LOCAL, LANDSCAPE, AND RIVERSCAPE VARIABLES AS PREDICTORS OF FISH ASSEMBLAGE RICHNESS IN TRIBUTARIES TO A MAINSTEM RIVER

by

Daniel David Homans

(under the direction of Mary C. Freeman)

ABSTRACT

The goal of this study was to determine the degree to which fish species richness in a stream reach is dependent on the condition of the upland landscape versus its location along the river network. I sampled reaches on 33 tributaries to the mainstem of the Upper Coosa River basin, Georgia. Species richness at each site was estimated for all species and three different sub-assemblages based on the richness observed in spatially and temporally replicated sampling. The relative importance of major landscape-level variables, local reach-level variables, and downstream riverscape variables for predicting assemblage species richness was calculated by developing and ranking competing multiple linear regression models. Richness of all but the lotic-lentic generalist assemblage was best predicted by drainage area and conductivity. I found little evidence that downstream factors influenced local fish species richness.

INDEX WORDS: AIC, stream fish assemblages, closed capture models, river networks, species richness, adventitious streams, river continuum, urban land use.

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B.S. Allegheny College, 2002

A Thesis Submitted to the Graduate Faculty of the University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2006

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May 2006

ACKNOWLEDGEMENTS

First and foremost I would like to thank Mary Freeman for her unending support and guidance throughout the design and implementation of this project, as well as her help interpreting the results. Also thanks to Bud Freeman and David Walters for securing funding for the red shiner project from which this study arose. All research on this project would not have been possible without the field and lab help of Casey Storey, Jane Rogers, Renee Machyousky, Paula Marcinek, Judith Barkstedt, Rebecca Coleman, Megan Hagler, Greg Anderson, and the greatest unpaid intern ever, Jenny Topilow. Also thanks to Seth Wenger for getting me started with the historical photos and with moral support during the modeling process.

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CHAPTER ONE

INTRODUCTION

Measures of fish species richness are one of the cornerstones of multimetric biological monitoring indices that are frequently used to measure stream health throughout the United States (Karr and Chu 1999). Fish species richness may also be seen as an indicator of conservation concern (Griffin 2003), especially in the southeastern United States where lotic fish diversity is high and many of the species are threatened or endangered endemics (Warren et al. 2000). In addition, richness can be used as a simple measure to evaluate which biotic and abiotic factors affect aquatic communities, which is one of the major goals of lotic ecology (Power et al. 1988).

At the most general level, fish diversity is limited by the total species pool present in an area, which is largely determined by long term climatic, physiographic, and geologic factors that have shaped the evolutionary history of a region (Jackson, Peres-Neto and Olden 2001). This total richness is then filtered by a number of biotic and abiotic factors acting at different spatial and temporal scales to determine local taxa composition.

A great deal of effort has been put towards determining what local factors limit fish diversity in a particular river reach. One of the most frequently cited local drivers of fish diversity is habitat complexity, which usually correlates positively with species richness (Gorman and Karr 1978). Habitat complexity is hypothesized to gradually increase as one moves downstream along the river continuum and thus drives trends in fish communities along the same ecological gradients as those laid out in the River Continuum Concept (Vannote et al. 1980). Oftentimes in-stream geomorphic patterns (i.e. Process Domains; Montgomery 1999) can shape fish communities independently of the variation along the river continuum (Walters et al. 2003). In addition to changes in habitat diversity, local biological factors such as competition and predation may play a role in determining fish species richness, although authors have had trouble showing this phenomenon at all but the smallest of spatial scales (see review in Jackson, Peres-Neto and Olden 2001). It is important to note that species richness may not be driven by either biological interactions or diversity of habitat in streams with highly variable flow that makes periodic extirpation of species more likely (Horwitz 1978, Angermeier and Schlosser 1989).

Another potentially important driver of fish species richness is the condition of the upland landscape. Anthropogenic changes to the upland landscape (e.g. urbanization, agriculture, clear-cutting) can lead to increased sediment introduction, nutrient addition, and direct contaminant pollution (see review by Allan 2004). All of these factors have been shown to alter fish assemblages by making stream reaches uninhabitable for sensitive fish species. In addition, increased impervious areas associated with urbanization can lead to greater hydrologic instability in streams, which has been shown to directly affect fish communities through changes in in-stream habitat (Wang et al. 2000, Walters, Leigh and Bearden 2003, Roy et al. 2005), and possibly via more frequent physical extirpation of species (e.g. by scouring). Though the effects of upland landscape on stream fishes are undeniable, there is still a great deal of debate over the effects of the landscape at different spatial scales (Wang et al. 2003, Scott et al. 2002, Fitzpatrick et al. 2001, Strayer et al. 2003), as well as the potential for effects across different temporal scales (Harding et al. 1998).

Although in-stream habitat and upslope land use are expected to play large roles in defining local fish richness, they do not show the whole picture. River reaches do not exist simply as a habitat patch at the bottom of a basin; rather they are patches along a hierarchical branching river network that continues both upstream and downstream. This "riverscape" view of the stream provides a useful context for thinking about fish community ecology because fish often have different life history stages that require movement within the network (Schlosser 1991, Fausch et al. 2002). The hierarchical and branching nature of river networks is also potentially important in defining geomorphic processes that structure local stream habitats (the "Network Dynamics Hypothesis"; Benda et al. 2004). When approaching fish richness from this riverscape perspective, it is important to note that effects can be transmitted from downstream factors (Pringle 1997), such as the presence of source or sink fish populations (Pulliam 1988). These factors are particularly notable when assessing fish communities near tributary junctures with large streams (Whiteside and McNatt 1972, Gorman 1986, Osbourne and Wiley 1992, Schaffer and Kerfoot 2004, Wilkinson and Edds 2001). In these situations, diverse large river populations may act as source populations from which individuals move into the "sink" of the tributary and thus boost local richness. Similarly, mainstem rivers may provide a more proximate source of species for recolonization after catastrophic events in tributaries, thus elevating the richness of tributaries near mainstem populations over that of similar streams which are farther from source populations.

Local in-stream factors, upland landscape factors, and riverscape factors provide the complete framework for predicting the richness of different species assemblages (defined, for example, by habitat affinities or life history characteristics) in any given river reach (Figure 1). Though a great deal of research has been directed to each of these factors separately, few studies have attempted to determine the importance of all three relative to one another. The primary objective of this study was to evaluate whether the richness of species in a reach of stream is best predicted by geomorphic and habitat characteristics occurring locally, landscape factors occurring upland of the reach, or network factors influencing the reach from downstream. Because these factors may affect different aspects of the species assemblage differently (Scott and Helfman 2001, Osbourne et al. 1992, Walters et al 2003, Roy et al. 2005) it was necessary to address not just the response of total species richness, but also the richness of specific subsets of the species pool where response would be expected to vary. Unlike many other studies of fish species richness, this assessment was made while attempting to account for imperfect species detection. Secondary objectives of this study were 1) to assess the relative dependence of richness on present versus historic land use, 2) to evaluate whether fish assemblage integrity was more associated with the impervious area measured at either the upstream catchment or local spatial scale, and 3) to determine how best to replicate sampling of sites in order to estimate assemblage richness while accounting for species non-detection.

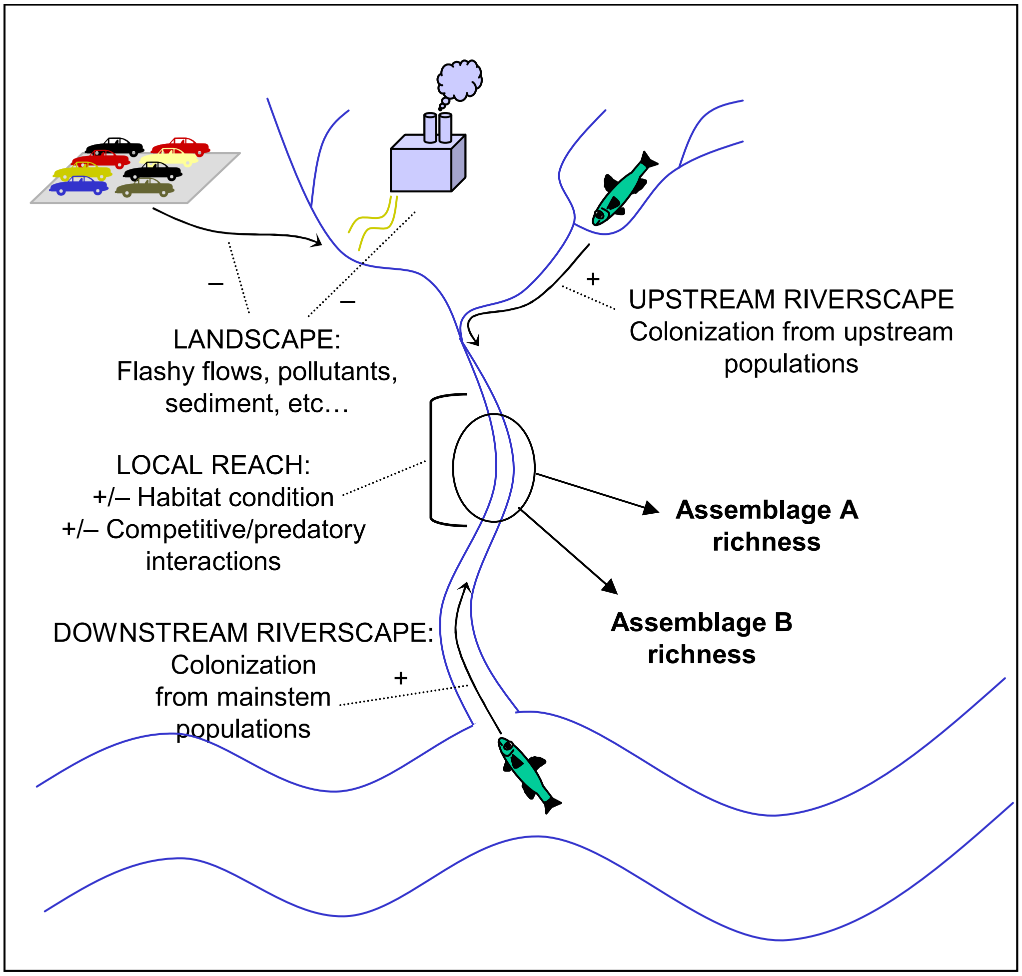

Figure 1. Conceptual model of forces affecting the richness of different fish assemblages in a stream reach.

CHAPTER TWO

METHODS

Study Region

Fish samples were collected from streams that feed into the contiguous mainstem channels of the Georgia portion of the Upper Coosa River System. For the purposes of this study, the mainstem channels were considered to be: the Coosa River upstream of Weiss Lake, the Oostanaula River, the Conasauga River upstream to Georgia Highway 76, and the downstream-most portions of the Etowah and Coosawattee Rivers (to Dykes Creek on the Etowah and to Crane Eater Creek on the Coosawattee; Figure 2). Flows in the mainstem, except for the Conasauga River, are partially regulated by the operation of Carters Reregulation Dam located 39 km upstream of Crane Eater Creek on the Coosawattee River, and Allatoona Dam located 65 km upstream of Dykes Creek on the Etowah River. Samples were collected from all accessible second-, third-, and fourth-order streams that entered into the main channel of the study area (Figure 2). Sample sites were located at the most downstream road crossing, unless sampling was impossible at this location due to water conditions or access issues; in these cases samples were collected from the next upstream road crossing. In the instances where both locations were inadequate, the stream was considered inaccessible and was not sampled. On two occasions, the downstream-most road crossing was located upstream of the first branching of the stream into two streams of second order or greater. In these situations, sample sites were located on the lowest road crossing of both branches. All sample sites were located within the Ridge and Valley physiographic province.

Fish Sampling

I sampled fishes at each site in order to estimate species richness for different subsets of the fish community while accounting for imperfect species detection (Williams, Nichols and Conroy 2002). Fish samples were collected from the nearest reach either upstream or downstream of the road crossing that encompassed both erosional and depositional habitat. A total of 30 kick-sets and/or seine hauls were performed using a backpack electrofisher in all representative habitats. Captured fish were identified in the field and released or were anesthetized and preserved in 10% formalin for lab identification (*Cyprinella lutrensis* and suspected *Cyprinella* hybrids were counted and preserved in ethanol for genetic analysis as a part of a separate study). All laboratory-identified specimens were archived in the Georgia Museum of Natural History.

To account for imperfect species detection, I obtained either spatial or temporal replicates of the fish samples. Spatial replication involved a second set of 30 kick-sets and/or seine hauls which were performed upstream of the first set. I performed spatial replication in all instances where there was no marked shift in habitat type or stream access and there was no addition of tributaries (14 of the 33 sites). Temporal replication involved returning to the site at least two days later and resampling the first spatial replicate using the same sampling protocol. I performed temporal replication at 8 randomly selected sites with spatial replicates and 8 randomly selected sites that lacked spatial replication. All primary sampling occurred between June 14th and July 22nd of 2005, and all temporal replication occurred between July 21st and August 5th 2005.

Reach-Scale Variable Sampling

I measured water quality and geomorphic variables at each site in order to quantify habitat factors hypothesized to influence local species richness. Stream baseflow turbidity was measured on 3 separate occasions using a Hach portable turbidity meter. Streams were considered at baseflow if no rain had been observed in the region for the preceding 72 hours and if water levels had leveled off on USGS stream gauges in the region. The three turbidity measurements were always made at least 2 weeks apart. Turbidity has been shown to influence lotic fish community structure (Walters, Leigh, and Bearden 2003). Stream conductivity was also measured using a Hydrolab® Datasonde 4a. Conductivity has been shown to influence fish communities (Fairchild et al 1998, Barko et al. 2004) and is often related to impaired urbanizing streams (Long and Schorr 2005, Roy et al. 2003).

Bed sediment size, stream depth, and average and maximum stream velocity were measured at ¼ channel-width intervals along the centerline of the stream for a distance of 25 times the channel width. In places where the length of stream sampled for fish exceeded 25 times stream width, sampling was continued at ¼-channel widths until the end of the fish sampling reach. In two streams, portions of the 25X channel width transect was unwadeable or inaccessible; in these instances, 100 samples were taken at intervals of 1/100th of the accessible length. Stream width was estimated by averaging the width measured at 5 randomly selected locations within the first 100 meters of the reach. If this average width was greater than 6 m (indicating a sampling transect >150 m in length) an additional 5 measurements were made over the next 100 m of stream to provide a better estimate of width over the length of the transect.

At each sampling point along the centerline, stream depth and water column velocity at 60% depth were measured using a top-setting wading rod and Marsh-McBirney velocity meter. I noted the presence of undercut banks, root mats, or large (>10 cm diameter) woody debris (LWD) in the cross section of the stream perpendicular to the centerline at the sampling point. Substrate particle size was recorded as the phi class (see Table 1) that was visually estimated to comprise the most of a ½ m diameter circle of stream bed centered on the sampling point. Each centerline sampling point was visually estimated as either erosional (as in riffles) or depositional (as in pools). In addition, percentage open canopy was measured using a spherical densiometer at every 20th sampling location. Velocity measurements were also taken in high flow areas throughout the sampled reach to estimate the maximum velocity of the reach.

Stream gradient was measured using total-station surveying equipment. Gradient measurements were made from riffle-top to riffle-top whenever possible; in the 8 instances where there was only access to one riffle, measurements were made from that riffle top to the farthest reachable area (always resulting in an overestimate of gradient). All geomorphic data were sampled between the 3rd of August and the 18th of October 2005.

Spatial Analysis

I developed a GIS in ArcMap 9.0 to quantify landscape and riverscape factors that have been hypothesized to influence local species richness, as follows.

Recent landscape

Recent land use for the upstream watersheds of each sampling site was calculated from the 1998 18-class land-use layer developed for the Georgia GAP project. These classifications were further grouped into 6 classes: open water, urban (including high and low intensity urban and transportation areas), forest (including evergreen, deciduous and mixed forests), cleared land (including clear cuts, bare rock and quarries), agriculture (including pasture and row crops), and wetlands (including forested and non-forested wetlands). In areas where portions of the drainage basins were out of state (primarily Coahulla Creek), data were patched in from the 1992 National Land Cover Dataset (NLCD) (see Appendix A). In addition to land use, percent of impervious area (IA) in the drainage basin and in a 1 km radius surrounding the sampling location was calculated from the 2001 NLCD (see Appendix B).

Historic landscape

A major confounding factor when relating stream communities to upland land use is the difficulty of separating present-day from historical influences (Allan 2004, Harding et al. 1998). To deal with this, I developed an historic land use layer based on scans of 1938 Soil Conservation Service Aerial Photograph index sheets available from the Georgia Aerial Photography collection located in the Digital Library of Georgia. Scanned images were georeferenced and mosaiced into a single image that covered the in-state extent of all sampled basins. Due to the vast differences in exposure of the original photographs as well as the differences in scan contrast between the separate index sheets, it was impossible to perform any automated classification scheme; instead areas of modified land were selected by hand in Adobe Photoshop. This generated a historic land use map with three classification levels: historically forested areas, historically non-forested areas, and areas of no data (out of state areas and areas where there were missing pieces on the index sheets). The proportion of historically non-forested area for each basin was calculated as the area classified as non-forested in the basin divided by the total area within the basin for which data were available (See Appendix C).

Downstream riverscape

Three downstream riverscape variables were assessed in the GIS—distance of the sample site to the mainstem, flow accumulation of the mainstem at the juncture, and downstream link. Distance to the mainstem was measured simply as the meters of stream that existed between the sample site and the centerline of the mainstem. This variable was included as a key element of the downstream riverscape because it has been shown to play a role in defining fish community in an adventitious stream (Schaffer and Kerfoot 2004; see also the C-link number of Fairchild et el. 1998). Flow accumulation of the mainstem at the juncture was measured as the number of 30mX30m flow accumulation cells that existed upstream and upslope of the juncture point where the sample stream meets the mainstem (though not including the drainage area of the sample stream itself). Downstream link (D-link), which has been used frequently as a measure of downstream network effects (Osbourne and Wiley 1992, Schaffer and Kerfoot 2004, Smith and Craft 2005), was recorded as the number of stream linkages upstream of the next stream juncture downstream of the study site. Though D-link has frequently been used to represent downstream proximity of larger rivers, it does not to reflect the proximity to a mainstem river if there are any small tributaries adding linkages between the sampling site and the mainstem river.

Statistical analysis

Testing comparability of replication methods

Before estimating the richness of species at each site it was necessary to determine whether temporal and spatial replicates were sufficiently comparable to be used together in richness models. I did this using data for the eight sites with both spatial and temporal replicates and modeling the likelihood of the data given that average species capture probability (p) is either: 1) constant across all spatial and temporal replicates (termed $p_{(\cdot)}$), 2) variable between spatial replicates and constant across temporal replicates (termed $p_{(\text{spatial})}$), 3) variable between temporal replicates and constant across spatial replicates (termed $p_{(\text{temporal})}$), or 4) variable for each individual sampling occasion (termed $p_{(\text{sample})}$). Estimates of the capture probabilities for these four scenarios were made using a Huggins closed-capture method, which fits a likelihood function to the observed capture histories for all species captured at the site across the three replicate samples (Huggins 1989). All models of capture probability included a covariate of species ubiquity, which was measured as the proportion of all of sample occasions in which the species was detected. This allowed some of the variation in detection among species to be accounted for by differences in commonness across the study region and improved model fit. All model fitting was performed with Program MARK v4.2 software.

The four models generated for each site were ranked according to their second order Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002). The models were also assigned a model weight (w_i) according to the formula $w_i = e^{(-½\ \Delta AICc)} / \Sigma e^{(-½\ \Delta AICc)}$, where ΔAICc equals the difference in AIC_c for each model compared to the best-supported model and the denominator is a sum of $e^{(-½\Delta AICc)}$ for all four models. This number can be viewed as the proportion of evidence that model *i* is the actual best model for the data given that the best model is in the model set (Burnham and Anderson 2002). To determine how well the different models fit the data in comparison to each other across sites, the ratios of w_i for $p_{(\cdot)}/p_{(spatial)}$, $p_{(\cdot)}/p_{(temporal)}$, and $p_{(\cdot)}/p_{(sample)}$ were calculated for each of the eight sites. Ratios greater than 1 supported the hypothesis that $p_{(\cdot)}$ models are the most parsimonious and thus supported estimating richness with models in which spatial and temporal replicates were treated identically.

Richness modeling

Species richness was evaluated for four different species assemblages: all species encountered, obligate lotic species, lotic/lentic generalist species (henceforth referred to as generalists), and local endemic species. Obligate lotic and generalist species were determined based on habitat classifications of Page and Burr (1998) and Boschung and Mayden (2004). Species were considered endemic if they were native to four or fewer drainages according to Warren et al. (2000). Stocked or recently introduced species (e.g. *Onchorynchus mykiss*, *Cyprinella lutrensis* and their hybrids) were not included in analyses as their occurrence at a site could be due to introduction patterns rather than environmental factors. *Gambusia holbrooki* and *G. affinis* were not separated because they occupy identical habitats and the frequent hybridization of the two species in the Upper Coosa makes separate identification difficult (Walters and Freeman 2000).

For each assemblage, a naïve estimate of species richness ($R_{(naïve)}$) for each site (*i*) was calculated as: $\Sigma R_s/S$, where R_s is the number of species found in sample *s* and S is the number of samples taken at the site. This estimation is a measure the number of species you would likely encounter during a single sampling occasion. The model M_h jackknife estimator (Burnham and Overton 1979) was also used to generate a modeled richness ($R_{(mh)}$) for the 22 sites that were sampled on at least two occasions. The model M_h is useful because it estimates the richness including non-detected species based on the assumption that species have varying capture probabilities and that this capture probability remains constant throughout all sampling occasions (the assumption tested with the Huggins closed-capture models; Burnham and Overton 1979). For the remaining 11 sites that were sampled only once, R_{mh} was estimated as the number of species observed at the site times the average of $R_{(mh)}/R_{(naïve)}$ across the sites with multiple samples. All jackknife estimations were run on CAPTURE 2 software.

Selection of predictor variables

Prior to modeling, variables were checked for normality and were transformed if necessary. In order to simplify the modeling process only the most informative predictor variables were retained for inclusion in final models. Both current forest cover and historic non-forested cover were retained in order to compare the effects of land use at different historical scales. Similarly, impervious coverage was included at both the basin-wide and 1 km radius scales because other authors have found varying effects at different spatial scales (Wang et al. 2003; see Allan 2004). All downstream riverscape variables (distance to mainstem, D-link, and mainstem flow accumulation) were also included because little work has been done to determine the most predictive variables relating to downstream riverscape.

To prevent the confusion that arises from the inclusion of correlated predictor variables, remaining variables were selected based on a matrix of Pearson's correlation coefficients calculated for all variables. With this matrix it was possible to identify groups of variables that were all highly correlated and select a single representative variable from the group for inclusion in the final analysis. Variables that showed no correlation to any other selected variables were also included for final analysis.

Regression models

Multiple linear regression models were used to determine the effect and relative importance of landscape, riverscape and local habitat variables on the richness of the different fish assemblages. For each fish assemblage, all possible models involving three or fewer of the 13 selected transformed predictor variables were generated (79 models total). The number of predictor variables in any given model was limited to 3 in order to reduce overfitting the models for the dataset of 33 sites (Burnham and Anderson 2002). Models were ranked according to their AIC_c values and assigned a model weight (w_i).

The relative variable importance of each predictor variable ($w_{+(j)}$) was computed as the sum of w_i for all models that contained the variable (j). This number can be viewed as the proportion of evidence in favor of the best model for the data including this variable provided that the best model is in the set of evaluated models (Burnham and Anderson 2002).

I used Monte Carlo tests to estimate the probability that the calculated values of $w_{+(j)}$ indicated a non-random effect of a variable in the predictive model set. The observed values of the variable in question were randomly reassigned among sites, all models were refit to the random data, and the $w_{+(j)}$ for the variable was reevaluated. This was repeated for 300 random shuffles of the data and reported as the proportion of random iterations in which $w_{+(j)}$ exceeded the $w_{+(j)}$ generated by the real data.

I estimated the size of effects of predictor variables on the richness of the different fish assemblages using regression coefficients averaged across all well-supported models in the model set (Burnham and Anderson 2002). This allows for use of multiple competing models to estimate effect size, thus accounting for uncertainty in selecting the best model. I did this by first selecting a "confidence set" of models that included all models with a w_i that exceeded $1/8*w_i$ of the best fitting model. To estimate variable effect size, model weights were recalculated using only the models in the confidence set that included the variable. The model averaged effect size of the variable was then estimated as $\Sigma w_i*\theta_i$ where θ_j indicates the effect size estimate for model j. In addition, the model averaged variance for the effect size was estimated as:

$$\left[\sum_{i=1}^{R} w_i \sqrt{\operatorname{var}(\hat{\theta}_i) + (\hat{\theta}_i - \hat{\bar{\theta}})^2}\right]^2$$

where R is the number of models containing the variable, $\hat{\theta}_i$ is the effect size of the variable in model i, $\operatorname{var}(\hat{\theta}_i)$ is the estimated variance of that effect size, and $\hat{\bar{\theta}}$ is the model averaged effect size (Burnham and Anderson 2002). Using this variance, 90% confidence intervals were placed around the effect size. Effect sizes with a 90%

confidence interval including zero indicated no clear relationship between the predictor variable and assemblage richness.

Table 1. Phi classification and descriptive classification of substrate particles. Measurements were made along the intermediate axis of particles. Negative phi values were used in order to maintain a positive relationship between phi and particle size.

phi	**particle size range (mm)**	**general classification**
1	<2	sand
2	2-4	gravel
3	5-8	gravel
4	9-16	gravel
5	17-32	gravel
6	33-64	gravel
7	65-128	cobble
8	129-256	cobble
9	257-512	cobble
10	>512	bedrock

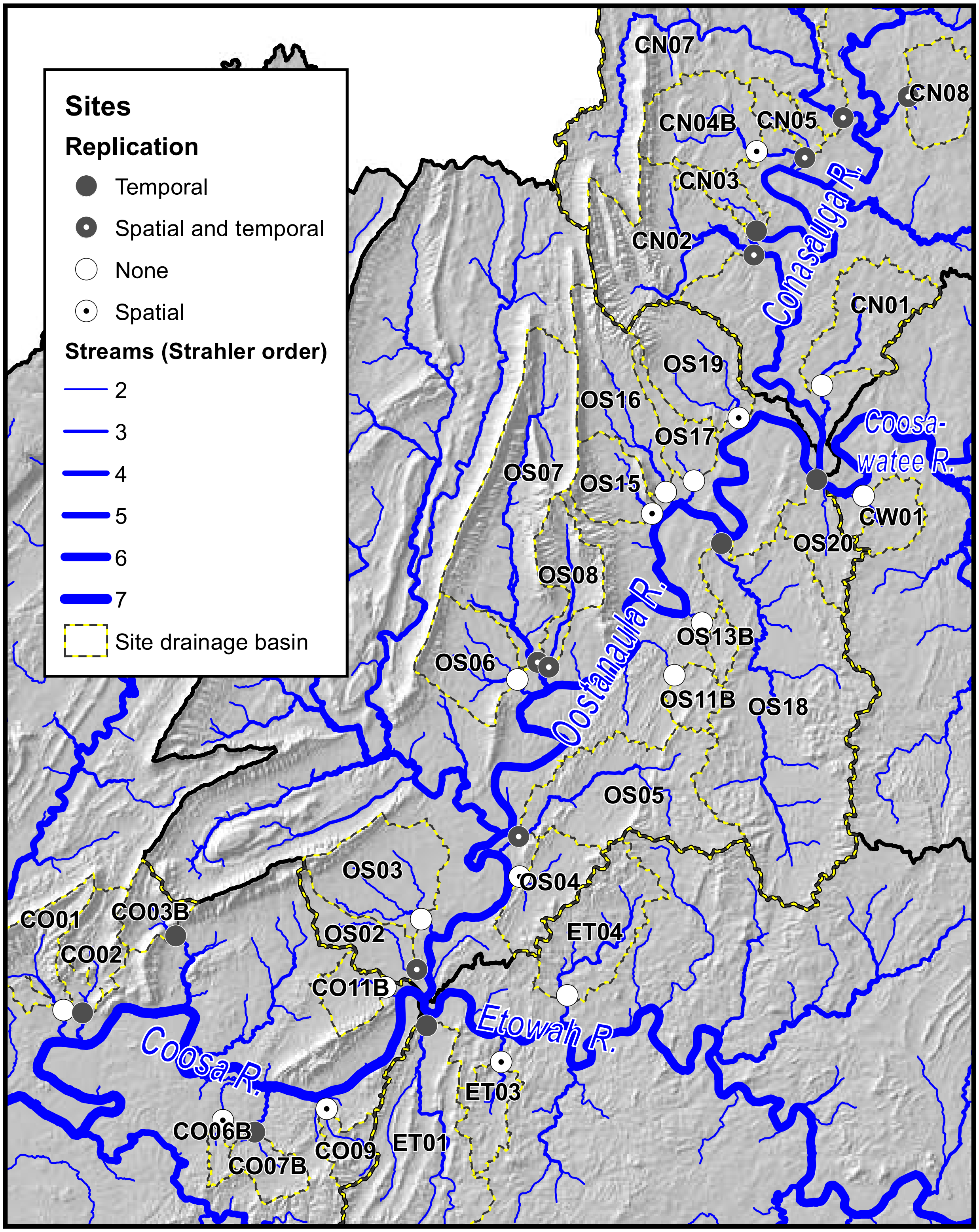

Figure 2. Map of the location of the 33 sample sites in Coosa River basin in northwest Georgia, USA.

CHAPTER THREE

RESULTS

Across the 33 sites and 63 sampling occasions, 49 different species were encountered. Thirty-one of the species were classified as obligate lotic, 15 were classified as endemic, and 14 were classified as lotic / lentic generalists (Table 2). All endemic species were considered obligate lotic.

Table 3 summarizes the results of the Huggins closed-capture models for the eight sites with both temporal and spatial replication. In all instances, $p_{(\cdot)}$ models were assigned a higher w_i than $p_{(spatial)}$ and $p_{(sample)}$ models. In addition, $p_{(\cdot)}$ models were also assigned higher w_i values than $p_{(temporal)}$ models for all but one site (CN07, Coahulla Creek) where the $p_{(temporal)}$ model outperformed the $p_{(\cdot)}$ model by a factor of 1.4. A one-tailed paired t-test confirmed that $p_{(\cdot)}$ models received higher w_i values than $p_{(spatial)}$ models ($t=6.88$, $p=0.0002$), $p_{(temporal)}$ models ($t=2.98$, $p=0.0204$), and $p_{(sample)}$ models ($t=9.93$, $p<0.0001$). $p_{(spatial)}$ models also tended to outperform $p_{(temporal)}$ models though a t-test failed to show a significant difference at $\alpha=0.05$ ($t=2.22$, $p=0.062$). Based on the strong support of models based on constant detection probabilities (i.e. $p_{(\cdot)}$ models), I used spatial and temporal replicates together to estimate species richness.

A summary of each assemblage's naïve ($R_{(naïve)}$) and jackknife modeled ($R_{(mh)}$) richness values for sites can be seen in Table 4. Naïve richness ranged from 5 to 22 for all species, 0 to 14 for obligate lotic species, 2 to 7 for generalist species and 0 to 8 for endemic species. $R_{(mh)}$ ranged from 7 to 35.53 for all species, 0 to 20.5 for obligate lotic species, 2 to 9.79 for generalists, and 0 to 11.64 for endemic species. The estimated average capture efficiency ($R_{(naïve)}$ / $R_{(mh)}$) used to calculate $R_{(mh)}$ for sites without replication was 0.670 for all species, 0.701 for obligate lotic species, 0.715 for generalist species and 0.687 for endemic species.

After data transformation and correlation analysis, 13 predictor variables were selected for final analysis (see Appendices D and E for data transformation and correlation information of unused variables). Five of these variables were upland landscape factors (proportion of basin forested, proportion of basin non-forested in 1938, basin-wide percent impervious area, 1-km radius percent impervious area, and conductivity), five were reach-scale factors (drainage area, proportion erosional habitat, average substrate particle size, proportion of sample reach dominated by gravel, and proportion of sample-point cross sections with large woody debris), and three were downstream network factors (distance to mainstem, D-link, and mainstem flow accumulation; Table 5). Although attempts were made to include only variables with minimal intercorrelations, some significant correlations still occurred (Table 6). In addition to the variables that were expected to be correlated (e.g. basinwide and local scale impervious surface, current forest and historic non-forest cover) substrate particle size was correlated with basin-wide forest cover (historical and current), distance to the mainstem was negatively correlated with the percent of basin-wide impervious area, and mainstem flow accumulation was correlated with basin-wide forest cover and impervious area as well as average substrate size. An estimate of the percent of calcareous geology (defined as areas classified as limestone, marble or dolomite in statewide surface geology GIS layer) showed low correlation with conductivity at the site ($r = 0.243$).

Table 7 summarizes the relative variable importance values (w_+) that were assigned to each variable for the complete $R_{(mh)}$ multilinear regression model sets ($R_{(naïve)}$ results were comparable and are included in Appendix G). Conductivity was rated as an important variable for all four assemblages. For all but generalist assemblages, conductivity had a $w_+ > 0.974$. The Monte-Carlo results strongly supported the hypothesis that the influence of conductivity was non-random, except for generalist species, for which 8.7% of the random data iterations resulted in a higher variable importance. Drainage area was also rated as an important variable for predicting the total species richness, obligate lotic richness and endemic richness (w_+= 0.998, 1.0, and 0.870 respectively). In Monte-Carlo analysis, these w_+ values were never exceeded by random iterations. In contrast, drainage area received the lowest w_+ value out of all variables for generalist species. In models for obligate lotic species and endemic species, the percent of erosional habitat received w_+ values that were exceeded by random iterations less than 10% of the time, though in both instances, the actual w_+ values (0.103 and 0.282 respectively) were much lower than the values observed for conductivity and drainage area. The only remaining variable which consistently yielded a higher w_+ value than randomized data was percentage of large woody debris in obligate lotic species richness models, though the direction of the effect was counter to that expected (see below) and the relative importance of the variable was relatively low (w_+=0.336).

Models selected for $R_{(mh)}$ confidence model sets can be seen in Table 8. There were 12 confidence models selected from the total richness model set, 7 from the obligate lotic model set, 12 from the endemic model set, and 73 from generalist model set. R^2 values for confidence models ranged between 0.616-0.649 for all species models, 0.703-0.746 for obligate lotic models, 0.488-0.545 for endemic species, and 0.005-0.231 for generalist models. All variables were included in at least one model for all confidence model sets with the exception of the obligate lotic richness set, which did not include 1938 non-forested cover, average substrate size, or any of the downstream riverscape variables. Conductivity and drainage area variables were included in all confidence models in the all-species, obligate lotic, and endemic model sets.

The model-averaged effect sizes for predictor variables showed similar trends to relative variable importance results (Figure 3; see Appendix H for raw data and Appendix G for $R_{(\text{naïve})}$ data). In all model sets, the 90% confidence intervals around the coefficients for conductivity did not contain zero; this was also the case for drainage area with the exception of generalist models. Other variables where the 90% confidence intervals around effect sizes did not cross zero were percent erosional habitat (for total species and endemic species richness models), percent large woody debris (for obligate lotic and endemic species richness models), percent gravel (for total species richness models), and local percent impervious area (for total species richness models).

Conductivity always showed a strong negative effect on richness. Likewise, except for generalists, the effect of drainage area was strongly positive. Percent erosional habitat had a strong positive effect on endemic species richness and a somewhat weaker positive effect on total species richness. Percent gravel also had a weakly positive effect on total species richness. For both endemic species and obligate lotic species richness, percent large woody debris had a moderately strong negative effect, though it also showed wide confidence intervals. Similarly, local percent impervious area had a moderately negative effect on total species models though its confidence intervals nearly overlapped zero.

Bivariate plots of obligate lotic richness (Figure 4) also show weak relationships between richness and percent large woody debris and basin-wide impervious area, and stronger relationships between richness and conductivity and drainage area. The basin-wide impervious area plot illustrates the considerable scatter in the data, but also indicates that assemblage richness is consistently low at transformed values of basin-wide impervious area higher than around 2 (6% basin-wide impervious area). The plot of richness in relation to occurrence of large woody debris also show high variability and, moreover, that when conductivity and drainage area are not accounted for, the relations trends positive rather than negative.

Table 2. List of species analyzed and their assemblage classification. Ubiquity = (total number of sampling occasions where the species was detected) / (total number of sampling occasions; n=63) Table continues on next page.

Species	Obligate lotic	Endemic	Lentic / lotic generalist	Ubiquity
Cyprinus carpio			X	0.016
Notemigonus crysoleucas			X	0.016
Semotilus atromaculatus	X			0.270
Rhinichthys atratulus	X			0.048
Notropis chrosomus	X	X		0.095
Notropis stilbius	X	X		0.317
Notropis xaenocephalus	X	X		0.254
Phenacobius catostomus	X	X		0.079
Campostoma oligolepis	X			0.889
Pimephales vigilax	X			0.206
Cyprinella callistia	X	X		0.032
Cyprinella trichroistia	X	X		0.048
Cyprinella venusta	X			0.524
Luxilus chrysocephalus	X			0.302
Lythrurus lirus	X	X		0.032
Moxostoma poecilurum	X			0.095
Moxostoma duquesnei	X			0.095
Moxostoma erythrurum	X			0.095
Hypentelium etowanum	X	X		0.603
Ictalurus punctatus			X	0.032
Noturus leptacanthus	X			0.048
Ameiurus natalis				0.079
Ameiurus nebulosus			X	0.016
Fundulus olivaceus	X			0.111
Fundulus stellifer	X	X		0.127
Gambusia sp.			X	0.556
Cottus carolinae zopherus	X	X		0.540

Table 2. Continued.

Species	Obligate lotic	Endemic	Lentic / lotic generalist	Ubiquity
Ambloplites ariommus				0.032
Lepomis auritus				0.778
Lepomis cyanellus			X	0.730
Lepomis gulosus			X	0.254
Lepomis macrochirus			X	0.905
Lepomis megalotis			X	0.619
Lepomis microlophus			X	0.349
Lepomis punctatus			X	0.413
Micropterus salmoides			X	0.397
Micropterus punctulatus	X			0.079
Micropterus coosae	X			0.159
Pomoxis nigromaculatus			X	0.143
Etheostoma coosae	X	X		0.540
Etheostoma jordani	X	X		0.206
Etheostoma rupestre	X	X		0.016
Etheostoma stigmaeum	X			0.429
Etheostoma trisella	X	X		0.032
Percina lenticula	X			0.016
Percina kathae	X	X		0.079
Percina nigrofasciata	X			0.571
Aplodinotus grunniens			X	0.016

Table 3. AIC_c model weights and their ratios for Huggins closed-capture models with probability of species encounter either identical across all replicates ($p_{(\cdot)}$), variable between spatial replicates and constant across temporal replicates ($p_{(spatial)}$), variable between temporal replicates and constant across spatial replicates ($p_{(temporal)}$), or variable for each individual sampling occasion ($p_{(sample)}$). T values reflect the test of H_0: $\ln(w_i \text{ ratio}) = 0$.

	Model weight (w_i)				**Ratio of model weights**			
site	$p_{(\cdot)}$	$p_{(spatial)}$	$p_{(temporal)}$	$p_{(sample)}$	$p_{(\cdot)}$/ $p_{(spatial)}$	$p_{(\cdot)}$/ $p_{(temporal)}$	$p_{(temporal)}$ / $p_{(spatial)}$	$p_{(\cdot)}$/ $p_{(sample)}$
CN02	0.452	0.151	0.285	0.113	3.00	1.59	1.89	4.00
CN05	0.456	0.208	0.254	0.082	2.20	1.79	1.22	5.53
CN07	0.303	0.107	0.428	0.162	2.84	0.71	4.02	1.87
CN08	0.386	0.217	0.299	0.097	1.78	1.29	1.38	3.97
OS02	0.327	0.294	0.290	0.089	1.11	1.13	0.98	3.67
OS05	0.515	0.185	0.226	0.074	2.78	2.28	1.22	7.00
OS07	0.466	0.207	0.244	0.083	2.25	1.91	1.18	5.59
OS08	0.465	0.200	0.200	0.135	2.32	2.32	1.00	3.45
mean	0.42	0.20	0.28	0.10	2.29	1.63	1.61	4.38
				t_7=	6.88	2.98	2.22	9.93
				p =	0.0002	0.0204	0.062	<0.0001

Table 4. Naïve ($R_{(naïve)}$) and modeled ($R_{(mh)}$) richness estimates for sampled sites.

Site	Stream Name	Spatial replication	Temporal replication	All species		Oblicate lotic		Lotic lentic generalists		Endemics	
				$R_{(mh)}$	$R_{(naïve)}$	$R_{(mh)}$	$R_{(naïve)}$	$R_{(mh)}$	$R_{(naïve)}$	$R_{(mh)}$	$R_{(naïve)}$
CN01	Polecat Creek			13.43	9	4.28	3	5.6	4	0	0
CN02	Swamp Creek	X	X	25.15	15	14.72	10	6.67	4	4	3.33
CN03	Jobs Creek	X		21.6	11.5	10.16	6.5	5.19	3.5	4	2
CN04B	Drowning Bear Creek		X	10.74	8	6.13	4.5	3	3	3.5	2.5
CN05	Little Creek	X	X	22.97	10.33	7.19	4.67	9.15	5	4.33	1.33
CN07	Coahulla Creek	X	X	31.88	12.33	20.5	10	8.01	2	7.33	3.67
CN08	Town Branch	X	X	15.34	9.67	5.67	4	6.67	4.33	2	2
CO01	Kings Creek			19.4	13	11.41	8	5.6	4	4.36	3
CO02	Mount Hope Creek	X		14.6	10	8.04	6.5	5	3	5	3
CO03B	Cabin Creek	X		11.5	10.5	6	6	4.5	3.5	3	3
CO06B	Hamilton Creek		X	10	8	1	1	6.5	5.5	0	0
CO07B	Webb Creek	X		19.51	15	13.07	9.5	5.5	4.5	4.5	3.5
CO09	UNT to Coosa		X	14.05	10.5	6	4	5.5	4.5	4	2
CO11B	Horseleg Creek			11.94	8	4.28	3	5.6	4	1.45	1
CW01	Crane Eater Creek			19.4	13	8.55	6	7	5	4.36	3
ET01	Silver Creek	X		24.61	16	18.09	12.5	5	3	9	7
ET03	UNT to Etowah		X	7	7	5	5	2	2	1	1
ET04	Dykes Creek			28.36	19	19.96	14	4.2	3	11.64	8
OS02	Little Dry Creek	X	X	13	8.33	1	0.33	9.33	6.33	0	0
OS03	Big Dry Creek			10.45	7	2.85	2	4.2	3	0	0
OS04	Dozier Creek		X	16.43	14	12.5	9.5	4	4	6.5	5.5
OS05	Woodward Creek	X	X	22	16.33	16	11	6.67	4.67	7	5.67
OS06	Lovejoy Creek			22.39	15	11.41	8	8.4	6	1.45	1
OS07	Johns Creek	X	X	28.68	16.33	17.11	12	6.32	3.67	9.33	6
OS08	Rocky Creek	X	X	35.53	19.67	18.09	12	11	6.67	11.26	6.67
OS11B	Robbins Creek			14.93	10	4.28	3	7	5	1.45	1
OS13B	UNT to Oostanaula			10.45	7	0	0	7	5	0	0
OS15	Bow Creek		X	21.13	13.5	10.72	6	7.5	6.5	2.5	1.5
OS16	Snake Creek			32.84	22	19.96	14	9.79	7	8.73	6
OS17	Graham Creek			7.46	5	0	0	4.2	3	0	0
OS18	Oothkalooga Creek	X		20.23	10.5	11.69	7	4.26	2.5	4.85	2
OS19	Dry Creek		X	23.89	20.5	14	12	8.04	6.5	5	5
OS20	Town Creek		X	23.89	11	7.29	3.5	7	5	3	1

Table 5. Descriptive statistics and transformation of variables used in final model building. Shapiro-Wilk test of transformed data indicates the degree to which the data could be drawn from a normal distribution. (as Pr<W increases, data more approximate a normal distribution). See Appendix A for variables not used in model building.

	Raw data					transformed data				Shapiro-Wilk test	
Variable	**Mean**	**St-Dev**	**Min**	**Max**	**Transform-ation**	**Mean**	**St-Dev**	**Min**	**Max**	**W**	**Pr<W**
Proportion of basin forested	0.558	0.163	0.187	0.867	none	0.558	0.163	0.187	0.867	0.982	0.832
Proportion of basin non-forested in 1938	0.436	0.182	0.106	0.742	none	0.436	0.182	0.106	0.742	0.964	0.328
% basinwide impervious area (IA)	3.88	5.33	0.10	23.27	ln(x+1)	1.178	0.861	0.099	3.189	0.927	0.029
% impervious area in 1 km radius	4.09	6.49	0.20	26.10	ln(x+1)	1.141	0.886	0.180	3.300	0.822	0.000
Conductivity (μS/cm)	233	85	88	573	ln(x+1)	5.40	0.32	4.49	6.35	0.927	0.030
Drainage area (km^2)	46.7	80.6	4.6	456.3	ln(x+1)	3.33	0.91	1.73	6.13	0.946	0.099
Proportion erosional habitat	0.281	0.147	0.060	0.562	arcsine($x^{1/2}$))	0.545	0.171	0.247	0.847	0.961	0.272
Particle size (phi)	4.06	1.34	1.63	7.99	none	4.06	1.34	1.63	7.99	0.952	0.155
Proportion of gravel (2-64 mm)	0.625	0.228	0.048	0.963	arcsine($x^{1/2}$))	0.923	0.260	0.220	1.376	0.970	0.475
Proportion of transects with large woody debris	0.133	0.137	0	0.660	arcsine($x^{1/2}$))	0.318	0.222	0	0.948	0.937	0.055
Distance to mainstem (m)	2280	1592	207	7832	ln(x+1)	7.51	0.73	5.34	8.97	0.949	0.121
D-link	613	783	2	2502	ln(x+1)	4.63	2.43	1.10	7.83	0.851	0.000
Drainage area of mainstem at juncture (km^2)	8357	4982	1342	17133	ln(x+1)	15.85	0.67	14.22	16.76	0.893	0.003

Table 6. Matrix of Pearson correlation coefficients for all predictive variables used in final model building. Bolded values indicate a p<0.05 for 33 sites. See Appendix B for correlation information of variables not used in final models.

% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation	
-0.671	**-0.596**	-0.241	-0.325	0.193	0.149	**0.417**	-0.080	0.135	0.105	0.208	**0.498**	**% basinwide forest cover**
	0.241	0.069	0.240	-0.034	-0.101	**-0.415**	-0.065	-0.056	-0.076	-0.216	**-0.437**	**% historical basin non-forested**
		0.586	0.277	0.093	-0.048	-0.126	0.071	-0.060	**-0.448**	0.204	**-0.476**	**basinwide %IA**
			0.283	0.187	-0.018	0.094	0.030	-0.189	-0.119	0.305	0.047	**1 km radius %IA**
				-0.083	-0.152	-0.145	-0.273	-0.287	0.278	-0.092	-0.045	**conductivity**
					0.293	-0.182	0.171	0.265	-0.055	0.245	-0.308	**drainage area**
						0.218	-0.072	-0.066	-0.145	-0.004	0.003	**% erosional habitat**
							-0.274	-0.301	0.237	-0.091	**0.420**	**average substrate size (phi)**
								0.132	-0.177	0.166	0.118	**% gravel substrate**
									-0.223	0.085	-0.131	**% LWD**
										-0.478	0.273	**distance to mainstem**
											0.146	**D-link**

Table 7. Relative variable importance values for models of all species (a), obligate lotic (b), endemic (c), and lotic/lentic generalist (d) base on $R_{(mh)}$ model sets (See Appendix 6 for $R_{(naïve)}$ results). Bolded values indicate Monte-Carlo results that did not exceed 10%. Table is continued on the next page.

a) All species

Variable	Relative variable importance	% of random iterations in excedance
conductivity	**0.992**	**0.0**
drainage area	**0.983**	**0.0**
1 km radius %IA	0.162	10.7
% gravel substrate	0.137	15.7
distance to mainstem	0.119	13.3
mainstem flow accumulation	0.081	26.0
% erosional habitat	0.077	26.0
D-link	0.054	43.7
average substrate size (phi)	0.048	46.3
basinwide %IA	0.045	56.3
% LWD	0.044	53.0
% historical basin non-forested	0.042	55.0
% basinwide forest cover	0.042	69.0

b) Obligate lotic species

Variable	Relative variable importance	% of random iterations in excedance
drainage area	**1.000**	**0.0**
conductivity	**0.998**	**0.0**
% LWD	**0.336**	**3.7**
% erosional habitat	**0.103**	**9.3**
1 km radius %IA	0.092	13.7
% gravel substrate	0.083	14.0
basinwide %IA	0.069	19.7
% basinwide forest cover	0.046	27.7
average substrate size (phi)	0.034	53.7
D-link	0.033	54.7
mainstem flow accumulation	0.030	63.0
distance to mainstem	0.027	77.7
% historical basin non-forested	0.027	84.7

Table 7. Continued.

c) Endemic species

Variable	Relative variable importance	% of random iterations in excedance
conductivity	**0.974**	**0.0**
drainage area	**0.870**	**0.0**
% erosional habitat	**0.282**	**7.0**
% LWD	0.189	11.3
average substrate size (phi)	0.090	22.3
% gravel substrate	0.075	31.7
mainstem flow accumulation	0.062	33.3
basinwide %IA	0.061	36.0
% basinwide forest cover	0.060	39.0
D-link	0.046	57.7
distance to mainstem	0.045	54.3
1 km radius %IA	0.038	86.7
% historical basin non-forested	0.038	84.7

d) Lotic / lentic generalist species

Variable	Relative variable importance	% of random iterations in excedance
conductivity	**0.422**	**8.7**
% LWD	0.237	18.7
% gravel substrate	0.229	19.7
% historical basin non-forested	0.224	24.7
distance to mainstem	0.196	22.3
average substrate size (phi)	0.193	24.7
mainstem flow accumulation	0.180	30.0
1 km radius %IA	0.144	43.3
basinwide %IA	0.142	45.3
D-link	0.131	43.7
% basinwide forest cover	0.120	54.0
% erosional habitat	0.108	75.3
drainage area	0.105	79.3

Table 8. Confidence model sets for multilinear regression of all species (a), obligate lotic (b), and endemic (c) species $R_{(mh)}$. Lotic/lentic generalist results (d) show only the top 10 confidence models as the confidence set included 73 models. Values for individual variables are the regression coefficients for transformed data. K=number of model parameters. Table is continued on the next page.

a) All species

intercept	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation	K	R^2	ΔAICc	Model weight
79.99					-13.73	3.94								4	0.616	0.00	0.173
73.32				-1.65	-12.36	4.28								5	0.649	0.12	0.163
70.09					-12.64	3.72			5.15					5	0.644	0.54	0.132
87.31					-12.65	3.90					-1.74			5	0.642	0.78	0.117
105.67					-13.95	3.60							-1.47	5	0.632	1.71	0.073
75.69					-13.33	3.63	5.82							5	0.632	1.71	0.073
81.65					-13.90	4.14						-0.30		5	0.625	2.31	0.054
83.82					-14.03	3.81		-0.44						5	0.622	2.59	0.047
82.62					-14.17	4.08				-2.36				5	0.620	2.74	0.044
78.12			-0.56		-13.30	4.00								5	0.620	2.78	0.043
79.30		-2.38			-13.41	3.94								5	0.619	2.83	0.042
79.21	0.59				-13.64	3.92								5	0.616	3.08	0.037

b) Obligate lotic species

intercept	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation	K	R^2	ΔAICc	Model weight
56.25					-11.07	4.55				-6.17				5	0.746	0.00	0.396
49.37					-9.94	4.18								4	0.703	2.03	0.143
45.06					-9.54	3.87	5.84							5	0.727	2.38	0.121
44.94				-1.10	-9.03	4.41								5	0.725	2.60	0.108
42.60					-9.19	4.03			3.52					5	0.723	2.82	0.097
46.09			-0.98		-9.18	4.29								5	0.720	3.17	0.081
44.02	4.06				-9.29	4.06								5	0.714	3.98	0.054

Table 8. Continued

c) Endemic species

intercept	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation	K	R^2	ΔAICc	Model weight
17.02					-3.54	0.90	3.40							5	0.545	0.00	0.211
22.50					-4.27	1.24				-2.67				5	0.544	0.03	0.208
19.53					-3.77	1.08								4	0.488	0.76	0.144
16.76					-3.56	1.17		0.32						5	0.520	1.71	0.090
10.40					-3.70	1.20							0.52	5	0.509	2.48	0.061
18.27			-0.37		-3.49	1.12								5	0.506	2.71	0.054
17.58					-3.56	1.04			1.01					5	0.500	3.09	0.045
17.46	1.57				-3.52	1.03								5	0.499	3.16	0.043
20.06					-3.83	1.15						-0.10		5	0.498	3.21	0.042
18.31					-3.95	1.09					0.29			5	0.496	3.37	0.039
19.65		0.44			-3.83	1.08								5	0.489	3.78	0.032
19.46				-0.02	-3.76	1.09								5	0.488	3.85	0.031

d) Lotic / lentic generalist species

intercept	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation	K	R^2	ΔAICc	Model weight
18.03					-2.18									3	0.122	0.00	0.059
20.62					-2.40			-0.35						4	0.177	0.69	0.042
15.45					-1.82					1.86				4	0.161	1.32	0.031
5.40										2.61				3	0.083	1.42	0.029
20.87		-2.88			-2.10			-0.51						5	0.231	1.53	0.028
15.01					-1.87				1.42					4	0.154	1.61	0.027
26.51					-2.23								-0.52	4	0.153	1.65	0.026
4.33									2.05					3	0.071	1.87	0.023
19.61					-1.94						-0.39			4	0.140	2.12	0.021
17.61		-1.38			-2.00									4	0.137	2.26	0.019

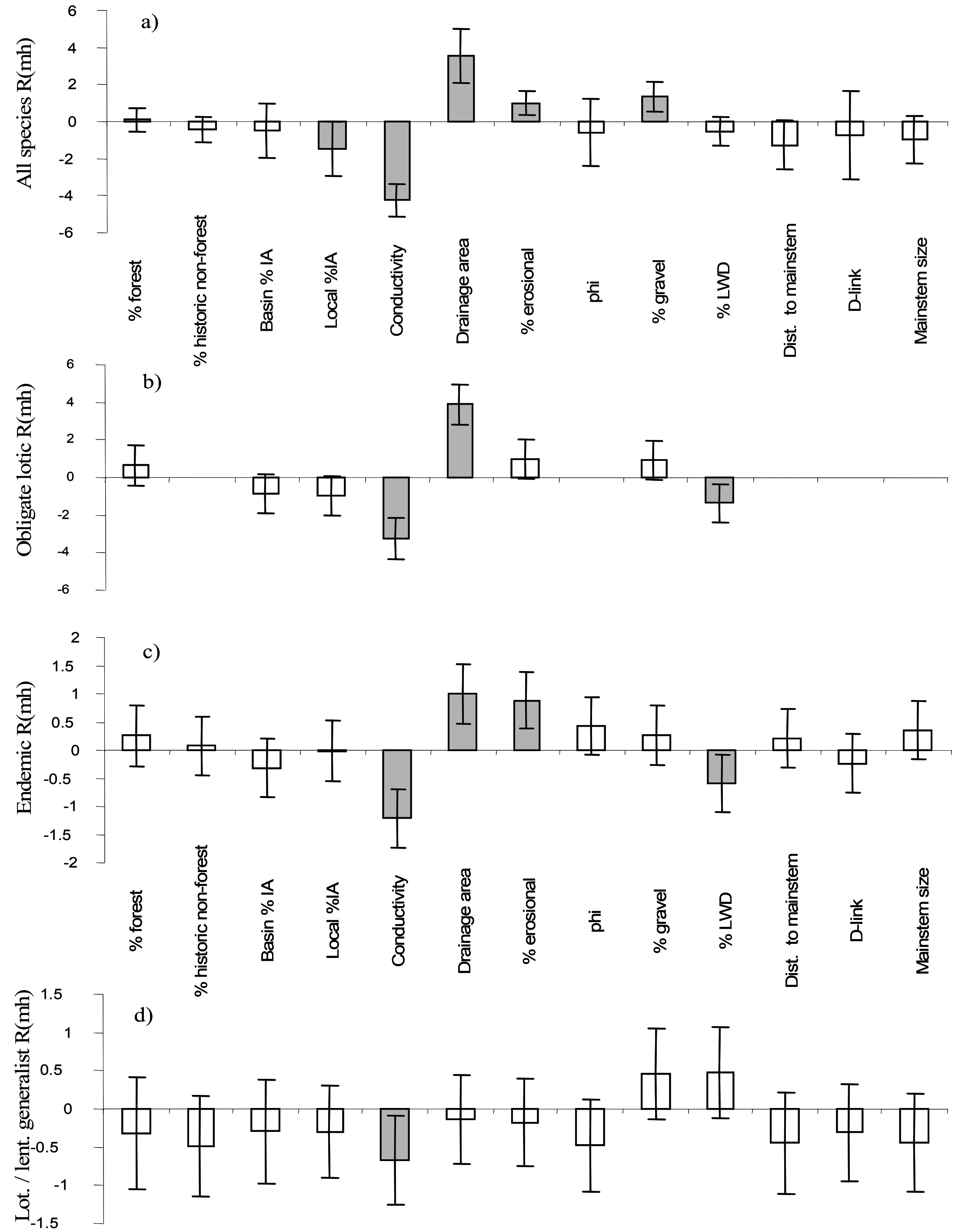

Figure 3. Model-averaged variable effect sizes on $R_{(mh)}$ for all species (a), obligate lotic (b), endemic (c), and lotic / lentic generalist (d) species. Bars indicate 90% confidence intervals with gray columns indicating confidence intervals that do not include zero. All effect sizes are multiplied by 1 standard deviation of the predictor variable mean in order to compare the relative effect of predictor variables on richness given the variance of values observed in the dataset.

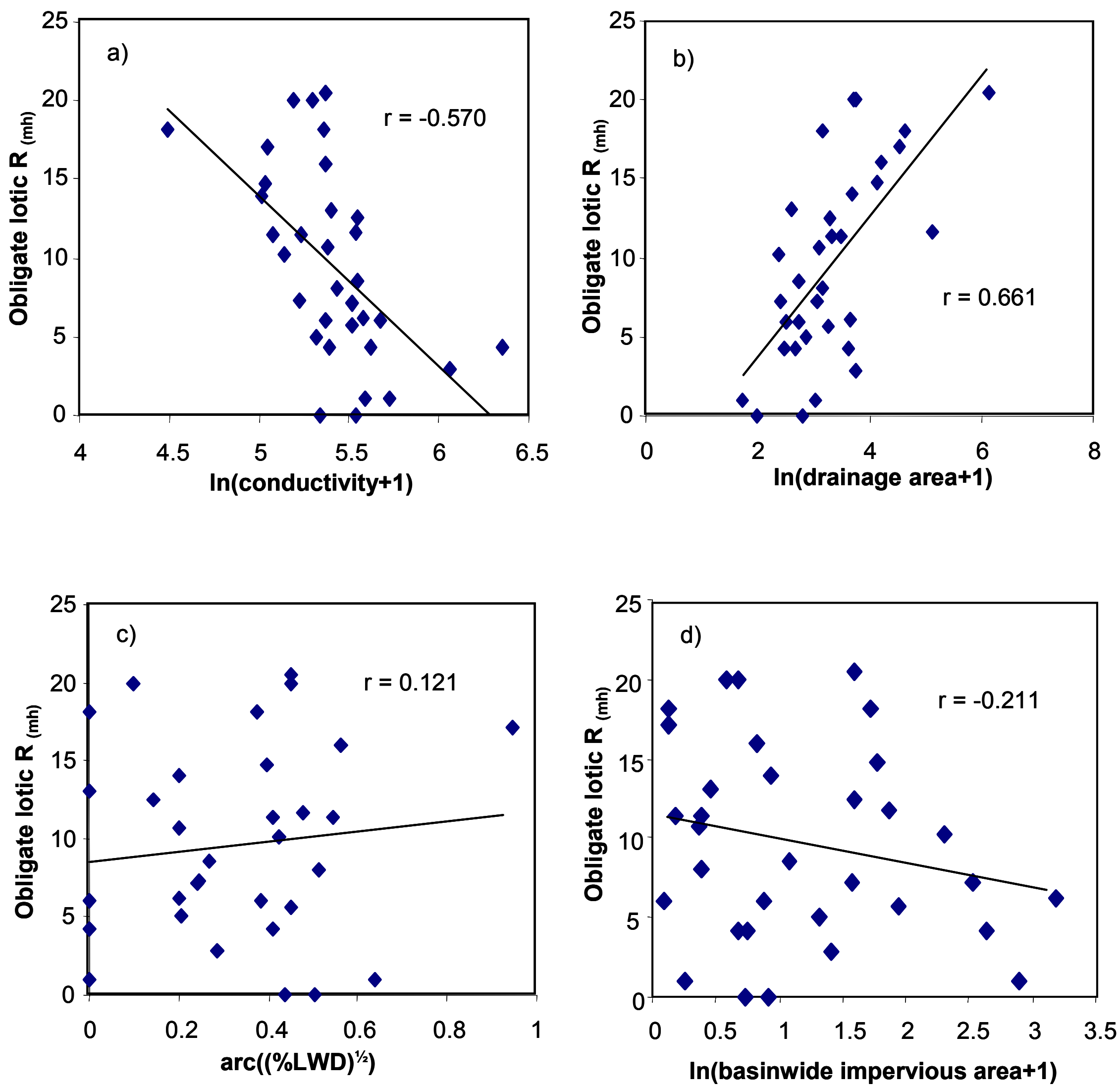

Figure 4. Obligate lotic modeled richness ($R_{(mh)}$) plotted against transformed values of conductivity (a), drainage area (b), percent large woody debris (c), and basinwide percent impervious area (d).

CHAPTER FOUR

DISCUSSION

Fish species richness observed in tributaries to the mainstem of the upper Coosa River system was most accurately predicted by drainage area, which is an indirect measure of in-stream habitat, and by specific conductivity of the stream, which is a direct measure of upland landscape effects. A number of additional in-stream habitat variables exhibited a significant but weaker influence on richness, such as the positive effects of percent erosional habitat and percent gravel in the sampled area, and negative effect of percent of sampled transects with large woody debris. The only remotely-sensed land cover variable showing any substantive relation to richness was the slightly negative effect of local percent impervious area on total species richness. Neither historic non-forested cover nor current forest cover was an important predictor of richness, thus precluding a comparison of historic to recent land cover effects. Counter to findings of other researchers, there was no discernable effect of the measured downstream riverscape variables on richness for any of the assemblages investigated. The ability to accurately predict species richness differed among assemblages, with obligate lotic richness being the most accurately predicted, followed by total species richness, and then endemic species richness. The R^2 values for models of generalist richness were always below 0.231, indicating that this assemblage could not be accurately predicted using the variables measured.

The analysis of replication techniques indicated that models estimating capture efficiency were more parsimonious if all sampling occasions were lumped together. Not only did this validate my use of all replicates together in jackknife models, it also showed that, for the most part, there was little variation in species detection across either spatial or temporal replicates. Nonetheless, comparing the two sampling approaches showed that models based on temporal variation in species detection generally were better supported than models based on spatial variation in species detection. This result indicates that detection varied more over time than it did over the distance between replicates. Though this may be due to changes in sampling efficiencies between visits, it seems more likely that the cause was a lack of true closure in the community as a result of fish species moving in or out of the sampling reach between visits at some sites. In the case of this dataset, temporal replicates were taken up to 43 days after the original sampling occasion, which allowed time for migratory species to move in or out, for floods to displace species, or to allow for species to recolonize after floods. Regardless, this study shows the utility of adding spatial and, if necessary, temporal replicates in lotic community studies; species detection is most likely always incomplete and replication can reduce the resulting bias with minimal additional effort (Yoccoz, Nichols and Boulinier 2001).

Effects of Landscape Factors on Fish Assemblages

One of the most interesting findings of this study was the strong negative correlation between specific conductivity of the streams sampled and the richness of all species assemblages measured. Since conductivity is largely determined by ionic input to the stream from uplands (e.g. agricultural runoff, point source pollutants, road runoff, surface geology runoff) it can considered a direct measure of upland landscape factors. Although others have found conductivity to correlate with fish community structure (Fairchild et al. 1998, Barko et al. 2004) and macroinvertebrate biotic indices (Roy et al. 2003), a lack of correlation with fish richness has been reported in a study of streams in the same region as the ones I sampled (Long and Schorr 2005). It is also important to note that though conductivity has frequently been shown to increase significantly with increasing urban area and impervious surfaces in the basin (Paul and Meyer 2001, Long and Schorr 2005), this was not the case for the range of impervious cover observed in this study. All streams sampled in this study were located in the Ridge and Valley physiographic province, which varies widely in its composition of calcareous surface geology. Though there would be reason to believe that differences in conductivity (and fish species richness) observed could be due to the differences in the geology of stream basins, this appearently was not the case as conductivity did not significantly correlate with percent calcareous geology.

In the context of this study, conductivity may be viewed as a direct measure of pollutant impacts to the stream. This is partially supported by anecdotal observations, such as in the case of site OS03, a stream with the second highest conductivity (427 μS/cm) even though it was located in a primarily forested watershed. In this instance the source of the elevated conductivity clearly was the leaking sewage pump station located directly upstream of the sampling site. Similar phenomena may be occurring upstream of other sites with elevated conductivity, and in many cases the presence of pollution sources may not be well indicated by urban land cover. The degree to which conductivity outperformed remotely-sensed landscape factors may be indicative of the lack of direct connection between landscape classes and stream impacts. Conductivity measurements would pick up the difference between a limed and sprayed field and an unmodified one, or a neighborhood full of leaking septic tanks versus one on a city sewer, whereas these differences would not be measured by remotely sensed data. This idea is further supported by the fact that a similar study found physicochemical measures of upland pollution to be more predictive of fish community condition than remotely-sensed land use data (Meador and Goldstein 2003). The results of my study highlight the need for regular monitoring of physicochemical conditions such as conductivity; these measurements are often simple to take and can implicate direct stressors of stream communities that may be overlooked by remote sensing.

Along with the strong relative support for conductivity as a predictor of fish assemblage diversity, percent impervious area within one kilometer of the site showed an additional negative impact on total fish species richness. The loss of fish species with increasing impervious area coverage was not a surprise, as it has been extensively shown in other studies (see review in Allan 2004). In the case of this study, the impact of impervious areas may represent the increase in flow variability that is often encountered in highly impervious basins (Roy et al. 2005), assuming that conductivity effectively accounted for the increase in pollution associated with increased impervious area.

When comparing basin-wide versus local impervious area, this study indicated that local impervious area was generally more predictive of total species richness. This increasing negative impact of impervious area on fish communities the closer it was to the sampling site has been seen in other studies (Wang, Lyons and Kanehl 2001), and is likely due to a gradual buffering and dilution of impacts the farther the site is from the impervious cover. Although species richness at my sites showed considerable variation in relation to basin-wide percent impervious area, richness of obligate lotic species was consistently low at high levels of impervious cover. This threshold response, though frequently encountered in urbanizing systems, is not well represented through linear modeling (Allan 2004), and may partially explain why basin-wide impervious area was not considered a strongly predictive variable of fish richness in any models.

Effects of Local Reach Factors and Drainage Area on Fish Assemblages

The second dominant factor that was found to drive fish assemblage richness, drainage area, was certainly to be expected. Researchers have consistently found species richness to increase downstream along the longitudinal profile of a stream (reviewed in Matthews 1986) and to increase with increasing stream order when compared to other streams in the same region (Whiteside and McNatt 1972, Paller 1994). The impact of drainage area should be especially apparent in this dataset, as drainage area for sampled sites ranged over two orders of magnitude (4.6 km^2 - 456 km^2).

Though the trend of increasing fish species richness with increasing drainage area is well known, the exact mechanisms behind this trend are not. One hypothesis for the increase in species richness with increasing stream size is that larger streams contain more complex habitat and thus can support more species (Schlosser 1982, Gorman and Karr 1978). This hypothesis can be somewhat intractable when it comes to consistent testing because complexity of habitat could be measured in a myriad of biologically significant ways. In the case of my dataset, the primary measures of habitat complexity either showed no correlation with drainage area (standard deviation of particle size, standard deviation of depth, and coefficient of variation of velocity) or a negative correlation with drainage area (coefficient of variation of depth). This suggests that, in this case, increases in species richness are not attributable to increases in habitat heterogeneity. A related explanation for increased richness with increasing stream drainage area is that larger streams have greater habitat volume (Angermeier and Schlosser 1989). This is apparent when looking at pool habitat, which often contains higher species diversity than riffle habitat (Schlosser 1982). In the streams studied here, the two variables measuring habitat volume, average width and depth, certainly increased with increasing drainage area, thus supporting the hypothesis that fish richness was driven by available habitat volume. Because drainage area is the primary factor defining many in-stream habitat variables (habitat volume, depth regime, velocity, etc.) it can be viewed largely as an in-stream habitat variable itself.

A third explanation for the decrease in fish species richness as one moves up a stream's longitudinal profile was put forth by Horwitz (1978). This study found stream flow variability was higher in the headwaters and that fish diversity was tightly inversely correlated with variability in flow. Horwitz explained this phenomenon as occurring either 1) because variability in the environment allowed generalist species to out-compete habitat specialists and thus prevented the increase in diversity associated with specialization, or 2) because flow variability increased the extirpation rate of species. These ideas shaped the "stochastic school" of thought that explains the lack of deterministic community structure (and minor role of interspecific competition) in streams as a result of high environmental variability (Grossman, Moyle and Whittaker, 1982). The results of my study do not contradict this rationale for the drainage area - species richness relationship, which in some ways may be viewed as an "upland riverscape" view of drainage area. All of the increases in total richness due to increases in drainage area (3.6 species per standard deviation of drainage area) could be attributed to accumulation of obligate lotic species (3.9 species per standard deviation of drainage area); this indicates that either Horwitz's first explanation is correct or that obligate lotic species are more easily extirpated and less likely to reestablish after hydrologic disturbances. Future studies could be useful in testing the habitat variability explanation of the drainage area - species richness relationship from Horowitz against the habitat volume explanation of Angermeier and Schlosser. Though experimental manipulation of habitat volume (via dredging or filling) or flow variability (via damming or storm flow retention) may be nearly impossible to achieve ethically and without significantly altering stream connectivity or local geomorphology, it may be possible to substitute time for space and compare species richness in streams between years of high and low flow variability.

Aside from the strong driving factors of stream drainage area, fish assemblage richness was significantly related to a few directly measured local habitat variables. Not surprisingly, endemic fish richness was positively related to percent erosional habitat, as this assemblage had a high percentage of riffle-specialist fishes (e.g. *Phenacobius catostomus, Cottus carolinae zopherus, Etheostoma jordani*.) and fewer pool specialist fishes (e.g. *Micropterus sp*., *Moxostoma sp*.). The percentage of gravel on the stream bed also had a small positive impact on total fish richness. Possibly, species richness increased with gravel because less of the habitat was devoted to suboptimal sand and bedrock substrates (Walters, Leigh and Bearden 2003). This trend was not more pronounced with regards to obligate lotic species as would be expected; I suspect this was due to both the high variability in obligate lotic species assemblages, and the small amount of assemblage variability left to be explained after conductivity and drainage area effects were taken into account.

Another local habitat variable that significantly altered species richness in sampled streams was the percent of sampled cross sections with large woody debris. This was a rather curious finding considering that the significant negative impact of woody debris on species diversity found in this study conflicts with the hypothesis that woody debris increases both habitat volume and diversity (Angermeier and Karr 1984). One possible explanation for the observed trend was that increased woody debris provided additional habitat for larger fish and generalists such as *Lepomis* and *Micropterus* species and proportionally less habitat for small riffle-dependent species. This scenario seems unlikely however, given that there was no correlation between percent erosional habitat and percent large woody debris. More than likely, the trend observed was simply an artifact of a few sites with higher diversity than would be predicted by conductivity and drainage area also lacking woody debris. Further, when not accounting for drainage area or conductivity, richness was positively associated large woody debris, suggesting that the negative influence of large woody debris in multivariate models lacked ecological significance.

Generalist species richness was not well predicted by any of the variables measured. The lack of strong predictive relations between generalist fish richness and direct measures of stream degradation indicates that, for the types of streams investigated in this study, inclusion of generalist species richness in any metrics of stream health would likely add extraneous variation without increasing predictive power. This is significant because others have used richness of generalist species in homogenization metrics to indicate degraded systems even in the absence of changes in the native endemic fish populations (Scott and Helfman 2001, Scott 2006). The lack of connection between generalist species richness and impairment in my study may be due to the fact that study streams were located in lowlands, that generalist species were classified somewhat differently than the cosmopolitan species used by others (Walters, Leigh and Bearden 2003, Scott and Helfman 2001) and that all sites may have experienced enough impairment to have lead to invasion by cosmopolitan species.

Effects of Downstream Riverscape Factors on Fish Assemblages

An unexpected result of this study was the lack of support for models that included downstream riverscape variables. Other authors have found notable differences between fish assemblages in adventitious streams (tributary streams flowing into a stream of much greater size) compared to assemblages in non-adventitious streams of comparable size (Whiteside and McNatt 1972, Osbourne and Wiley 1992, Fairchild et al. 1998, Grenouillet, Pont and Herisse 2004, Schaefer and Kerfoot 2004, Smith and Craft 2005). Often, assemblages in adventitious streams are characterized by the presence of species usually found only in mainstem rivers. However, I collected relatively few species that would be characterized as mainstem fishes and most of the common fish from the regional species pool that were not collected were species more frequently encountered in large streams (Freeman et al. 2005, Boschung and Mayden 2004). This lack of big river fish is even more surprising when considering that some samples were taken on tributaries essentially where they joined the backwater channel of the mainstem.

One explanation for the lack of mainstem fishes in my samples could be that the source populations of these fishes in the mainstem may already be depressed as a result of habitat degradation and thus fail to provide frequent migrants to tributary streams. It is also possible that mainstem species are less likely to occur in tributaries during baseflow conditions than during high flows, when tributaries may provide refuge. However, because basin-wide impervious area was higher at sites closer to the mainstem, it is possible that increases in richness resulting from proximity of the mainstem were masked by a decrease in richness due to the increase in basin-wide impervious cover. Conversely, this trend may have resulted in basin-wide impervious area underperforming as a predictor variable. Additionally, streams that were in close proximity to the mainstem could have experienced additional impacts and elevated levels of habitat variability because water levels are variable over much of the mainstem due to the operation of the hydroelectric dams located upstream on the Etowah and Coosawattee Rivers. This impact is even apparent in tributaries to the lower Oostanaula River which fill with high waters backflowing up the Oostanaula River during periods of water release from Allatoona Dam on the Etowah River.

Though all downstream riverscape variables measured in this study failed as strong predictors of fish assemblage richness, there may be other unmeasured downstream factors that are tempering these results. For instance, distance to the mainstem may fail to be predictive because it fails to take into account what type of habitat exists over that distance; fish have been shown to migrate different distances through different habitats (Albanese, Angermeier, and Dorai-Raj 2004). Additionally, if riverscape trends are driven by source-sink dynamics, then downstream riverscape effects in tributaries may be more determined by the quality of habitat patches in the mainstem and the distance between sampling locations and those patches.

Conclusions

There are excellent conceptual reasons to believe that fish species richness in tributary streams is driven by a combination of variables relating to in-stream habitat, land use on the upland landscape, and the downstream riverscape context of a site. This study's failure to show strong effects from all of these factors is likely due to the spatiotemporal context in which these variables were analyzed. The upper Coosa River river system has experienced extensive historic agricultural impacts, increasing urban impact, occasional industrial point source impacts, and effects of hydroelectric dam operation, and it is likely that the fish richness in mainstem tributaries is affected by stressors propagated from both upstream and downstream. It is also likely that these stressors were not always clearly measured in this study by in-stream habitat condition or remotely-sensed upland land uses. Regardless, this study does highlight 1) the utility of a simple water-quality measure, conductivity, for tracking potential stress to fish communities, 2) the importance of understanding where a stream is along the river continuum when performing community analyses, and 3) the utility of assessing fish communities using the estimated richness of multiple biologically-defined fish assemblages.

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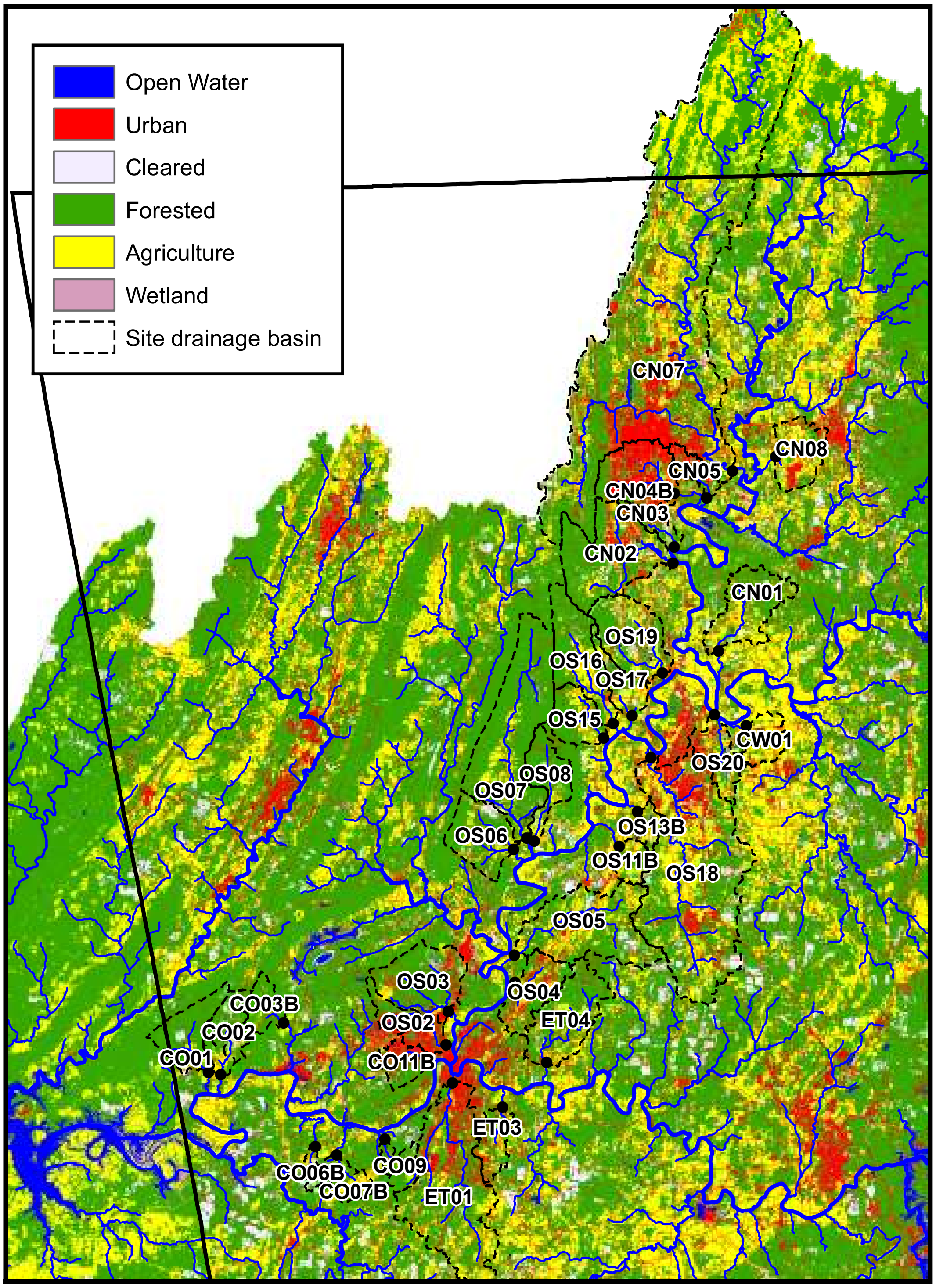
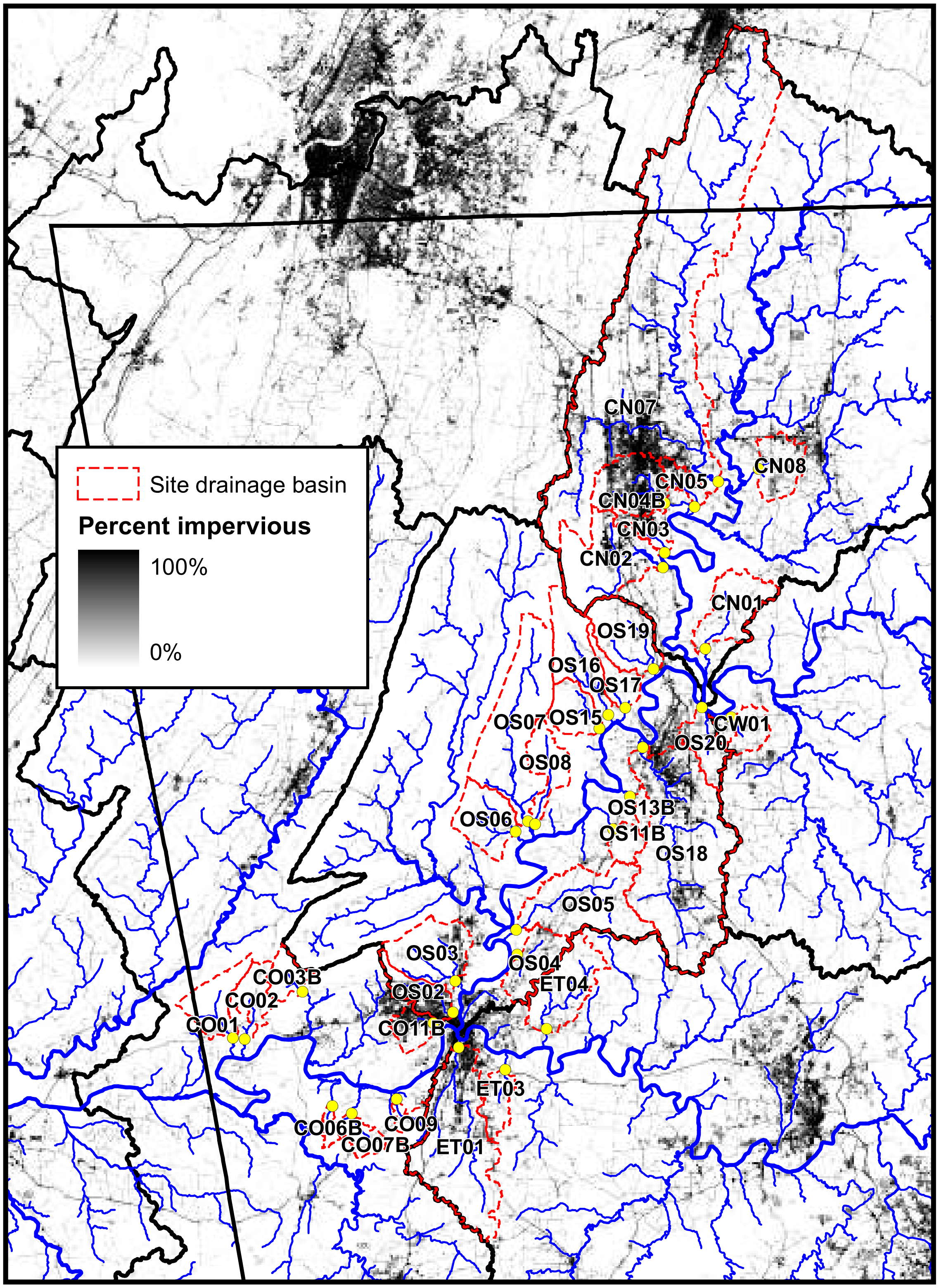
APPENDICES

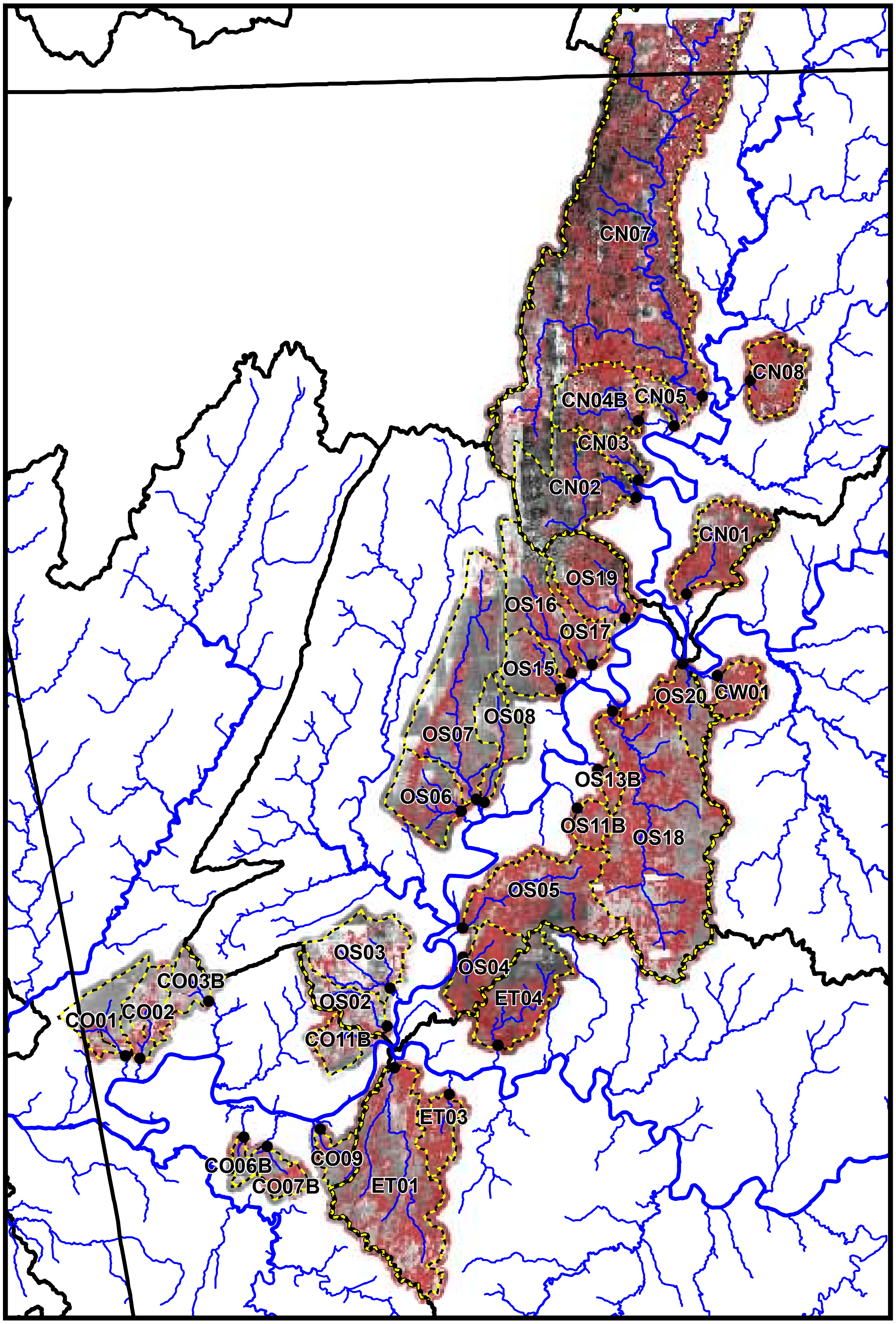
APPENDIX A. Land use classification of sample site drainage basins. Instate portions of the land use layer were generated from the 18-class land use layer developed for the Georgia-GAP project. Out of state portions were patched in from the 1992 National Land Cover Database.



APPENDIX B. Impervious area classification of sample site drainage basins. Impervious area layer was generated from the 2001 National Land Cover Dataset.



APPENDIX C. Historic aerial photography. This layer was generated from 1938 Soil Conservation Service aerial photograph index sheets. Areas classified as non-forested are highlighted in red.



APPENDIX D. Descriptive statistics for variables not included in final models. Shapiro-Wilk test of transformed data indicates the degree to which the data could be drawn from a normal distribution. (as Pr<W increases, data more approximate a normal distribution). Continued on next page.

Variable	Raw data Mean	StDev	Min	Max	Transform-ation	transformed data Mean	StDev	Min	Max	Shapiro-Wilk test W	Pr<W
tubidity (NTU)	8.21	7.64	1.29	36.49	ln(x+1)	1.989	0.653	0.828	3.624	0.953	0.167
% gradient	0.303	0.269	-0.035	1.444	ln(x+1)	0.248	0.177	-0.036	0.894	0.892	0.003
width (m)	6.4	2.5	2.8	12.5	ln(x+1)	1.949	0.324	1.345	2.605	0.976	0.648
proportion open water in basin	0.007	0.006	0.001	0.028	arcsine($x^{1/2}$))	0.076	0.033	0.030	0.169	0.899	0.005
proportion urban land in basin	0.153	0.132	0.031	0.561	arcsine($x^{1/2}$))	0.377	0.170	0.178	0.847	0.882	0.002
proportion agriculture in basin	0.215	0.129	0.029	0.670	arcsine($x^{1/2}$))	0.466	0.158	0.171	0.959	0.956	0.203
proportion cleared land in basin	0.065	0.074	0.001	0.449	arcsine($x^{1/2}$))	0.239	0.111	0.037	0.735	0.749	<0.001
proportion wetland in basin	0.003	0.002	0	0.009	arcsine($x^{1/2}$))	0.053	0.020	0.011	0.095	0.952	0.150
maximum velocity at site (m/s)	0.57	0.26	0.03	1.12	none	0.565	0.255	0.030	1.120	0.984	0.904
average depth (m)	0.37	0.18	0.19	0.97	ln(x+1)	0.311	0.122	0.173	0.680	0.869	0.001
standard deviation of depth	0.21	0.06	0.13	0.36	ln(x+1)	0.188	0.052	0.119	0.310	0.929	0.033

APPENDIX D. Continued.

Variable	Raw data: Mean	StDev	Min	Max	Transform-ation	transformed data: Mean	StDev	Min	Max	Shapiro-Wilk test: W	Pr<W
average velocity (m/s)	0.110	0.091	0	0.298	ln(x+1)	0.101	0.080	0	0.261	0.906	0.008
standard deviation of velocity	0.103	0.055	0	0.208	none	0.103	0.055	0	0.208	0.979	0.769
standard deviation of particle size	1.48	0.45	0.86	2.72	none	1.483	0.452	0.864	2.724	0.942	0.078
proportion sand (<2 mm)	0.128	0.151	0	0.590	arcsine($x^{1/2}$))	0.299	0.238	0	0.876	0.940	0.070
proportion cobble (64-512mm)	0.095	0.182	0	0.740	arcsine($x^{1/2}$))	0.220	0.268	0	1.036	0.785	<0.001
proportion bedrock	0.152	0.185	0	0.679	arcsine($x^{1/2}$))	0.316	0.284	0	0.969	0.903	0.006
proportion of transects with rootmats	0.037	0.053	0	0.239	arcsine($x^{1/2}$))	0.149	0.131	0	0.511	0.903	0.006
proportion of transects with undercut banks	0.007	0.013	0	0.041	arcsine($x^{1/2}$))	0.039	0.073	0	0.205	0.568	<0.001
coefficient of variation of depth	0.6	0.2	0.3	1.0	none	61.200	18.232	30.962	99.473	0.947	0.107
coefficient fo variation of velocity	147.2	117.1	0	612.3	ln(x+1)	4.688	1.028	0	6.419	0.730	<0.001
proportion open canopy	0.3	0.2	0	0.7	ln(x+1)	3.048	0.843	1.027	4.299	0.955	0.192

APPENDIX E. Matrix of Pearson correlation coefficients for all transformed predictive variables. Bolded values indicate a $p<0.05$ for 33 sites. Continued on next 2 pages.

	particle size (phi)	st.dev. of particle size	% sand (<2 mm)	% of gravel (2-64 mm)	% cobble (64-512mm)	% bedrock	% erosional habitat	% gradient	% LWD	% of transects with rootmats	% with undercut banks	average depth (m)	CV of depth
particle size (phi)	**1.000**	-0.144	**-0.779**	-0.274	**0.770**	0.234	0.218	**0.680**	-0.301	0.336	-0.089	**-0.459**	**0.612**
st.dev. of particle size	-0.144	**1.000**	0.287	-0.236	0.188	0.113	-0.082	0.023	0.304	-0.001	0.188	0.070	-0.244
% sand (<2 mm)	**-0.779**	0.287	**1.000**	-0.095	**-0.367**	**-0.405**	-0.072	**-0.446**	**0.377**	-0.017	-0.019	**0.499**	**-0.490**
% of gravel (2-64 mm)	-0.274	-0.236	-0.095	**1.000**	**-0.566**	**-0.493**	-0.072	**-0.431**	0.132	-0.139	0.136	0.116	-0.020
% cobble (64-512mm)	**0.770**	0.188	**-0.367**	**-0.566**	**1.000**	0.052	0.187	**0.633**	-0.249	0.282	-0.045	-0.225	**0.353**
% bedrock	0.234	0.113	**-0.405**	**-0.493**	0.052	**1.000**	-0.092	0.267	-0.147	-0.081	-0.038	**-0.419**	0.058
% erosional habitat	0.218	-0.082	-0.072	-0.072	0.187	-0.092	**1.000**	**0.476**	-0.066	-0.001	0.092	**-0.366**	0.210
% gradient	**0.680**	0.023	**-0.446**	**-0.431**	**0.633**	0.267	**0.476**	**1.000**	-0.301	0.083	-0.056	**-0.418**	**0.401**
% LWD	-0.301	0.304	**0.377**	0.132	-0.249	-0.147	-0.066	-0.301	**1.000**	0.320	0.321	0.143	-0.191
% of transects with rootmats	0.336	-0.001	-0.017	-0.139	0.282	-0.081	-0.001	0.083	0.320	**1.000**	0.007	-0.058	0.221
% with undercut banks	-0.089	0.188	-0.019	0.136	-0.045	-0.038	0.092	-0.056	0.321	0.007	**1.000**	0.055	-0.045
average depth (m)	**-0.459**	0.070	**0.499**	0.116	-0.225	**-0.419**	**-0.366**	**-0.418**	0.143	-0.058	0.055	**1.000**	**-0.667**
CV of depth	**0.612**	-0.244	**-0.490**	-0.020	**0.353**	0.058	0.210	**0.401**	-0.191	0.221	-0.045	**-0.667**	**1.000**
st. dev. of depth	-0.002	-0.036	0.124	0.227	0.007	**-0.479**	-0.269	-0.148	0.092	0.139	0.078	**0.621**	0.118
average velocity (m/s)	-0.260	0.000	0.296	0.165	-0.123	**-0.360**	**0.709**	0.071	0.021	-0.113	0.088	0.176	**-0.359**
maximum velocity at site (m/s)	0.124	0.167	0.061	-0.012	0.173	-0.180	**0.688**	**0.372**	0.111	0.051	0.224	0.040	-0.059
st. dev. of velocity	-0.083	0.115	0.143	0.079	-0.021	-0.195	**0.815**	0.249	0.083	-0.093	0.106	0.058	-0.206
CV of velocity	0.053	0.106	-0.026	-0.067	-0.014	0.157	-0.056	0.049	0.200	0.176	0.114	0.009	0.253
width (m)	-0.252	0.023	0.279	0.155	-0.158	-0.342	0.123	-0.009	0.117	-0.136	-0.099	**0.539**	**-0.554**
Drainage area (km2)	-0.182	0.066	0.266	0.171	-0.084	**-0.423**	0.293	-0.044	0.265	-0.019	0.080	**0.453**	**-0.455**
% open canopy	-0.231	-0.282	0.301	0.214	-0.109	**-0.481**	0.151	-0.110	0.019	-0.094	-0.139	**0.374**	-0.258
% of basin non-forested in 1938	**-0.415**	0.199	0.175	-0.065	-0.250	0.194	-0.101	**-0.425**	-0.056	-0.237	0.104	0.158	**-0.356**
% of basin forested	**0.417**	-0.102	-0.074	-0.080	**0.349**	-0.235	0.149	0.318	0.135	**0.432**	-0.118	0.046	0.320
% agriculture in basin	**-0.436**	0.126	**0.369**	-0.123	-0.317	0.155	0.119	**-0.344**	0.036	-0.137	0.024	0.210	**-0.375**
% cleared land in basin	-0.160	0.018	-0.040	0.331	-0.203	-0.035	-0.341	-0.338	-0.104	-0.124	0.133	-0.039	0.044
% urban land in basin	-0.073	0.107	-0.187	0.077	-0.031	0.118	-0.103	0.058	-0.126	-0.290	0.098	-0.159	-0.153
% open water in basin	**-0.357**	-0.025	0.156	0.069	-0.223	0.105	-0.011	-0.212	0.158	-0.129	0.067	-0.195	-0.059
% wetland in basin	-0.169	0.109	0.160	-0.141	0.057	0.063	-0.151	-0.180	0.047	0.063	-0.007	-0.236	-0.018
% basin impervious area (IA)	-0.126	0.209	-0.092	0.071	-0.016	0.064	-0.048	0.070	-0.060	-0.296	0.093	-0.086	-0.244
% 1 km radius impervious area	0.094	0.033	-0.170	0.030	0.195	-0.049	-0.018	0.132	-0.189	-0.095	0.128	-0.134	-0.067
tubidity (NTU)	**-0.446**	-0.064	**0.436**	0.036	-0.276	-0.214	-0.029	-0.222	0.137	-0.102	0.049	**0.427**	-0.317
Conductivity (mS/cm)	-0.145	-0.172	0.143	-0.273	0.039	-0.007	-0.152	-0.135	-0.287	-0.129	0.042	0.248	-0.145
Distance to mainstem (m)	0.237	**-0.502**	-0.202	-0.177	0.031	0.087	-0.145	-0.077	-0.223	0.058	-0.091	0.122	0.139
D-link	-0.091	0.257	0.087	0.166	0.092	-0.280	-0.004	0.036	0.085	-0.141	0.111	0.008	-0.166
Mainstem size	**0.420**	-0.311	**-0.474**	0.118	0.149	0.115	0.003	0.152	-0.131	0.106	0.108	-0.314	**0.525**

APPENDIX E. Continued.

	st. dev. of depth	average velocity (m/s)	maximum velocity at site (m/s)	st. dev. of velocity	CV of velocity	width (m)	Drainage area (km2)	% open canopy	% of basin non-forested in 1938	% of basin forested	% agriculture in basin	% cleared land in basin	% urban land in basin
particle size (phi)	-0.002	-0.260	0.124	-0.083	0.053	-0.252	-0.182	-0.231	**-0.415**	**0.417**	**-0.436**	-0.160	-0.073
st.dev. of particle size	-0.036	0.000	0.167	0.115	0.106	0.023	0.066	-0.282	0.199	-0.102	0.126	0.018	0.107
% sand (<2 mm)	0.124	0.296	0.061	0.143	-0.026	0.279	0.266	0.301	0.175	-0.074	**0.369**	-0.040	-0.187
% of gravel (2-64 mm)	0.227	0.165	-0.012	0.079	-0.067	0.155	0.171	0.214	-0.065	-0.080	-0.123	0.331	0.077
% cobble (64-512mm)	0.007	-0.123	0.173	-0.021	-0.014	-0.158	-0.084	-0.109	-0.250	**0.349**	-0.317	-0.203	-0.031
% bedrock	**-0.479**	**-0.360**	-0.180	-0.195	0.157	-0.342	**-0.423**	**-0.481**	0.194	-0.235	0.155	-0.035	0.118
% erosional habitat	-0.269	**0.709**	**0.688**	**0.815**	-0.056	0.123	0.293	0.151	-0.101	0.149	0.119	-0.341	-0.103
% gradient	-0.148	0.071	**0.372**	0.249	0.049	-0.009	-0.044	-0.110	**-0.425**	0.318	**-0.344**	-0.338	0.058
% LWD	0.092	0.021	0.111	0.083	0.200	0.117	0.265	0.019	-0.056	0.135	0.036	-0.104	-0.126
% of transects with rootmats	0.139	-0.113	0.051	-0.093	0.176	-0.136	-0.019	-0.094	-0.237	**0.432**	-0.137	-0.124	-0.290
% with undercut banks	0.078	0.088	0.224	0.106	0.114	-0.099	0.080	-0.139	0.104	-0.118	0.024	0.133	0.098
average depth (m)	**0.621**	0.176	0.040	0.058	0.009	**0.539**	**0.453**	**0.374**	0.158	0.046	0.210	-0.039	-0.159
CV of depth	0.118	**-0.359**	-0.059	-0.206	0.253	**-0.554**	**-0.455**	-0.258	**-0.356**	0.320	**-0.375**	0.044	-0.153
st. dev. of depth	**1.000**	-0.161	0.005	-0.101	0.294	0.159	0.164	0.204	-0.184	**0.454**	-0.159	-0.065	**-0.358**
average velocity (m/s)	-0.161	**1.000**	**0.698**	**0.854**	-0.275	**0.509**	**0.635**	**0.392**	0.084	-0.010	0.283	-0.134	-0.086
maximum velocity at site (m/s)	0.005	**0.698**	**1.000**	**0.856**	-0.146	**0.387**	**0.513**	0.336	-0.042	0.146	0.193	-0.324	-0.111
st. dev. of velocity	-0.101	**0.854**	**0.856**	**1.000**	-0.081	**0.470**	**0.569**	**0.365**	0.080	0.000	0.302	-0.313	-0.043
CV of velocity	0.294	-0.275	-0.146	-0.081	**1.000**	-0.194	-0.179	-0.296	-0.006	-0.010	0.117	0.262	-0.223
width (m)	0.159	**0.509**	**0.387**	**0.470**	-0.194	**1.000**	**0.888**	**0.527**	-0.038	0.107	0.009	**-0.368**	0.116
Drainage area (km2)	0.164	**0.635**	**0.513**	**0.569**	-0.179	**0.888**	**1.000**	**0.492**	-0.034	0.193	0.028	-0.329	0.003
% open canopy	0.204	**0.392**	0.336	**0.365**	-0.296	**0.527**	**0.492**	**1.000**	-0.041	0.093	0.145	-0.190	-0.188
% of basin non-forested in 1938	-0.184	0.084	-0.042	0.080	-0.006	-0.038	-0.034	-0.041	**1.000**	**-0.671**	**0.767**	-0.062	0.237
% of basin forested	**0.454**	-0.010	0.146	0.000	-0.010	0.107	0.193	0.093	**-0.671**	**1.000**	**-0.495**	-0.300	**-0.608**
% agriculture in basin	-0.159	0.283	0.193	0.302	0.117	0.009	0.028	0.145	**0.767**	**-0.495**	**1.000**	-0.071	-0.222
% cleared land in basin	-0.065	-0.134	-0.324	-0.313	0.262	**-0.368**	-0.329	-0.190	-0.062	-0.300	-0.071	**1.000**	-0.079
% urban land in basin	**-0.358**	-0.086	-0.111	-0.043	-0.223	0.116	0.003	-0.188	0.237	**-0.608**	-0.222	-0.079	**1.000**
% open water in basin	-0.329	0.071	-0.046	0.017	-0.130	-0.049	-0.017	0.103	0.300	-0.324	0.133	0.004	0.295
% wetland in basin	**-0.381**	-0.100	-0.159	-0.173	-0.278	-0.207	-0.135	-0.043	0.166	-0.316	-0.094	0.126	**0.434**
% basin impervious area (IA)	**-0.353**	0.050	0.022	0.079	-0.302	0.167	0.093	-0.083	0.241	**-0.596**	-0.172	-0.089	**0.964**
% 1 km radius impervious area	-0.245	0.055	0.044	-0.005	**-0.372**	0.264	0.187	0.173	0.069	-0.241	-0.270	-0.104	**0.596**
tubidity (NTU)	0.110	**0.367**	0.253	0.216	-0.196	**0.455**	**0.436**	0.190	0.152	0.001	0.190	-0.120	-0.020
Conductivity (mS/cm)	0.041	-0.036	-0.229	-0.115	-0.130	-0.039	-0.083	0.009	0.240	-0.325	0.037	0.077	0.292
Distance to mainstem (m)	0.173	-0.224	-0.284	-0.285	0.196	-0.028	-0.055	0.010	-0.076	0.105	0.013	0.121	-0.320
D-link	-0.021	0.153	-0.018	-0.001	-0.238	0.223	0.245	-0.042	-0.216	0.208	**-0.355**	-0.057	0.186
Mainstem size	0.157	-0.254	-0.191	-0.279	-0.018	-0.323	-0.308	-0.092	**-0.437**	**0.498**	**-0.383**	0.127	**-0.404**

APPENDIX E. Continued.

	% open water in basin	% wetland in basin	% basin impervious area (IA)	% 1 km radius impervious area	tubidity (NTU)	Conductivity (mS/cm)	Distance to mainstem (m)	D-link	Mainstem size
particle size (phi)	**-0.357**	-0.169	-0.126	0.094	**-0.446**	-0.145	0.237	-0.091	**0.420**
st.dev. of particle size	-0.025	0.109	0.209	0.033	-0.064	-0.172	**-0.502**	0.257	-0.311
% sand (<2 mm)	0.156	0.160	-0.092	-0.170	**0.436**	0.143	-0.202	0.087	**-0.474**
% of gravel (2-64 mm)	0.069	-0.141	0.071	0.030	0.036	-0.273	-0.177	0.166	0.118
% cobble (64-512mm)	-0.223	0.057	-0.016	0.195	-0.276	0.039	0.031	0.092	0.149
% bedrock	0.105	0.063	0.064	-0.049	-0.214	-0.007	0.087	-0.280	0.115
% erosional habitat	-0.011	-0.151	-0.048	-0.018	-0.029	-0.152	-0.145	-0.004	0.003
% gradient	-0.212	-0.180	0.070	0.132	-0.222	-0.135	-0.077	0.036	0.152
% LWD	0.158	0.047	-0.060	-0.189	0.137	-0.287	-0.223	0.085	-0.131
% of transects with rootmats	-0.129	0.063	-0.296	-0.095	-0.102	-0.129	0.058	-0.141	0.106
% with undercut banks	0.067	-0.007	0.093	0.128	0.049	0.042	-0.091	0.111	0.108
average depth (m)	-0.195	-0.236	-0.086	-0.134	**0.427**	0.248	0.122	0.008	-0.314
CV of depth	-0.059	-0.018	-0.244	-0.067	-0.317	-0.145	0.139	-0.166	**0.525**
st. dev. of depth	-0.329	**-0.381**	**-0.353**	-0.245	0.110	0.041	0.173	-0.021	0.157
average velocity (m/s)	0.071	-0.100	0.050	0.055	**0.367**	-0.036	-0.224	0.153	-0.254
maximum velocity at site (m/s)	-0.046	-0.159	0.022	0.044	0.253	-0.229	-0.284	-0.018	-0.191
st. dev. of velocity	0.017	-0.173	0.079	-0.005	0.216	-0.115	-0.285	-0.001	-0.279
CV of velocity	-0.130	-0.278	-0.302	**-0.372**	-0.196	-0.130	0.196	-0.238	-0.018
width (m)	-0.049	-0.207	0.167	0.264	**0.455**	-0.039	-0.028	0.223	-0.323
Drainage area (km2)	-0.017	-0.135	0.093	0.187	**0.436**	-0.083	-0.055	0.245	-0.308
% open canopy	0.103	-0.043	-0.083	0.173	0.190	0.009	0.010	-0.042	-0.092
% of basin non-forested in 1938	0.300	0.166	0.241	0.069	0.152	0.240	-0.076	-0.216	**-0.437**
% of basin forested	-0.324	-0.316	**-0.596**	-0.241	0.001	-0.325	0.105	0.208	**0.498**
% agriculture in basin	0.133	-0.094	-0.172	-0.270	0.190	0.037	0.013	**-0.355**	**-0.383**
% cleared land in basin	0.004	0.126	-0.089	-0.104	-0.120	0.077	0.121	-0.057	0.127
% urban land in basin	0.295	**0.434**	**0.964**	**0.596**	-0.020	0.292	-0.320	0.186	**-0.404**
% open water in basin	**1.000**	**0.683**	0.332	0.284	0.279	0.044	**-0.441**	-0.044	-0.128
% wetland in basin	**0.683**	**1.000**	**0.484**	**0.521**	0.119	**0.369**	**-0.375**	0.100	-0.151
% basin impervious area (IA)	0.332	**0.484**	**1.000**	**0.586**	0.056	0.277	**-0.448**	0.204	**-0.476**
% 1 km radius impervious area	0.284	**0.521**	**0.586**	**1.000**	-0.042	0.283	-0.119	0.305	0.047
tubidity (NTU)	0.279	0.119	0.056	-0.042	**1.000**	0.182	-0.052	-0.067	-0.236
Conductivity (mS/cm)	0.044	**0.369**	0.277	0.283	0.182	**1.000**	0.278	-0.092	-0.045
Distance to mainstem (m)	**-0.441**	**-0.375**	**-0.448**	-0.119	-0.052	0.278	**1.000**	**-0.478**	0.273
D-link	-0.044	0.100	0.204	0.305	-0.067	-0.092	**-0.478**	**1.000**	0.146
Mainstem size	-0.128	-0.151	**-0.476**	0.047	-0.236	-0.045	0.273	0.146	**1.000**

APPENDIX F. Raw un-transformed data for predictive variables used in final models. Continued on next page.

SiteID	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation
CN01	0.559	0.586	0.010	0.013	573	36.1	0.100	1.63	0.000	0.400	4120	12	3345250
CN02	0.658	0.208	0.049	0.027	152	62.2	0.400	3.79	0.150	0.500	628	460	3164650
CN03	0.487	0.397	0.091	0.002	170	10.0	0.289	4.22	0.170	0.553	207	441	3051820
CN04B	0.306	0.458	0.233	0.090	264	37.4	0.220	3.88	0.040	0.495	4421	12	2978110
CN05	0.409	0.495	0.114	0.007	247	10.2	0.244	4.65	0.057	0.919	1376	16	2978110
CN07	0.531	0.457	0.039	0.006	215	456.3	0.410	2.77	0.190	0.750	2211	315	2309440
CN08	0.288	0.715	0.060	0.012	249	24.9	0.110	2.41	0.190	0.580	1906	6	1491260
CO01	0.838	0.173	0.002	0.005	160	26.8	0.080	3.94	0.270	0.963	2526	2502	19036300
CO02	0.704	0.296	0.005	0.007	227	23.1	0.552	3.10	0.241	0.841	2729	2490	18983200
CO03B	0.867	0.106	0.001	0.004	215	14.4	0.562	7.99	0.000	0.048	6085	5	18930900
CO06B	0.385	0.224	0.003	0.007	267	4.6	0.096	4.42	0.000	0.893	7832	4	18669300
CO07B	0.547	0.358	0.006	0.006	220	12.6	0.324	4.93	0.000	0.814	3957	7	18583600
CO09	0.731	0.379	0.014	0.006	291	11.4	0.210	4.38	0.140	0.560	1202	6	18580100
CO11B	0.544	0.330	0.131	0.191	274	13.6	0.070	4.93	0.000	0.710	1254	2402	18495400
CW01	0.187	0.742	0.020	0.013	255	14.8	0.500	3.21	0.070	0.460	2061	4	3968830
ET01	0.541	0.516	0.046	0.207	211	103.0	0.500	3.69	0.000	0.860	1005	981	8555770
ET03	0.516	0.727	0.027	0.039	204	16.6	0.136	5.18	0.042	0.610	2065	957	8317780
ET04	0.696	0.465	0.010	0.035	179	42.2	0.540	5.31	0.010	0.770	2224	13	8179310
OS02	0.385	0.273	0.169	0.261	305	19.9	0.245	3.30	0.356	0.730	866	1414	9885130
OS03	0.713	0.221	0.031	0.130	427	42.0	0.370	7.09	0.080	0.240	2435	1410	9858560
OS04	0.503	0.672	0.039	0.020	255	26.3	0.300	4.33	0.020	0.470	1466	1396	9685060
OS05	0.555	0.566	0.013	0.007	214	67.2	0.324	4.39	0.284	0.902	1913	18	9683720

APPENDIX F. Continued.

SiteID	% basinwide forest cover	% historical basin non-forested	basinwide %IA	1 km radius %IA	conductivity	drainage area	% erosional habitat	average substrate size (phi)	% gravel substrate	% LWD	distance to mainstem	D-link	mainstem flow accumulation
OS06	0.690	0.361	0.005	0.008	186	32.3	0.180	3.96	0.160	0.400	2026	15	8435400
OS07	0.822	0.243	0.001	0.004	155	91.2	0.280	3.44	0.660	0.633	2477	41	8371790
OS08	0.765	0.174	0.001	0.008	88	22.9	0.204	5.71	0.133	0.770	1979	41	8371790
OS11B	0.507	0.656	0.011	0.022	218	11.0	0.274	5.50	0.160	0.226	3921	3	8099150
OS13B	0.425	0.730	0.015	0.030	207	6.3	0.202	2.24	0.234	0.653	1666	2	8032150
OS15	0.685	0.340	0.004	0.011	216	21.0	0.300	2.61	0.040	0.540	1696	1084	7969180
OS16	0.647	0.367	0.008	0.010	198	39.9	0.240	3.72	0.190	0.800	1028	1075	7925700
OS17	0.464	0.592	0.011	0.008	253	15.4	0.060	2.77	0.180	0.240	2391	1063	7849130
OS18	0.458	0.550	0.055	0.085	254	167.0	0.270	3.46	0.210	0.859	1979	43	7806580
OS19	0.560	0.491	0.016	0.058	150	39.3	0.200	4.21	0.040	0.710	1196	1012	7459030
OS20	0.433	0.513	0.039	0.008	184	20.4	0.490	2.70	0.060	0.730	395	994	7359300

APPENDIX G. Parameter estimates and relative variable importance values for naïve richness models. Bolded values indicate a variable with a 90% confidence interval that does not cross zero for parameter estimates and Monte-Carlo results that did not exceed 10% for relative variable importance. Table is continued on the next page.

a) All species

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**48.172**	**11.225**	**14**	**66.635**	**29.708**
basinwide %IA	**log**	**-1.199**	**0.662**	**1**	**-0.110**	**-2.288**
conductivity	**log**	**-7.639**	**1.879**	**14**	**-4.548**	**-10.729**
drainage area	**log**	**1.581**	**0.641**	**12**	**2.636**	**0.526**
% LWD	arc	-4.121	2.685	1	0.296	-8.538
% basinwide forest cover	none	3.951	3.702	1	10.040	-2.138
% erosional habitat	arc	4.127	3.624	2	10.089	-1.834
% gravel substrate	arc	1.923	2.298	1	5.703	-1.856
mainstem flow accumulation	log	0.608	0.889	1	2.071	-0.855
D-link	log	-0.150	0.243	1	0.250	-0.550
1 km radius %IA	log	-0.406	0.688	1	0.725	-1.538
average substrate size (phi)	none	0.208	0.441	1	0.934	-0.517
% historical basin non-forested	none	-1.131	3.243	1	4.204	-6.465
distance to mainstem	log	-0.159	0.822	1	1.192	-1.511

Variable	Relative variable importance	% of random iterations in excedance
conductivity	**0.974**	**0.000**
drainage area	**0.656**	**2.667**
basinwide %IA	**0.235**	**9.333**
% erosional habitat	0.135	19.667
% LWD	0.126	21.667
% basinwide forest cover	0.125	23.667
% gravel substrate	0.106	29.667
distance to mainstem	0.072	44.667
mainstem flow accumulation	0.065	64.000
1 km radius %IA	0.060	69.000
D-link	0.059	71.000
average substrate size (phi)	0.058	78.333
% historical basin non-forested	0.057	80.333

b) Obligate lotic

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**38.177**	**9.402**	**6**	**53.642**	**22.712**
conductivity	**log**	**-7.323**	**1.605**	**6**	**-4.683**	**-9.963**
drainage area	**log**	**2.514**	**0.540**	**6**	**3.402**	**1.625**
% LWD	**arc**	**-5.042**	**2.128**	**1**	**-1.542**	**-8.542**
basinwide %IA	log	-0.896	0.557	1	0.021	-1.813
% basinwide forest cover	none	4.400	3.034	1	9.390	-0.590
% erosional habitat	arc	4.107	2.850	1	8.795	-0.581
average substrate size (phi)	none	0.495	0.357	1	1.082	-0.093

Variable	Relative variable importance	% of random iterations in excedance
drainage area	**0.998**	**0.000**
conductivity	**0.997**	**0.000**
% LWD	**0.413**	**2.333**
basinwide %IA	**0.093**	**9.333**
% basinwide forest cover	0.073	15.000
% erosional habitat	0.071	18.667
average substrate size (phi)	0.065	18.667
mainstem flow accumulation	0.041	32.667
% gravel substrate	0.037	36.000
1 km radius %IA	0.033	41.667
D-link	0.026	60.667
distance to mainstem	0.024	74.667
% historical basin non-forested	0.023	84.000

APPENDIX G. Continued.

c)Endemic

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**26.063**	**8.184**	**11**	**39.525**	**12.602**
% erosional habitat	**arc**	**5.386**	**2.610**	**2**	**9.679**	**1.093**
conductivity	**log**	**-5.341**	**1.327**	**11**	**-3.158**	**-7.525**
drainage area	**log**	**1.590**	**0.479**	**10**	**2.378**	**0.801**
% gravel substrate	**arc**	**3.058**	**1.763**	**2**	**5.957**	**0.158**
% LWD	arc	-2.461	1.970	1	0.780	-5.702
D-link	log	-0.178	0.174	1	0.108	-0.465
average substrate size (phi)	none	0.322	0.315	1	0.841	-0.196
mainstem flow accumulation	log	0.485	0.643	1	1.543	-0.573
basinwide %IA	log	-0.358	0.502	1	0.467	-1.184
1 km radius %IA	log	-0.350	0.497	1	0.468	-1.168
% basinwide forest cover	none	1.891	2.711	1	6.350	-2.568

Variable	Relative variable importance	% of random iterations in excedance
conductivity	**0.975**	**0.000**
drainage area	**0.889**	**0.000**
% erosional habitat	**0.358**	**2.667**
% gravel substrate	**0.192**	**7.000**
% LWD	0.071	23.333
average substrate size (phi)	0.057	34.667
D-link	0.055	35.333
% basinwide forest cover	0.052	37.333
mainstem flow accumulation	0.044	41.667
basinwide %IA	0.044	52.333
1 km radius %IA	0.043	52.000
distance to mainstem	0.034	86.333
% historical basin non-forested	0.033	98.667

d)Lotic / lentic generalists

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**9.211**	**4.105**	**42**	**15.963**	**2.459**
conductivity	log	-1.161	0.721	14	0.025	-2.348
drainage area	**log**	**-0.583**	**0.256**	**35**	**-0.162**	**-1.003**
basinwide %IA	log	-0.419	0.327	11	0.119	-0.957
distance to mainstem	log	-0.458	0.378	8	0.164	-1.080
average substrate size (phi)	none	-0.216	0.181	4	0.081	-0.514
% gravel substrate	arc	0.916	0.904	6	2.403	-0.571
% historical basin non-forested	none	-1.365	1.353	7	0.861	-3.590
% LWD	arc	0.899	1.088	5	2.688	-0.891
% erosional habitat	arc	-1.290	1.479	5	1.142	-3.723
1 km radius %IA	log	-0.029	0.277	2	0.427	-0.485
% basinwide forest cover	none	-0.564	1.939	3	2.625	-3.752
D-link	log	-0.012	0.098	2	0.149	-0.172
mainstem flow accumulation	log	-0.029	0.357	2	0.559	-0.617

Variable	Relative variable importance	% of random iterations in excedance
drainage area	**0.633**	**2.333**
conductivity	0.273	12.667
basinwide %IA	0.227	19.333
distance to mainstem	0.184	29.000
% historical basin non-forested	0.158	35.000
average substrate size (phi)	0.147	41.333
% erosional habitat	0.144	34.000
% gravel substrate	0.139	41.333
% basinwide forest cover	0.119	58.333
% LWD	0.117	50.333
D-link	0.110	64.000
mainstem flow accumulation	0.106	63.667
1 km radius %IA	0.104	75.333

APPENDIX H. Parameter estimates for $R_{(mh)}$ richness models. Bolded values indicate variables with a 90% confidence interval that do not cross zero. Table is continued on the next page.

a) All species

variable	transform-ation	parameter estimate	standard error	models including parameter	0.90 CI	0.10 CI
intercept	**-**	**80.271**	**4.245**	**12**	**87.253**	**73.290**
conductivity	**log**	**-13.231**	**1.668**	**12**	**-10.487**	**-15.975**
drainage area	**log**	**3.928**	**0.986**	**12**	**5.550**	**2.305**
1 km radius %IA	**log**	**-1.649**	**0.998**	**1**	**-0.008**	**-3.291**
% gravel substrate	**arc**	**5.148**	**1.836**	**1**	**8.167**	**2.129**
distance to mainstem	log	-1.735	1.093	1	0.063	-3.534
mainstem flow accumulation	log	-1.474	1.150	1	0.418	-3.365
% erosional habitat	**arc**	**5.824**	**2.286**	**1**	**9.585**	**2.064**
D-link	log	-0.305	0.604	1	0.688	-1.297
average substrate size (phi)	none	-0.444	0.814	1	0.894	-1.782
% LWD	arc	-2.355	2.045	1	1.009	-5.719
basinwide %IA	log	-0.557	1.023	1	1.127	-2.240
% historical basin non-forested	none	-2.377	2.208	1	1.255	-6.008

b) Obligate lotic species

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**49.885**	**12.154**	**7**	**69.877**	**29.894**
conductivity	**log**	**-10.073**	**2.091**	**7**	**-6.633**	**-13.512**
drainage area	**log**	**4.300**	**0.712**	**7**	**5.470**	**3.129**
% LWD	**arc**	**-6.170**	**2.795**	**1**	**-1.573**	**-10.767**
% erosional habitat	arc	5.836	3.677	1	11.884	-0.212
1 km radius %IA	log	-1.095	0.720	1	0.090	-2.280
% gravel substrate	arc	3.519	2.429	1	7.514	-0.476
basinwide %IA	log	-0.977	0.734	1	0.230	-2.184
% basinwide forest cover	none	4.061	4.012	1	10.659	-2.538

APPENDIX H. Continued.

c)Endemic species

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**19.703**	**6.278**	**12**	**30.028**	**9.377**
% erosional habitat	**arc**	**5.193**	**1.793**	**12**	**8.142**	**2.243**
conductivity	**log**	**-3.777**	**0.992**	**1**	**-2.145**	**-5.409**
drainage area	**log**	**1.094**	**0.357**	**12**	**1.682**	**0.507**
% LWD	**arc**	**-2.668**	**1.414**	**12**	**-0.343**	**-4.993**
average substrate size (phi)	none	0.321	0.230	1	0.699	-0.057
mainstem flow accumulation	log	0.524	0.471	1	1.298	-0.251
basinwide %IA	log	-0.373	0.368	1	0.232	-0.979
% gravel substrate	arc	1.014	1.233	1	3.042	-1.014
% basinwide forest cover	none	1.574	2.003	1	4.869	-1.721
D-link	log	-0.099	0.130	1	0.115	-0.312
distance to mainstem	log	0.288	0.438	1	1.008	-0.432
% historical basin non-forested	none	0.441	1.741	1	3.306	-2.423
1 km radius %IA	log	-0.016	0.371	1	0.595	-0.626

d)Lotic / lentic generalist species

Variable	Transform-ation	Parameter estimate	Standard error	Models including parameter	0.90 CI	0.10 CI
intercept	**-**	**15.599**	**8.471**	**73**	**29.532**	**1.665**
conductivity	**log**	**-2.103**	**1.112**	**40**	**-0.273**	**-3.933**
average substrate size (phi)	none	-0.361	0.276	15	0.094	-0.815
% LWD	arc	2.149	1.635	21	4.839	-0.541
% historical basin non-forested	none	-2.694	2.181	15	0.893	-6.281
% gravel substrate	arc	1.780	1.396	16	4.077	-0.516
mainstem flow accumulation	log	-0.651	0.578	13	0.299	-1.602
distance to mainstem	log	-0.614	0.557	12	0.303	-1.530
% basinwide forest cover	none	-1.957	2.739	4	2.549	-6.463
% erosional habitat	arc	-1.057	2.034	3	2.289	-4.402
D-link	log	-0.127	0.159	9	0.135	-0.389
1 km radius %IA	log	-0.337	0.414	7	0.345	-1.019
drainage area	log	-0.157	0.388	4	0.482	-0.796
basinwide %IA	log	-0.343	0.482	8	0.451	-1.136

APPENDIX I. Fishes encountered at each site.

SPECIES	CN01	CN02	CN03	CN04B	CN05	CN07	CN08	CO01	CO02	CO03B	CO06B	CO07B	CO09	CO11B	CW01	ET01	ET03	ET04	OS02	OS03	OS04	OS05	OS06	OS07	OS08	OS11B	OS13B	OS15	OS16	OS17	OS18	OS19	OS20
Ambloplites ariommus																X		X															
Ameiurus natalis					X							X	X												X								
Amerius nebulosus																											X						
Aplodinotus grunniens						X																											
Campostoma oligolepis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X		X	X	X
Cottus carolinae zopherus		X	X			X		X	X			X			X	X	X	X			X	X	X	X	X			X	X		X	X	
Cyprinella callistia						X																											
Cyprinella lutrensis	X																											X			X	X	X
Cyprinella trichroistia																									X				X				
Cyprinella venusta	X	X	X	X	X	X		X				X				X		X				X	X	X	X			X	X		X	X	X
Cyprinella venusta X lutrensis	X	X	X			X																										X	X
Cyprinus carpio																											X						
Etheostoma coosae		X	X	X	X		X	X		X			X		X	X		X			X	X		X	X	X		X			X	X	X
Etheostoma jordani																X		X			X	X		X	X				X				
Etheostoma rupestre						X																											
Etheostoma stigmaeum		X			X	X		X	X			X				X		X			X	X	X	X	X			X	X		X	X	X
Etheostoma trisella																						X											
Fundulus olivaceus		X						X				X												X	X								
Fundulus stellifer																X		X				X			X				X				
Gambusia affinis	X		X	X	X						X		X	X					X			X	X		X	X	X		X		X	X	X
Gambusia holbrooki				X			X				X											X	X		X		X	X			X		X
Gambusia sp.				X	X		X				X		X			X			X						X		X	X	X		X	X	X
Hypentelium etowanum		X		X	X	X	X		X	X		X	X		X	X		X			X	X		X	X				X		X	X	
Ictalurus punctatus						X																X											
Lepomis auritus	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lepomis cyanellus		X	X	X	X		X		X	X	X	X	X	X	X		X		X		X	X	X		X	X	X	X	X	X	X	X	
Lepomis gulosus		X			X		X				X		X		X				X	X						X				X		X	X
Lepomis macrochirus	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
Lepomis megalotis		X	X		X	X		X		X		X		X		X		X	X	X	X	X	X	X	X	X		X	X		X	X	
Lepomis microlophus			X		X		X	X			X				X				X			X	X	X	X			X	X		X	X	X
Lepomis punctatus	X	X					X		X	X	X	X	X		X	X			X	X	X			X	X	X						X	
Luxilus chrysocephalus		X	X														X	X			X	X	X		X	X		X	X			X	
Lythrurus lirus																								X	X								

APPENDIX I. Continued.

SPECIES	CN01	CN02	CN03	CN04B	CN05	CN07	CN08	CO01	CO02	CO03B	CO06B	CO07B	CO09	CO11B	CW01	ET01	ET03	ET04	OS02	OS03	OS04	OS05	OS06	OS07	OS08	OS11B	OS13B	OS15	OS16	OS17	OS18	OS19	OS20
Micropterus coosae						X				X		X				X		X			X								X			X	
Micropterus punctulatus		X																				X		X								X	
Micropterus salmoides	X	X			X	X	X	X	X	X	X		X					X	X					X	X		X	X	X			X	X
Moxostoma duquesnei		X														X						X			X			X					
Moxostoma erythrurum		X				X						X				X																X	
Moxostoma poecilurum						X																		X					X		X		
Notemigonus crysoleucas																																	X
Notropis chrosomus									X			X		X											X								
Notropis stilbius		X	X	X		X										X		X			X			X	X				X		X	X	X
Notropis xaenocephalus					X			X		X						X		X			X	X		X	X							X	
Noturus leptacanthus						X																		X									
Oncorhynchus mykiss																		X															
Percina kathae						X			X			X	X					X															
Percina lenticula						X																											
Percina nigrofasciata	X	X	X	X		X	X	X	X	X		X	X			X					X		X	X	X	X			X		X	X	
Phenacobius catostomus																X								X									
Pimephales vigilax		X	X			X														X			X					X	X		X		X
Pomoxis nigromaculatus															X				X				X		X			X	X	X			X
Rhinichthys atratulus															X		X																
Semotilus atromaculatus			X		X		X		X			X		X	X		X						X	X	X			X					