams of restricted areas (e.g., Ozark minnow, bigeye shiner, and common shiner). Therefore, rarity *per se* does not appear necessarily related to model performance. Extremely common species also had poor fits in this study (Fig 2), probably because some important local habitat variables or biological processes (e.g., food supplies and predations) were missed from our modeling. This non-linear relationship between

rarity and model performance contrasts with their positive and consistent relationships in previous studies (McPherson and Jetz 2007; Newbold et al. 2009; Franklin et al. 2009).

Prediction uncertainty, an important issue in species modeling, can be affected by multiple sources (Beale and Lennon 2012). The uncertainty associated with modeling *per se* in the present study appeared to be minor ($CV < 0.1$). However, the overall prediction accuracy was not high in the validation (i.e., low correlation r , Table 2). One possible explanation is that all the validation sites used were in a single river basin, but the models were built to achieve a state-wide statistical optimum. A more probable explanation is that our modeling did not consider replicate variability and seasonal and inter-annual variation, all of which can be substantial (Grossman et al. 1990; Peterson and Rabeni 1995). Incorporating local habitat variables and weather conditions in the sampling year into modeling could improve model accuracy, but constrain model applicability.

To ensure the applicability of models to unsampled streams reaches, we also had to exclude several other environmental factors which are known to be important to fish abundance, a step that may contributed to the low R^2 for many species models. Among these factors are water quality and flow stability and discharge (Allen 2004; Blann et al. 2009). Although we included a range of landscape variables that are normally used to predict these factors (Richards et al. 1996; Tong and Chen 2002; Frederico et al. 2014), their direct modeling and prediction at the reach level could significantly improve fish model performance. Biological processes, such as competition and predation can also play a significant role in explaining species abundance and distribution (Godsoe and Harmon 2012; Trainor and Schmitz 2014), but were not included in our models, either, because these types of data are rarely available from field surveys and not available at unsampled sites. Imperfect and variable catchability of fish individuals likely further affected the R^2 values. Fish catchability often varies with habitat characteristics (Bayley and Austen 2002; Price and Peterson 2010). Individual catchability can be incorporated into species-abundance modeling, but such studies are normally focused on a single species (e.g., Wenger and Freeman 2008). It is a challenge to incorporate the catchability for a large number of species in a region as this requires collecting multiple spatial or temporal replicates and detailed habitat information at large numbers of sites (Johnson 2008; Bank-Leite et al. 2015). The statistical adjustments for catchability, however, may be not always effective (Welsh et al. 2013, but see Guillera-Arroita et al. 2014).

It is even more challenging to model rare species, like those recorded at <10 sites in the present study while such models are most needed for conservation. Routine fish monitoring needs to be supplemented by additional field sampling that target specific rare species and use the most effective

collection methods for these species. Joint species distribution models that use information from co-occurrence of rare species with common ones (Harris 2015; Ovaskainen et al. 2015) may also be useful to cope with this challenge.

In sum, the performances of abundance models differed among species with intermediately-common species typically fitted best. Natural environmental variables, particularly climate, appeared to be most important for the abundance of individual species, but land use and spatial connections were also strongly related to many species. Most fish species positively responded to the increase in percent agricultural land in the watershed and the distance to dams/impoundments. There are multiple challenges in accurately predicting species abundance, modeling remained to be a powerful tool for resource management and aquatic ecology, and its utility will only improve over time as more robust algorithms and high-resolution GIS habitat data, and more fish samples become available.

Acknowledgements

Authors are grateful to Tim Lambert for help with GIS mapping, to all field crew members who have collected fish samples from IL streams, and to Bob Illyes who has managed the fish database in the decades. This research was supported mainly by INHS General Revenue Fund, and supplemented by Federal Aid in Sport Fish Restoration Project F-69-R.

References

Allan J.D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annu Rev Ecol Syst.* **35**: 257-284.

Allen, A.W., and Vandever, M.W. 2012. Conservation Reserve Program (CRP) contributions to wildlife habitat, management issues, challenges and policy choices—an annotated bibliography: U.S. Geological Survey Scientific Investigations Report 2012–5066, 185 p.

Andrewartha, H.G., and Birch, L.C. 1954. The distribution and abundance of animals. University of Chicago Press.

Banks-Leite, C., Pardini, R., Boscolo, D., Cassano, C.R., Puttker, T., Barros, C.S. and Barlow, J. 2014. Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. *J. Appl. Ecol.* **51**: 849-859.

- 431 Barbet-Massin, M., Thuiller, W., and Jiguet, F. 2010. How much do we overestimate future local
432 extinction rates when restricting the range of occurrence data in climate suitability models?
433 *Ecography*, **33**: 878-886.
- 434 Bayley, P.B., Larimore, R.W. and Dowling, D.C. 1989. Electric seine as a fish-sampling gear in streams. *T.*
435 *Am. Fish. Soc.* 118: 447–453.
- 436 Bayley, P.B., and Austen, D.J. 2002. Capture efficiency of a boat electrofisher. *T. Am. Fish. Soc.* **131**:435-
437 451.
- 438 Beale, C.M., and Lennon, J.J. 2012. Incorporating uncertainty in predictive species distribution modelling.
439 *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**: 247-258.
- 440 Blann, K.L., Anderson, J.L., Sands, G.R., and Vondracek, B. 2009. Effects of Agricultural Drainage on
441 Aquatic Ecosystems: A Review. *Crit. Rev. Env. Sci. Tec.* **39**: 909–1001.
- 442 Brenden, T.O., Wang, L., Seelbach, P.W., Clark, R. D., Wiley, M.J., and Sparks-Jackson, B.L. 2006. A
443 spatially constrained clustering program for river valley segment delineation from GIS digital river
444 networks. *Environ. Modell. Softw.* **23**: 638-649.
- 445 Breiman, L. 2001. Random forests. *Machine Learning*, **45**: 5–32.
- 446 Breiman, L., Friedman, J., Stone, C. J. and Olshen, R. A. 1984. Classification and regression trees. CRC
447 press, New York.
- 448 Burkhead, N.M. 2012. Extinction rates in North America freshwater fishes, 1900-2010. *Bioscience*, **62**:
449 798-808.
- 450 Cao, Y., Stodola, A., Douglass, S., Shasteen, D., Cummings, K., Holtrop, A.M. 2015. Modeling and
451 mapping the distribution, diversity, and abundance of freshwater mussels (Family Unionidae) in
452 wadeable streams of Illinois, USA. *Freshwater Biol.* **60**: 1379-1397.
- 453 Cutler, D.R., Edwards, T.C. Jr., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J. and Lawler, J.J. 2007. Random
454 forests for classification in ecology. *Ecology*, **88**: 2783–2792.
- 455 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz,
456 W., Kissling, W.D., Kuhn, I., Ohlemuller, R., Peres-Neto, P.R., Reieking, B., Schroder, B., Schurr, F.M.,
457 and Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species
458 distributional data: a review. *Ecography*, **30**: 609-628.
- 459 Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C. and Sullivan, C.
460 A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.*
461 **81**: 163-182.

- 462 Elith, J., and Leathwick, J. 2009. Species distribution models: ecological explanation and prediction
463 across space and time. *Annu. Rev Ecol. Syst.* **40**: 677-697.
- 464 Esselman, P.C., and Allan, J.D. 2010. Relative influences of catchment- and reach-scale abiotic factors on
465 freshwater fish communities in rivers of northeastern Mesoamerica. *Ecology of Freshwater Fish* **19**:
466 439-454.
- 467 Forbes, S. A. 1908. The fishes of Illinois. Illinois State Laboratory of Natural History.
- 468 Franklin, J., Wejnert, K.E., Hathaway, S.A., Rochester, C.J. and Fisher, R.N. 2009. Effect of species rarity
469 on the accuracy of species distribution models for reptiles and amphibians in southern California.
470 *Diversity and Distribution*, **15**: 167-177.
- 471 Frederico, R.G., De Marco, Jr. P. and Zuanon, J. 2014. Evaluating the use of macroscale variables as
472 proxies for local aquatic variables and to model stream fish distributions. *Freshwater Biol.* **59**: 2303-
473 2314.
- 474 Gaston, K. J., and McArdle, B. H. 1994. The temporal variability of animal abundances: measures,
475 methods and patterns. *Philos. T. Roy. Soc. B.* **345**: 335-358.
- 476 Godsoe, W., and Harmon, L.J. 2012. How do species interactions affect species distribution models.
477 *Ecography*, **35**: 811-820.
- 478 Grossman, G.D., Dowd, J.F., and Crawford, M. 1990. Assemblage stability in stream fishes: A review.
479 *Environmental Management*, **14**: 661-671.
- 480 Guillera-Aroita, G., Lahoz-Monfort, J.J., Mackenzie, D.I., Wintle, B.A., and McCarthy, M.A. 2014. Ignoring
481 imperfect detection in biological surveys is dangerous: a response to "Fitting and Interpreting
482 Occupancy Models". *PLos One* **9**: e99571.
- 483 Harris, D.J. 2015. Generating realistic assemblages with a Joint Species Distribution Model. *Methods in*
484 *Ecology and Evolution* (in press, DOI: 10.1111/2041-210X.12332).
- 485 Hinz Jr. L.C., Metzke, B.A. and Holtrop, A.M. 2011. *Evaluating water temperature, habitat and fish*
486 *communities in candidate coolwater streams in Illinois*. Prepared for: Illinois Department of Natural
487 Resources. State Wildlife Grant / Project Number (T-13-P-001). Illinois Natural History Survey
488 Technical Report 2011 (21), Champaign, Illinois, USA.
- 489 Holtrop, A.M., Cao, Y., and Dolan, C.R. 2010. Estimating sampling effort required for characterizing
490 species richness and site-to-site similarity in fish assemblage surveys of Wadeable Illinois streams. *T.*
491 *Am. Fish. Soc.* **139**: 1421-1435.

- IL-EPA. 1996. Quality assurance and field methods manual for IDNR Division of Fisheries: IEPA basin surveys in rivers and streams. Illinois Department of Environmental Protection, Bureau of Water, Division of Water Pollution Control. Springfield, IL.
- IL-DNR. 2010. Fisheries manual of operation: filed sampling protocols for rivers and streams. IL-DNR, Division of Fisheries/Illinois Natural History Survey, 1816 S Oak Street, Champaign, IL 61820.
- Iverson, L.R. 1989. Land use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. *Landscape Ecology* 2:45-61.
- Johnson, D.H. 2008. In defense of indices: the case of bird surveys. *J. Wildl. Manage.* **72**: 857-868.
- Karpievitch, Y.V., Hill, E.G., Leclerc, A.P., Dabney, A.R. and Almeida, J. S. 2009. An introspective comparison of random forest-based classifiers for the analysis of cluster-correlated data by way of RF++. *PLoS ONE* **4**, e7087.
- Kuhn, M., and Johnson, K. 2013. *Applied predictive models*. Springer, New York, USA.
- Larimore, R.W., and Smith, P.W. 1963. The fishes of Champaign County, Illinois as affected by 60 years of stream changes. Illinois Natural History Survey, Champaign, IL, USA.
- Lawrence, D.J., Larsen, E.R., Liermann, C.A.R., Mims, M.C., Pool, T.K., and Olden, J.D. 2011. National parks as protected areas for US freshwater fish. *Conserv. Lett.* **4**: 364-371.
- Lyons, J., Stewart, J.S., and Mitro, M. 2010. Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, USA. *J. Fish Biol.* **77**: 1867-1898.
- McKenna, J.E., and Johnson, J.H. 2011. Landscape models of Brook trout abundance and distribution in lotic habitat with field validation. *N. Am. J. Fish. Manage.* **31**: 742-756.
- McKenna J.E., Carlson, D.M., and Payne-Wynne, M. 2013. Predicting locations of rare aquatic species' habitat with a combination of species-specific and assemblage-based models. *Diversity and Distributions*, **19**: 503-517.
- McPherson, J.M., and Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30**: 135-151.
- Merovich, G.T., Petty, J.T., Strager, M.P., and Fulton, J.B. 2013. Hierarchical classification of stream condition: a house-neighborhood framework for establishing conservation priorities in complex riverscapes. *Freshwater Sci.* **32**: 874-891.
- Moyle, P.B. and Herbold, B. 1987. Life-history patterns and community structure in stream fishes of Western North America: comparisons with eastern North America and Europe. In *Community and Evolutionary Ecology of North American Stream Fishes* (W.J. Matthews and D.C. Heins, eds.), pp. 25–32. Norman, OK: University of Oklahoma Press.

- 524 Newbold, T., Reader, T., Zalat, S., Ei-Gabbas, A., and Gilbert, F. 2009. Effect of characteristics of butterfly
525 species on the accuracy of distribution models in an arid environment. *Biodivers. Conserv.* **18**:
526 3629-3641.
- 527 Nislow, K. H., Hudy, M., Letcher, B. H., and Smith, E. P. 2011. Variation in local abundance and species
528 richness of stream fishes in relation to dispersal barriers: implications for management and
529 conservation. *Freshwater Biol.* **56**: 2135-2144.
- 530 Oakes, R.M., Gido, K.B., Falke, J.A., Olden, J.D., and Brock, B.L. 2005. Modeling of stream fishes in the
531 Great Plains, USA. *Ecol. Freshwater Fish*, **14**: 361-374.
- 532 Oberdorff, T., Pont, D., Hugueny, B., and Chessel, D. 2001. A probabilistic model characterizing fish
533 assemblages of French rivers: a framework for environmental assessment. *Freshwater Biol.* **46**: 399-
534 415.
- 535 Olden, J.D., Jackson, D.A., and Peres-Neto, P.R. 2002. Predictive models of fish species distributions: A
536 note on proper validation and chance predictions. *T. Am. Fish. Soc.* **131**: 329-336.
- 537 Ovaskainen, O., Roy, D.B., Fox, R., Anderson, B.J. 2015. Uncovering hidden spatial structure in species
538 communities with spatially explicit joint species distribution models. *Methods in Ecology and*
539 *Evolution* (in press, doi: 10.1111/2041-210X.12502).
- 540 Paul, M.J., and Meyer, J.L. 2001. Streams in the urban landscape. *Annu. Rev. Ecol. Syst.*, **32**:333-65
- 541 Peterson J. T., and Rabeni, C.F. 1995. Optimizing sampling effort for sampling warm water stream fish
542 communities. *North American Journal of Fisheries Management*, **15**: 528-541.
- 543 Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., and Araújo,
544 M.B. 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton,
545 New Jersey, USA.
- 546 Pineda, E., Lobo, J.M. 2009. Assessing the accuracy of species distribution models to predict amphibian
547 species richness patterns. *Journal of Animal Ecology*, **78**: 172–180.
- 548 Price, A.L., and J. T. Peterson. 2010. Estimation and modeling of electrofishing capture efficiency for
549 fishes in wadeable warmwater Streams. *N. Am. J. Fish. Manage.* **30**:481–498.
- 550 Radinger, J. and Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries*, **15**:
551 456-473.
- 552 Richards, C., Johnson, L.B., and Host, G.E. 1996. Landscape-scale influences on stream habitats and biota.
553 *Can. J. Fish. Aquat. Sci.* **53**(suppl. 1): 295-311.
- 554 Royle, J.A., Kery, M., Goutier, R., and Smith, H. 2007. Hierarchical spatial models of abundance and
555 occurrence from imperfect survey data. *Ecol. Monogr.* **77**: 465-481.

- Seelbach, P.W., Hinz, L.C., Wiley, M.J., and Cooper, A.R. 2010. Use of multiple linear regression to estimate flow regimes for all rivers across Illinois, Michigan, and Wisconsin. Research Report 2095, Fisheries Division, Michigan Department of Natural Resources and Environment, P.O. Box 30466, Lansing, MI 48909, USA.
- Smith, P.W. 1979. The fishes of Illinois. University of Illinois Press, Urbana and Chicago, USA.
- Smith, G.R., Badgley, C., Eiting, T.P., and Larson, P.S. 2010. Species diversity gradients in relation to geological history in North American freshwater fishes. *Evol Ecol Res* **12**: 693–726.
- Soininen, J., and Luoto, M. 2014. Predictability in species distributions: a global analysis across organisms and ecosystems. *Global Ecol. Biogeogr.* **23**: 1264–1274.
- Steen, P.J., Zorn, T.G., Seelbach, P.W., and Schaeffer, J.S. 2008. Classification tree models for predicting distributions of Michigan stream fish from landscape variables. *T. Am. Fish. Soc.* **137**: 976–996.
- Stoll, S., Sundermann, A., Lorenz, A.W., Kail, J., and Haase, P. 2013. Small and impoverished regional species pools constrain colonisation of restored river reaches by fishes. *Freshwater Biol.* **58**: 664–674.
- Stoll, S., Kail, J., Lorenz, A.W., Sundermann, A., and Haase, P. 2014. The importance of the regional species pool, ecological species traits and local habitat conditions for the colonization of restored river reaches by fish. *PLOS ONE*, **9**(1), e84741.
- Strayer, D. L. and Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *J. N. Am. Ben. Soc.* **29**: 344–358.
- Stuart-Smith, R., Bates, A.E., Lefcheck, J., Duffy, E.J., Baker, S.C., Thomson, R., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoidi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G., Strain, E.M.A., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, **501**: 539–542.
- Tong, S.T.Y. and Chen, W.L. 2003. Modeling the relationship between land use and surface water quality. *J. Environ. Manage.* **66**: 377–393.
- Trainor, A.M., and Schmitz, O.J. 2014. Infusing considerations of trophic dependencies into species distribution modeling. *Ecol. Lett.* **17**: 1507–1517.
- Utz, R.M. 2014. Are we overlooking landscape-scale threats to common freshwater fishes? *Fisheries*, **39**: 294–297.
- Wang, L.Z., Lyons, J., Kanehl, P., Bannerman, R., and Emmons, E. 2000. Watershed urbanization and changes in fish communities in southern Wisconsin streams. *J. Am. Water Resour. As.* **36**: 1173–1189.

586 Wang, L.Z., Infante, D., Lyons, J., Stewart, J., and Cooper, A. 2011. Effects of dams in river networks on
587 fish assemblages in non-impoundment section of rivers in Michigan and Wisconsin, USA. *River Res.*
588 *Appl.* **27**: 473-487.

589 Welch, A.H., Lindenmayer, D.B., and Donnelly, C.F. 2013. Fitting and interpreting occupancy models.
590 *PLoS One* **8**: e52015.

591 Wenger, S.J., and Freeman, M.C. 2008. Estimating species occurrence, abundance, and detection
592 probability using zero-inflated distributions. *Ecology*, **89**: 2953-2959.

Draft

Table 1. Random-forests regression models for 97 fish species that were recorded at >10 reaches in small Wadeable streams ($\leq 18\text{m}$) in Illinois, USA, and the importance of different types of environmental variables for 50 species with $R^2 \geq 0.2$, measured with the number of variables ranking a type in the top 10 predictors and the highest rank (in parentheses) (N = number of sites where a species was recorded; mtry = the number of variables used for a split, Clim = climate, Con = connection, LU = land use, SS = stream size, Soil = soil permeability, Geo = geology, Top = topography, also see Appendix 2).

Scientific Name	Common Name	N	R^2	mtry	Clim	Con	LU	Soil	SS	Geo	Top
Amiidae (1)											
<i>Amia calva</i>	Bowfin	33	0.08	3							
Aphredoderidae (1)											
<i>Aphredoderus sayanus</i>	Pirate perch	189	0.42	4	3(1)		1(8)	2(4)		2(6)	2(9)
Atherinidae											
<i>Labidesthes sicculus</i>	Brook silverside	12	0.05	2							
Catostomidae (15)											
<i>Carpionodes carpio</i>	River carpsucker	129	0.17	3							
<i>Carpionodes cyprinus</i>	Quillback	228	0.22	4	3(1)		2(5)		2(2)	1(6)	2(4)
<i>Carpionodes velifer</i>	Highfin carpsucker	45	0.07	2							
<i>Catostomus commersonii</i>	White sucker	542	0.33	5	3(2)		3(6)		2(1)	1(9)	1(4)
<i>Erimyzon oblongus</i>	Creek chubsucker	181	0.38	5	3(1)	1(7)	1(5)	4(4)		1(10)	
<i>Hypentelium nigricans</i> *	Northern hog sucker	209	0.40	6	3(1)	1(4)	2(6)			3(3)	1(10)
<i>Ictiobus bubalus</i>	Smallmouth buffalo	52	0.02	2							
<i>Ictiobus cyprinellus</i>	Bigmouth buffalo	63	0.02	2							
<i>Ictiobus niger</i>	Black buffalo	18	0.00	2							
<i>Minytremia melanops</i>	Spotted sucker	108	0.11	3							
<i>Moxostoma anisurum</i>	Silver redhorse	85	0.14	2							
<i>Moxostoma duquesnei</i>	Black redhorse	65	0.25	4	2(1)	1(5)	3(3)	1(10)	2(7)	1(8)	
<i>Moxostoma erythrum</i>	Golden redhorse	346	0.33	5	3(1)	1(6)	2(5)	1(4)	2(7)	1(8)	
<i>Moxostoma macrolepidotum</i>	Shorthead redhorse	213	0.21	4	3(1)	1(4)	1(8)		2(5)	1(10)	2(6)
Centrarchidae (14)											
<i>Ambloplites rupestris</i>	Rock bass	126	0.37	5	3(2)	2(1)	1(8)	1(10)		2(6)	1(3)
<i>Centrarchus macropterus</i>	Flier	25	0.12	2							
<i>Lepomis cyanellus</i>	Green sunfish	626	0.25	6	3(1)	3(7)	2(6)	2(2)			
<i>Lepomis gibbosus</i>	Pumpkinseed	14	0.23	5	3(3)	3(1)	1(9)	1(2)		2(7)	
<i>Lepomis gulosus</i>	Warmouth	85	0.31	5	3(1)		2(8)	2(2)		1(5)	2(6)
<i>Lepomis humilis</i>	Orangespotted sunfish	152	0.15	5							
<i>Lepomis macrochirus</i>	Bluegill	555	0.26	4	3(1)		2(4)	2(8)		2(7)	1(5)
<i>Lepomis megalotis</i>	Longear sunfish	356	0.51	5	3(1)		2(7)	2(5)		2(9)	1(3)
<i>Lepomis microlophus</i>	Redear sunfish	73	0.05	2							
<i>Micropterus dolomieu</i>	Smallmouth bass	221	0.42	5	3(1)	3(4)	1(8)	1(9)		2(6)	
<i>Micropterus punctulatus</i>	Spotted bass	65	0.18	4							
<i>Micropterus salmoides</i>	Largemouth bass	515	0.12	5							
<i>Pomoxis annularis</i>	White crappie	80	0.10	2							
<i>Pomoxis nigromaculatus</i>	Black crappie	85	0.01	2							

Table 1 continues

Clupeidae (1)											
<i>Dorosoma cepedianum</i>	Gizzard shad	275	0.18	4							
Cottidae (1)											
<i>Cottus caroliniae</i>	Banded sculpin	27	0.23	4	3(4)		4(2)	1(10)	1(3)		1(1)
Cyprinidae (30)											
<i>Campostoma anomalum</i>	Central stoneroller	504	0.48	6	3(2)		1(6)	2(3)	1(9)	1(10)	2(1)
<i>Campostoma oligolepis</i>	Largescale stoneroller	38	0.36	6	3(2)	1(5)	2(6)	1(7)		3(1)	
<i>Carassius auratus</i>	Goldfish	16	0.08	2							
<i>Ctenopharyngodon idella</i>	Grass carp	27	0.00	2							
<i>Cyprinella lutrensis</i>	Red shiner	353	0.47	6	3(1)	1(7)	1(9)	2(4)		2(8)	1(3)
<i>Cyprinella spiloptera</i>	Spotfin shiner	214	0.38	6	3(1)	1(10)	1(9)	2(4)		3(6)	
<i>Cyprinella whipplei</i>	Steelcolor shiner	88	0.41	8	3(1)		4(3)		1(7)	2(2)	
<i>Cyprinus carpio</i>	Common carp	390	0.11	3							
<i>Hybognathus nuchalis</i>	Silvery minnow	62	0.13	3							
<i>Luxilus chrysocephalus</i>	Striped shiner	284	0.57	6	3(2)	2(1)	2(5)			2(6)	1(8)
<i>Luxilus cornutus</i> *	Common shiner	87	0.58	7	3(1)		2(4)	2(5)	1(10)	2(6)	
<i>Lythrurus fumeus</i>	Ribbon shiner	31	0.12	2							
<i>Lythrurus umbratilis</i>	Redfin shiner	414	0.28	5	3(2)		2(1)	3(4)		1(7)	1(6)
<i>Nocomis biguttatus</i> *	Hornyhead chub	326	0.57	6	3(1)	3(4)	3(6)	1(10)			
<i>Notemigonus crysoleucas</i>	Golden shiner	174	0.22	6	3(1)	1(10)	2(6)	2(4)		2(3)	
<i>Notropis atherinoides</i>	Emerald shiner	102	0.16	3							
<i>Notropis blennioides</i>	River Shiner	13	0.05	2							
<i>Notropis boops</i>	Bigeye shiner	13	0.35	4			2(2)	2(1)	3(7)	1(10)	2(3)
<i>Notropis buccatus</i>	Silverjaw minnow	132	0.43	8	3(1)		1(10)	2(3)		2(7)	2(4)
<i>Notropis dorsalis</i>	Bigmouth shiner	245	0.35	6	3(1)		2(5)	2(6)		1(8)	2(2)
<i>Notropis nubilus</i>	Ozark minnow	14	0.50	5	3(1)		3(5)	1(10)		3(2)	
<i>Notropis percobromus</i>	Carmine shiner	80	0.34	7	3(2)	1(1)	1(7)	1(9)		4(5)	
<i>Notropis stramineus</i> *	Sand shiner	441	0.40	6	3(1)	1(8)	2(3)	2(5)		1(9)	1(6)
<i>Phenacobius mirabilis</i>	Suckermouth minnow	316	0.24	6	3(4)	1(9)	2(3)		1(8)	1(10)	2(1)
<i>Phoxinus erythrogaster</i>	Southern redbelly dace	56	0.18	3							
<i>Pimephales notatus</i>	Bluntnose minnow	648	0.22	4	2(1)		1(6)	2(5)	2(3)	1(4)	2(8)
<i>Pimephales promelas</i>	Fathead minnow	126	0.11	2							
<i>Pimephales vigilax</i>	Bullhead minnow	78	0.20	7	3(3)		2(4)	2(7)	3(1)		
<i>Rhinichthys atratulus</i>	Blacknose dace	84	0.21	5	3(1)		3(7)	1(6)		1(9)	2(2)
<i>Semotilus atromaculatus</i>	Creek chub	528	0.30	6	3(3)		1(7)		4(1)		2(4)
Esocidae (2)											
<i>Esox americanus</i>	Grass pickerel	187	0.29	6	2(1)		2(3)	2(2)		1(4)	3(5)
<i>Esox Lucius</i>	Northern pike	25	0.13	3							
Fundulidae (2)											
<i>Fundulus notatus</i>	Blackstripe topminnow	393	0.31	4	3(1)		3(6)	2(4)			2(7)
<i>Fundulus olivaceus</i>	Blackspotted topminnow	105	0.70	5	3(1)	1(10)	2(3)			3(7)	1(6)

Table 1 continues

Gasterosteidae (1)										
<i>Culaea inconstans</i>	Brook stickleback	12	0.05	2						
Ictaluridae (9)										
<i>Ameiurus melas</i>	Black bullhead	112	0.13	2						
<i>Ameiurus natalis</i>	Yellow bullhead	497	0.14	5						
<i>Ictalurus punctatus</i>	Channel catfish	244	0.22	3	2(8)		2(4)		4(1)	1(6) 1(5)
<i>Noturus exilis</i>	Slender madtom	44	0.12	4						
<i>Noturus flavus</i> *	Stonecat	166	0.24	5	3(1)	1(8)	2(6)	1(9)		1(10) 2(4)
<i>Noturus gyrinus</i>	Tadpole madtom	142	0.11	2						
<i>Noturus miurus</i>	Brindled madtom	30	0.22	4	3(1)	1(8)	2(7)	1(4)		2(3) 1(6)
<i>Noturus nocturnus</i>	Freckled madtom	37	0.07	2						
<i>Pylodictis olivaris</i>	Flathead catfish	40	0.10	2						
Lepisosteidae (2)										
<i>Lepisosteus osseus</i>	Longnose gar	17	0.00	2						
<i>Lepisosteus platostomus</i>	Shortnose gar	45	0.02	2						
Moronidae (2)										
<i>Morone chrysops</i>	White bass	21	0.04	2						
<i>Morone mississippiensis</i>	Yellow bass	12	0.02	2						
Percidae (13)										
<i>Etheostoma asprigene</i>	Mud darter	32	0.00	2						
<i>Etheostoma blennioides</i>	Greenside darter	44	0.37	7	3(1)	2(2)	1(3)	1(7)		2(9) 1(5)
<i>Etheostoma caeruleum</i>	Rainbow darter	74	0.18	5						
<i>Etheostoma chlorosomum</i>	Bluntnose darter	20	0.01	2						
<i>Etheostoma flabellare</i>	Fantail darter	175	0.37	5	3(1)		1(10)	2(5)		3(6) 1(4)
<i>Etheostoma nigrum</i> *	Johnny darter	422	0.25	4	3(1)	1(6)	2(4)	2(8)		1(9) 1(7)
<i>Etheostoma spectabile</i>	Orangethroat darter	245	0.28	5	3(2)		1(8)	2(4)	1(9)	3(1)
<i>Etheostoma zonale</i>	Banded darter	97	0.37	6	2(1)	1(6)	1(9)	2(7)		3(2) 1(5)
<i>Percina caprodes</i>	Logperch	86	0.08	2						
<i>Percina maculate</i>	Blackside darter	228	0.22	5	3(4)	3(1)	1(10)	2(2)		1(9)
<i>Percina phoxocephala</i>	Slenderhead darter	109	0.18	5						
<i>Percina sciera</i>	Dusky darter	28	0.05	2						
<i>Stizostedion vitreum</i>	Walleye	20	0.04	3						
Poeciliidae (1)										
<i>Gambusia affinis</i>	Mosquitofish	171	0.21	6	3(1)		2(4)			2(6) 3(5)
Sciaenidae (1)										
<i>Aplodinotus grunniens</i>	Freshwater drum	131	0.12	3						
Umbridae (1)										
<i>Umbra limi</i>	Central mudminnow	19	0.10	2						
Number of species ranking the type of variables as top 10 or top 3 predictors (# top 10/# top 3)					49/43	25/6	50/10	39/7	17/7	42/7 35/10

* species used for assessing modeling uncertainty.

Table 2. Twenty-eight fish species recorded in ≥ 5 reaches collected from Kaskaskia River Basin, Illinois, and the Spearman correlations between their observed (Obs) and predicted abundances (log-transformed) (Pred) (N = number of samples where a species was recorded, average = number of individuals per sample, SD = standard deviation, * $p < 0.05$).

Common Name	N	Average	SD	Spearman r for Obs-Pred	Model R^2
Bigmouth shiner	35	32.8	103.8	0.41*	0.35
Blackside darter	17	0.5	2.0	0.48*	0.22
Bluegill	72	20.8	43.5	0.47*	0.26
Bluntnose minnow	86	77.4	221.1	0.51*	0.22
Blackstripe topminnow	74	30.3	148.5	0.26*	0.31
Bullhead minnow	4	0.4	2.7	0.00	0.20
Chanel catfish	4	0.5	4.1	0.57*	0.22
Central stoneroller	72	78.3	187.9	0.40*	0.48
Creek chub	92	140	317.1	0.34*	0.30
Creek chubsucker	43	10.6	39.9	0.41*	0.38
Golden redbhorse	6	0.90	5.8	0.26*	0.30
Golden shiner	16	1.0	3.8	0.00	0.22
Green sunfish	99	44.9	106.0	0.26*	0.25
Grass pickerel	16	2.3	9.8	0.63*	0.29
Hornyhead chub	13	1.6	6.7	0.56*	0.57
Johnny darter	70	24.8	46.0	0.31*	0.25
Longear sunfish	38	4.6	10.5	0.30*	0.51
Orangethroat darter	29	10.9	49.6	0.00	0.28
Quillback	5	0.4	3.3	0.43*	0.22
Pirate perch	39	21.0	60.7	0.54*	0.42
Redfin shiner	41	8.6	21.0	0.24*	0.28
Red shiner	71	67.1	220.2	0.50*	0.47
Sand shiner	56	60.6	153.8	0.36*	0.40
Silverjaw minnow	47	31.3	77.9	0.57*	0.43
Striped shiner	13	1.4	4.9	0.52*	0.57
Suckermouth minnow	38	8.8	24.7	0.39*	0.24
White sucker	55	12.4	31.1	0.23*	0.33
Max	99	164	317.1	0.57	0.57
Min	4	0.4	2.0	0.00	0.20
Average	43	26.8	71.7	0.37	0.35

Captions

Fig. 1. Locations of 701 fish sampling sites in wadeable streams of Illinois, USA with bold boundary for Kaskaskia River Basin where validation samples were collected (HUC8 = US-GS Hydrological Unit Code 8).

Fig. 2. Correlations between R^2 -values in RF regression and species prevalence (number of sites where a species was recorded) (dotted line is a polynomial fitting).

Fig. 3. Spatial pattern in the number of fish individuals for central stoneroller (left) and smallmouth bass (right) per 1000m² across wadeable streams with wet-channel width ≤ 18 m in Illinois, USA, based on random-forests model predictions (NA = not applicable water bodies, mainly lakes, large rivers, and wide streams). The local watershed (see definition in text) of a stream reach is mapped.

Fig. 4. Example partial-dependence plots of random-forests regression showing the relationships between log-transformed species abundance (y-axes) and different environmental variables (as described in Appendix 2) (x-axis with the observed range highlighted) with Panel a: WT_GDD = average growing-degree-day in the total watershed, b) Damdn_L = distance (km) from a downstream dam, c) WT_Agri = proportion of agricultural land in the total watershed, d) WT_Perm = average soil permeability in the total watershed, e) BR50 = bedrock depth ≤ 50 feet, and f) WP_Slope = average slope of the total watershed; species are labelled as follows: BLG = Bluegill, CMS = Common shiner, FAD = Fantail darter, GOS = Golden shiner, GSF = Green sunfish, HOC = Hornyhead chub, LOS = Longear sunfish, NHS = Northern hogsucker, PRP = Pirate perch, RDS = Redfin shiner, SFS = Spotfin shiner, SHR = Shorthead redhorse, SMB = Smallmouth bass, STS = Striped shiner (Y2 = the second y-axis).

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Appendix 1. Overview of 70 stream/lake fish modeling studies published in peer-reviewed journals during 2000-2015 (Den = density; DC = density class; PA = presence-absence). Web of Science and Google Scholar were used for search with the combinations of several terms as key words: freshwater, stream, river, fish, habitat/niche/distribution model, climate changes, and land use.

Authors	Journal	Year	Species	# of Sites	Study Area	Country	Type	Predictors
Porter et al.	N. Am. J. Fish Manage.	2000	13	48	Blackwater R. Basin (BC)	Canada	PA	habitats & watershed
Oberdorff et al.	Freshwater Biol.	2001	34	650	Nation-wide	France	PA	climate, habitats, watershed
Olden & Jackson	Freshwater Biol.	2002	27	286	Algonquin Park (ON)	Canada	PA	lake-local habitat
Olden et al.	T. Am. Fish. Soc.	2002	14	48	Blackwater R. Basin (BC)	Canada	PA	watershed
	T. Am. Fish. Soc.	2002	26	89	Petawawa R. Basin (ON)	Canada	PA	lake morphology;
Argent et al.	Fish Res	2003	153	NA	State-wide (PA)	USA	PA	watershed basin variables (GIS)
Dominguez et al.	Conserv Biol	2005	41	551	Central Mexico	Mexico	PA	Climate & topography (GIS)
Leathwick et al.	Freshwater Biol.	2005	15	9866^	Nation-wide	New Zealand	PA	watershed/reach GIS
McNyset	Ecol Freshw. Fish	2005	12	38-141*	State-wide (KS)	USA	PA	Landscape_GIS
Oakes et al.	Ecol Freshw. Fish	2005	38	120	Big Blue R. Basin	USA	PA	Watershed-GIS
Rashleigh et al.	N. Am. J. Fish. Manage.	2005	13	264	Mid-Atlantic Highland	USA	PA	local habitats
Chessman	Mar. Freshwater Res.	2006	54	85	New South Wales	Australia	PA	Watershed size & Altitude (GIS)
Gido et al.	AFS Symposium	2006	41	150	Lower Kansas R. Basin	USA	PA	Landscape_GIS
Ruiz & Peterson	T. Am. Fish. Soc.	2007	46	257	Flint R. Basin	USA	PA	Landscape-GIS
Buisson et al.	Ecol Freshw. Fish.	2008	28	141	Adour-Garonne Basin	France	PA	watershed & habitat
Dauwalter & Rahel	Aquatic. Conserv.	2008	1	289	Black Hill Forest	USA	PA	Landscape_GIS
Lassalle et al.	Freshwater Biol.	2008	28	136 (basins)	Europe	Europe	PA	Landscape_GIS
McCleary & Hassan	Can. J. Fish. Aquat. Sci.	2008	3	692	Rocky Mountains	Canada	PA	habitat & landuse
Sharma & Jackson	Can. J. Fish. Aquat. Sci.	2008	1	4181^	North America	North America	PA	Climate-GIS
Wenger et al.	Can. J. Fish. Aquat. Sci.	2008	5	357^	Etowah R. Basin (GA)	USA	PA	local, historic & current land use
Essekman & Allan	Freshwater Biol.	2010	63	303	Belize Coast	Belize	PA	watershed-GIS
Lyons et al.	J. Fish. Biol.	2010	50	282	State-wide (WI)	USA	PA	watershed-GIS
Grenouillet et al.	Ecography	2011	35	1110	Nation-wide	France	PA	climate, habitats, watershed
Anderson et al	T. Am. Fish. Soc	2012	1	40	Etowah R. Basin (GA)	USA	PA	local habitats & watershed
Groce et al.	T. Am. Fish. Soc	2012	1	19	Arkansas R. Basin (CO)	USA	PA	local habitats
Logez et al.	Ecol Freshw. Fish	2012	21	1548	14 countries	Europe	PA	flow , Temp & watershed size
Markovic et al.	PLOS One	2012	38		Nation-wide	Germany	PA	GIS (climate, hydrology, topography)
Michel & Knouft	PLOS One	2012	5	1	one stream (MO)	USA	PA	Habitats
Mouton et al.	Ecol Model	2012	1	1	River Grote Nete	Belgium	PA	local habitats
Richardo et al.	Freshwater Biol.	2012	4	167	Amazon R. Basin	Brazil	PA	GIS (Landscape)
Sindt et al.	N. Am. J. Fish. Manage	2012	10	86	Mississippi R. Basin (IA)	USA	PA	watershed_GIS
Zarkami et al.	Ecol Model	2012	1	75	Flanders	Belgium	PA	local habitat , WQ,
Albanese et al.	Ecol Freshw. Fish	2013	1	115	Coosawatee R. Basin (GA)	USA	PA	watershed & habitats
Black et al.	SE Naturalist	2013	1	72	Upper Cumberland R Basin	USA	PA	local habitats
Comte & Grenouillet	Diversity & Distribution	2013	35	839	Nation-wide	France	PA	climate & watershed (GIS)
Filipe et al.	Diversity Distrib	2013	1	3843	3 EU basins	Europe	PA	GIS (climate, landuse)
Hopkins & Roush	Ecol Freshw. Fish	2013	6	239^	Upper Kentucky R Basin	USA	PA	Landscape_GIS
Nowosad & Taylor	Can. J. Zool.	2013	1	60	Lower Fraser R.	Canada	PA	local habitat & fish

Appendix 1 continued

Appendix-1 continues

Authors	Journal	Year	Species	# of Sites	Study Area	Country	Type	Predictors
Ptolemy	N. Am. J. Fish. Manage	2013	2	649	BC and West-coastal US	US & Canada	PA	habitats & watershed
Wuellner et al.	J. Fish. Biol.	2013	20	120	Great Plains (MT)	USA	PA	local habitat & watershed
Dextrase et al.	Freshwater Biol.	2014	2	151	Grand & Thames R. Basin (ON)	Canada	PA	Local habitat & Watershed
Frederico et al.	Freshwater Biol.	2014	6	380	Amazon R. Basin	Brazil	PA	climate, soil, & veg. (GIS)
Grenouillet & Comte	Global Change Biology	2014	32	3549	Nation wide	France	PA	climate, habitats, watershed
Lauzeral et al.	Ecography	2014	31	1110	National- wide	France	PA	Watershed and habitat
Shea et al.	River Res. Appl.	2014	15	6	Elk R. Basin (TN,AL)	USA	PA	flow & temperature
Veza et al.	Aquat. Sci.	2014	1	95	Alps	Italy	PA	local habitats
Yoshihiro et al.	Popul Ecol.	2014	2	48	Two streams (Central Brazil)	Brazil	PA	flow
Askeyev et al.	Environ Biol Fish	2015	26	245	Nation wide	Tartarstan	PA	Local habitat, Elevation
Bouska et al.	Hydrobiologia	2015	14	12	Midwest states	USA	PA	GIS (Geo, landuse, climate)
Clavero1 & Hermoso	J. Appl. Ecol.	2015	1	5427	Nation-wide	Spain	PA	Topography, distance to sea
Comte & Grenouillet	Diversity & Distribution	2015	16	3627	Nation-wide	France	PA	Climate, topography
Guo et al.	Ecol. Model.	2015	92	135	Nation-wide lakes	China	PA	Climate, lake location, size
Kanno et al.	T. Am. Fish. Soc.	2015	1	559	State-wide (CT)	USA	PA	GIS (Geo, landuse, climate)
Kwon et al.	Ecol. Inform.	2015	22	960	Nation-wide	South Korea	PA	Climate, topography, hydrology
Huang & Frimpong	PLOS One	2015	76	1933	Four US basins	USA	PA	GIS (Geo, land use, climate)
Labay et al.	Environ Manag.	2015	100	269	Texas	USA	PA	GIS (climate, geology, topography)
Marie et al.	Aquatic Conserv.	2015	35	139	North France	France	PA	Local and GIS
Harig & Fausch	Ecol. Appl.	2002	1	27	2 streams in Colorado R. Basin	USA	DC	habitats & watershed
Bouchard & Boisclair	Can. J. Fish. Aquat. Sci.	2008	1	32	Saite-Marguerite R. (QC)	Canada	Den	local & longitudinal
Steen et al.	T. Am. Fish. Soc.	2008	93	66-1242*	State-wide (MI)	USA	PA	watershed (reach)_GIS
			46	subset	State-wide (MI)	USA	DC	watershed (reach)_GIS
Wenger & Freeman	Ecology	2008	1	215	Etowah (GA)	USA	PA & Den	local habitat
McKenna & Johnson	N. Am. J. Fish. Manage	2011	1	7800	State-wide (NY)	USA	Den	Watershed
Boone et al.	Environmetrics	2012	1	28	Albert & Mary R. Basins (QLD)	Australia	Den	local and watershed
Maloney et al.	Env. Model Assess.	2012	30	1640	State-wide (MD)	USA	PA & Den	watershed (GIS)
McMillan et al.	T. Am. Fish. Soc.	2013	1	7	Calawah R. Basin (WA)	USA	Den	local habitats
Stewart-Koster et al.	Ecography	2013	1	28	Albert & Mary R. Basins (QLD)	Australia	PA & Den	local and watershed
Anlauf-Dunn et al	Can. J. Fish. Aquat. Sci.	2014	1	651	Coastal watersheds (OR)	USA	PA & Den	habitats
Troia & Gido	Ecosphere	2014	6	221	Big Blue R. Basin (KS)	USA	Den	habitat & watershed
Cianfrani et al.	Ecol. Model.	2015	1	21	One catchment in Switzerland	Switzerland	Den	Climate, land-cover
Lamoureux & Olivier	Freshwat. Biol	2015	14	9	A catchment	Germany	Den	Hydraulic condition
Walsworth & Budy	TAFS	2015	3	22	A catchment (UT)	US	Den	Habitats, invasive species

* varying with species

^ Number of records

Appendix 2. Description of 65 variables used for random-forests regression (WT = total watershed, W = local watershed, R = riparian zone in a local watershed, RT = riparian zone in the total watershed).

Variables	Description	Variables	Description
Stream Size (5)		Landuse (12) (2002)	
Link	number of upstream 1 st -order streams	R_Water	% water in riparian zone (W)
Dlink	link of downstream reach	RT_Grass	% grassland in riparian zone (WT)
Order	stream Order (Shreve)	W_Forest	% forest (W)
Downorder	order of downstream reach	W_Agril	% agricultural land (W)
WT_Area (km ²)	size of the total watershed	W_Grass	% Grass land (W)
		W_Urban	% urban land (W)
		W_Water	% water (W)
		W_Wet	% wetland (W)
Climate (3) (1961-1990)		WT_Forest	% forest (WT)
WT_GDD	Growing-degree-days (WT)	WT_Urban	% urban land (WT)
WT_JMin (C°)	July-minimum Temp (WT)	WT_Grass	% grass land (WT)
WT_Precip (mm)	Annual precipitation (WT)	WT_Agril	% agricultural land (WT)
Geology (22)		Connections (15)	
Chan_BR50	channel bedrock depth<15m	Bigriver	0 = no direct connection to a river with the total watershed >1000 km ² ; 1 = yes
Chan_BR100	15m ≤ channel bedrock depth <30m	Damdn_L (m)	distance to the closest downstream dam
Chan_BRG100	channel bedrock depth ≥ 30m	Damdnst	1 = downstream dam; 0 = not
WT_BR50	% of WT with bedrock depth < 15m	Damup_L (m)	distance to the closest upstream dam
WT_BR100	% of WT with 15m ≤ bedrock depth ≤ 30m	Damupst	1 = upstream dam, 0 = not
WT_BRG100	% of WT with bedrock depth ≥ 30m	Missi	0 = dam/waterfall between target reach and Mississippi River; 1 = no
WT_Carb	% of WT with carbonate (bedrock)	Pond	1 = a pond within the reach; 0 = no
WT_Sand	% WT for sand (bedrock)	Pondarea (km ²)	size of within-reach pond
WT_Shale	% WT for shale (bedrock)	Ponddn_L (m)	distance to the nearest downstream pond of ≥ 0.04 km ²
WT_Rocky	% WT for bedrock-colluvium (deposit)	Ponddn_S (km ²)	size of downstream pond ≥ 0.04 km ²
WT_Alluv	% of WT for alluvium (deposit)	Ponddn_S (km ²)	size of downstream pond ≥ 0.04 km ²
WT_CMorai	% of WT for coarse moraine (deposit)	Ponddnst	1 = downstream pond ≥ 0.04, 0 = no
WT_Coars	% of WT for coarse (deposit)	Pondup_L (m)	distance to the nearest upstream pond of ≥ 0.02km ²
WT_Collu	% of WT for colluviums (deposit)	Pondup_S (acre)	size of nearest downstream pond ≥ 0.04 km ²
WT_Dune	% of WT for dune (deposit)	Pondup_S (acre)	size of nearest downstream pond ≥ 0.04 km ²
WT_Fine	% of WT for all-form-fine (deposit)	Pondupst	1 = upstream pond ≥ 0.02km ² , 0 = no
WT_Lacus	% of WT for lacustrine (deposit)	Topography (5)	
WT_Loess	% of WT for loess (deposit)	Sinuosity	(Channel length)/(downstream distance)
WT_MMora	% of WT for medium moraine (deposit)	W_Area (km ²)	Size of the local watershed
WT_OWash	% of WT for outwash (deposit)	W_Slope (%)	ArcInfo SLOPE command: arctangent(rise/run) × 57.296°
WT_PMuck	% of WT for peat-muck (deposit)	WT_Slope (%)	ArcInfo SLOPE command: arctangent(rise/run) × 57.296°
WT_ICont	% of WT for ice contact (deposit)	Chan-Grad (m)	Elevation change (m)/channel length (m)
Soil (4)			
W_Darcy	Average Darcy Number		
WT_Darcy	Average Darcy Index		
W_Perm	Average Soil permeability (W)		
WT_Perm	Average Soil Permeability (WT)		

Appendix 3. Number of species that showed different types of directional responses to 38 environmental variables ranked as the top 10 predictors at least by one species in IL Wadeable streams (see Appendix 2 for variable descriptions).

Major Categories	Variables	Positive	Negative	multimodal	Total
Climate	WT_GDD	12	26	11	49
	WT_Jmin	16	23	8	47
	WT_Precip	19	23	4	46
Stream size	Link	11	5		16
	WT_Area	7	7		14
Soil	WT_Perm	20	8	8	36
	W_Perm	11	8	6	25
	WT_Darcy	1	1		2
	W_Darcy	1			1
Topography	WT_Slope	13	12	7	32
	W_Slope	10	5	3	18
	CH_Grad	4	2		6
Landuse	WT_Forest	11	15	9	35
	WT_Agri	25	5	3	33
	RT_Grass	3	2		5
	WT_Grass	3	2		5
	R_Water	1	3		4
	W_Forest	2	1		3
	W_Wet		2		2
Geology	WT_BR50	8	16	5	29
	WT_BG100	11	4		15
	WT_Alluv	4	1	1	6
	WT_Mmora	5			5
	WT_Rocky	4			4
	WT_Collu	3			3
	WT_Fine	1	1	1	3
	WT_Shale	2	1		3
	WT_Carbon	1	1		2
	WT_Lacus	1			1
	WT_Owash			1	1
Connection	Damdn_L	13	2	2	17
	Ponddn_L	9	1		10
	Ponddn_S	9		1	10
	Dlink	2	2		4
	BigRiver	1			1
	Downorder	1			1