EVALUATING CONNECTIVITY IN THREE WATERSHEDS IN THE SOUTHEASTERN UNITED STATES

by

EVAN ROBERT COLLINS

(Under the Direction of Nathan Nibbelink)

ABSTRACT

Fragmentation of hydrologic connectivity is one of many threats to aquatic biodiversity. Increasingly, culverts installed at road-stream crossings have been identified as a significant contributor in fragmentation. Culverts present an interesting challenge for researchers and those seeking to restore connectivity in that they are often not complete barriers to fish passage and are numerous on the landscape. The purposes of this study are to approach these problems with the use of spatial analysis and predictive modelling. This study utilizes random forest modelling and identifies a suite of environmental gradients that relate to impassable culverts. The necessity of rigorous classification of field data to be used to train models is highlighted. Predictions from the random forest models are used to explicitly state the cumulative effect of culverts on overall connectivity for the first time. Finally, this study guides managers by recommending that restoration activities focus on smaller, species-specific scales.

INDEX WORDS: Hydrologic connectivity, Fish passage, Culvert passability, Random forest, Restoration prioritization, Road-crossings

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CHAPTER 1

INTRODUCTION

Freshwater ecosystems support an impressive amount of the world's biodiversity (Darwall and Freyhof 2016). For instance approximately 25% of all vertebrates occur in these ecosystems (Stiassny 1996). Unfortunately, these systems are also some of the most threatened, especially in terms of freshwater fishes (Darwall and Freyhof 2016). This is a pattern that is consistent when the scale of analysis is reduced to the southeastern United States. The Southeast possesses the greatest freshwater species richness and endemism in North America (Abell et al. 2000). Simultaneously, approximately 20% of its fish fauna is at risk of extinction (Jelks et al. 2008).

One factor that has led to higher levels of imperilment among aquatic species in the Southeast is increased levels of development and urbanization (Wenger et al. 2010, Jelks et al. 2008, Folkerts 1997). One facet of urbanization that is directly relevant to aquatic habitat degradation is the increased demand for transportation infrastructure that can accommodate growing urban and suburban populations. At the interface between transportation corridors and streams, road-crossings directly interact with lotic ecosystems and potentially act as barriers to fish movement (Januchowski-Hartley et al. 2014, Anderson et al. 2012, Warren and Pardew 1998). It can safely be assumed that an increase in the quantity and size of roads built as a result of growing human populations increases the potential for habitat degradation and fragmentation of hydrologic connectivity. Fragmentation of hydrologic connectivity has been identified as one of the major threats to freshwater biodiversity (Closs et al. 2016, Gido et al. 2016, Nilsson et al. 2005, Leirman et al. 2005).

Hydrologic connectivity is defined in a broad ecological context as: “water-mediated transport of matter, energy, or organisms within or between elements of the hydrologic cycle” (Pringle 2001). This transport may occur across several interfaces; between the stream and groundwater, the stream and its floodplain, and the stream’s longitudinal length. Although connectivity can refer to interactions occurring in several different directions, the placement of structures across a stream channel primarily affects longitudinal connectivity. Loss of longitudinal connectivity may decrease a species’ ability to maintain populations in less suitable habitat (Warren and Pardew 1998), increase chances of extinction (Winston et al. 1991), or cause decreases in fish abundance and richness in a given stream network (Nislow et al. 2011).

Research and discussions of hydrologic connectivity and fragmentation are often focused on dams. There is a substantial amount of literature documenting how dams alter and fragment habitats, water temperature regimes, nutrient and hydrologic cycles, and act as barriers to movement of animals, nutrients, and materials (Olden 2016, Januchowski-Hartley et al. 2013, Zheng et al. 2012, Soballe et al. 1992). In contrast, the influence of road crossings on smaller lotic systems are less understood. Increasingly, however, road-stream crossings with installed culverts have been found to have the ability to decrease connectivity in lotic ecosystems (Diebel et al. 2015, Januchowski-Hartley et al. 2013, Diebel et al. 2010, Kemp and O’Hanley 2010, Gibson et al. 2005). Like dams, road crossings have the potential to fragment stream habitat and obstruct fish movement (Diebel et al. 2015, Norman et al. 2009, Nislow et al. 2011, Warren and Pardew 1998). Unlike dams, road crossings are not always absolute barriers (Anderson et al. 2012). Road crossings can vary from completely passable to impassable depending on physical structure characteristics, such as type, structure installation, and time of year among other variables (Anderson et al. 2012). For example, free span bridges typically do not decrease connectivity in lotic systems, but improperly installed culvert crossings can often decrease connectivity and impede fish movement and have the potential to affect population genetics of fishes (Evans et al. 2015, Prowell et al. 2012). While culverts are physically smaller than dams, and may at least allow some fish movement (Anderson et al. 2012, Norman et al. 2009, Warren and Pardew 1998), they outnumber dams across a watershed. At least one study found approximately 38 times more culverts than dams in a large Midwestern watershed (Januchowski-Hartley et al. 2013).

Although there is still a good deal of uncertainty regarding what factors constrain movements of stream fishes (Winter and Van Denson 2001), research by Januchowski-Hartley et al. (2014), Anderson et al. (2012), and Coffman (2005) has led to the identification of physical traits of culverts and environmental factors that influence fish movement and decrease connectivity. Coffman (2005) has created conceptual models that can be used to estimate passablity of culverts to smaller bodied fishes; Anderson et al. (2012) have developed Bayesian Belief Networks to classify field surveyed culverts while accounting for passability uncertainty; and Januchowski-Hartley et al. (2014) were the first to identify landscape variables that are related to culvert impassabilty.

The term “passability” is used to describe how an installed structure affects fish movement. Throughout the literature there is variation in how passability is defined (see Kemp and O’Hanley 2010 for a synthesis of passability definitions). While passability is a characteristic of a particular structure, it generally needs to be considered in terms of a fish species or swimming guild. Passability of a structure can vary between different species or within a single species based on differing body sizes, swimming abilities, life stages, or simply an individual organism’s motivation to move (Inbid).

To date, there have been relatively few studies that have attempted to assess connectivity with culverts explicitly in consideration across large, multi-watershed regions. The largest efforts have primarily focused in the Great Lakes watershed (Januchowski-Hartley et al. 2014 and Januchowski-Hartley et al. 2013) and Washington State (Washington State Department of Transportation [WSDOT] 2014). Some of the largest scales studies in the Southeast are more regionally specific (Anderson et al. 2012) or only encompass single watersheds (Chipola River surveys, USFWS pers comm). Given the richness of fish species in the Southeast and their level of imperilment, more research is needed so we can begin to understand the quantity and influence of small barriers in this geographically and biologically diverse region.

Motivation for action

Currently, it has been found that the general public has a more positive attitude toward stream restoration and may be more willing to assume the cost of structure replacement for increased hydrologic connectivity (Januchowski-Hartley 2013). This sentiment is apparent by the steady increase in dam removal projects across the United States where local communities and governments have found decommissioning of a structure and restoration of lotic habitat connectivity to outweigh the original benefits of the dam (Zheng et al. 2012, Poff and Hart 2002). Given that a properly installed culvert has both societal benefits, such as accommodating flood stage flows and ecological benefits, such as allowing passage of aquatic organisms (Prowell et al. 2012) we might assume the public would be willing to support the remediation of improperly installed road crossings that could benefit stream connectivity. With opportunities for removal and remediation of barriers at road-crossings available, methods are needed to efficiently identify culverts that impede fish movement in a region and their cumulative effects on overall connectivity, how landscape level environmental gradients influence passablity of culverts, and to determine how to achieve the greatest benefits from culvert remediation and removal.

Study Objectives

Culverts are often chosen for installation due to their lower cost (Gibson et al. 2005). A large number of new installations fail to meet recommendations set by state and federal agencies to accommodate fish passage (Prowell et al. 2012, Gibson et al. 2005). Despite understanding that even new road-crossings may act as barriers, there is uncertainty regarding the quantity of these potential barriers that are on the landscape and their precise, cumulative effect on connectivity and fish.

In a study of the Great Lakes watershed, Januchowski-Hartley et al. (2013) identified 268,818 road crossings that could be potential barriers to fish movement, 38 times the number of dams in the same system. Similarly, a study in Nova Scotia, Canada found that 25 out of 47 sampled culverts were barriers to fish (Gibson et al. 2005). These studies expose road-crossings as a significant factor when considering hydrologic connectivity, however actual passability estimates for culverts were still not determined. Furthermore, large scale studies on culverts are largely absent from the Southeastern U.S.

Given the uncertainty surrounding culvert abundance and passability, region-wide surveys are clearly desirable. The field effort required to exhaustively survey all road crossings, however, is cost prohibitive. In this study we use a geographic information system (GIS) and modeling approaches (random forest) to help determine if and how environmental variables influence culvert passability and then produce predictive models to estimate passability of culverts not surveyed. We further utilize these predictive passability models to understand the total effect of culverts on connectivity in a large watershed and explore how managers may maximize the benefits gained from culvert remediation or removal to improve connectivity.

The broad objectives of this thesis are to identify environmental gradients that influence culvert passability. We hypothesize that features like stream gradient, topographic variation, land cover and land use, among others, influence erosional processes and therefore may lead to perched culverts which preclude fish from entry. We use the environmental variables to produce predictive models that can estimate culvert passability and quantify the effects of culverts on longitudinal hydrologic connectivity in large, species-rich watersheds.

Predictive models were built using random forest, a decision tree based machine learning algorithm. Random forest is defined by Breiman (2001) as a classifier consisting of a collection of tree structured classifiers comprised of independent identically distributed random vectors where each tree contributes (votes) to a prediction for x. A single tree within a random forest is built using a random subset of the training data.

Models are based on sites surveyed across three different watersheds in the southeastern United States that encompass the diversity of geology and human development that occur in the region with the hope that the models will be transferable throughout the region. Predictions derived from models will be incorporated into a barrier removal prioritization algorithm that utilizes the Dendritic Connectivity Index (DCI) as a measure of connectivity (Cote 2009). The results of this algorithm will be analyzed to determine how much connectivity is restored from the removal or remediation of individual prioritized culverts and how increases in the number of culverts removed influence overall connectivity. This information could be useful to managers for identifying regions with an increased risk of habitat fragmentation from road crossings and targeting those areas for focused surveys and remediation. Further, this process will also ensure candidate sites for removal or remediation will have the greatest benefit to aquatic organisms.

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CHAPTER 2

ESTIMATING BARRIER PASSABILITY USING RANDOM FOREST MODELS[1]

[1] Collins, E., T. Prebyl, D. Elkins, N. Nibbelink. To be submitted to *Diversity and Distributions*

Abstract

Assessing fragmentation of lotic systems caused by culverts at road crossings has been a challenge for quantifying structural connectivity and ultimately, aquatic conservation. This study identified landscape gradients that can help managers understand what factors influence culvert impassability, compared methodologies of classifying training data, and produced predictive passability models using random forest models to predict impassability of culverts. Results of this study indicate that environmental gradients derived from widely available geographic datasets can inform impassability across the landscape. The use of these gradients can be used to build random forest models and these models are a feasible method to predict impassable structures. Managers and decision makers, however, should be aware of the somewhat modest predictive ability (generally AUC<0.7) of these models. Additionally, we found that the predictive ability can be improved by ensuring a more accurate classification of training data derived from the field. This is one of only two studies that assess the use of predictive models to quantify impassability across large spatial extents and the first time this methodology has been applied to the southeastern U.S.

Introduction

Habitat fragmentation is a well-known challenge to conservation and to conservation of lotic systems in particular. Connectivity (hydrological and ecological) of rivers and streams is sensitive to single fragmentation events due to the dendritic structure of the system (Fagan 2002). As a result of this sensitivity, the effects of relatively few fragmentation events have a greater influence in lotic systems than in terrestrial systems. The likelihood of fragmentation increases with growing human populations and, more directly, an increasing need for infrastructure. Specifically, dams and linear structures, such as pipelines and roads, have the potential to increase fragmentation in lotic systems.

Road crossings over streams and rivers have been found to negatively affect fish population dynamics by reducing migration, thus causing decreases in fish abundance and richness in a given stream network (Pépino M et al. 2012, Nislow et al. 2011, Warren and Pardew 1998). These negative effects are often dependent on the structure put in place that allows for the conveyance of water beneath the road (Warren and Pardew 1998). Road engineers are presented with a choice of structures to place in streams that broadly includes bridges or culverts. Culverts are often chosen for installation due to their more modular nature, ease of placement in the stream, and ultimately, their lower cost when compared to bridges (Gibson et al. 2005). Free span bridges typically do not create physical barriers to fish movement because they allow the natural bed to remain intact and natural hydrologic process to persist despite alteration to the stream by construction activities. A properly sized and placed culvert may also provide adequate space and substrate to mimic the natural stream bed. Improperly installed culverts, however, can decrease connectivity and impede fish movement via higher water velocities, minimal natural substrate, shallow water depth within the culvert, or scour from erosion creating artificial waterfalls (Prowell et al. 2012). Unfortunately, a large number of new culvert installations fail to meet recommendations set by state and federal agencies to accommodate fish passage and therefore act as barriers (or partial barriers) to fish movement (Prowell et al. 2012, Gibson et al. 2005). In addition to variation in passability among structure types, temporal variation also exists (Kemp and O'Hanley 2010). The passability of a particular structure has the potential to exhibit periodic variation as a function of flows. In dry periods, there may be too little water depth to allow for fish passage. In wet periods, velocities may be too high for fish to move through the structure (Januchowski-Hartley 2014, Kemp and O'Hanley 2010).

There is substantial uncertainty regarding the number of potential barriers on the landscape and their cumulative effect on ecological connectivity and fish populations. Given this uncertainty, region-wide surveys are clearly desirable, such as those conducted by the U.S. Forest Service (Coffman et al. 2006a, Coffman et al. 2006b, Steele et al. 2007). Field surveys, however, can be cost-prohibitive due to the large number of potential structures on the landscape. For example, 268,818 road crossings were estimated in the Great Lakes watershed (769,989 km^2; Januchowski et al. 2013) and between 3,000- 13,000 road crossings were identified in watersheds approximately 160 times smaller than the Great Lakes in our study!

Conservation and river restoration actions need guidance to help focus efforts that address connectivity that might otherwise be too overwhelming an undertaking. In this study, we use a geographic information system (GIS) and machine learning algorithms (random forest) in lieu of large-scale, region-wide surveys as a way to identify culverts that are likely to be barriers to fish passage and regions where passage problems are likely to occur. Here we hypothesize that geomorphometric variables influence erosional patterns and fish passability through road culverts. Further, we hypothesize that landscape gradients calculated from widely-available geographic data can be used to estimate the likelihood that individual structures or groups of structures will have passability problems. Therefore, our objectives are to identify environmental gradients that influence fish passability through culverts and develop passability predictions across three large watersheds. In addition, we compare two approaches for measuring passability of field surveyed culverts and evaluate which methods are better suited for training predictive models.

Methods

Study Area

The extent of this study encompasses three watersheds across the southeast; the Chipola River, Etowah River, and Nolichucky River basins. These three watersheds were chosen because they encompass the geographic and biologic diversity of the Southeast. Because imperiled aquatic species occur in these three watersheds past studies on connectivity and habitat fragmentation have occurred here and we determined more research on the topic could aid conservation efforts in each watershed.

The Chipola River flows into the Apalachicola River shortly downstream of the Dead Lakes. It drains an area of about 3,330 km^2 in the Gulf Coastal Plain of Alabama and Florida. The headwaters of this drainage are north of Dothan, Alabama. This city is the only major developed area within the watershed. Land uses and cover in this watershed consist of peanut and cotton farms, silviculture, and bottomland deciduous forest. The Chipola River basin is home to one fish species (Alabama Shad, *Alosa alabamae*) listed as threatened by the American Fisheries Society (Jelks et al. 2008, NatureServe 2015).

The Etowah River is part of the larger Coosa River system and, ultimately, the Mobile River Basin. It drains an area of about 4,800 km^2 across the Piedmont, Ridge and Valley, and Blue Ridge within Georgia. The Etowah River supports a number of imperiled aquatic species, including three federally listed fish species (Amber darter, *Percina antesella*; Etowah darter, *Etheostoma etowahae*; and Cherokee darter, *Etheostoma scotti*). Four additional imperiled species identified by the American Fisheries Society (AFS) occur in the Etowah River system and include one AFS endangered species (Coosa madtom, *Noturus sp. cf. munitus*), two AFS threatened species (Holiday darter, *Etheostoma brevirostrum* and Bridled darter, *Percina kusha*), and one AFS vulnerable species (Coosa chub, *Macrohybosis sp. cf. aestivalis*; Jelks et al. 2008, NatureServe 2015). Due to the Etowah River's proximity to the Atlanta metropolitan area, urban development continues to be a major threat to the persistence of aquatic species and the overall health of the aquatic ecosystem (Wenger et al. 2010, Burkhead et al. 1997). The presence of imperiled aquatic species and threats from development has drawn past researchers to study freshwater connectivity with a focus on road-stream crossings in the Etowah River basin (Anderson et al. 2012, Millington 2004). These past studies provide an opportunity to evaluate the benefits of higher resolution, field acquired data as opposed to rapid survey data when classifying passability of road-stream crossings to fish movement.

The Nolichucky River is part of the Tennessee River system, a Mississippi River drainage. The Nolichucky River's headwaters begin in North Carolina and flow west into Tennessee. The watershed drains an area of approximately 4,500 km^2 within the Blue Ridge and Ridge and Valley geophysical provinces. Land cover is predominantly deciduous forest in the Blue Ridge portion and agriculture in the Ridge and Valley portion of the watershed. Two federally listed species (Chucky madtom and Snail darter) and one additional AFS (American Fisheries Society) imperiled fish species (Blotchside logperch) are found in the Nolichucky River basin (Jelks et al. 2008, NatureServe 2015).

Source Data and Data Preparation

Road crossings were initially identified with a GIS by intersecting the National Hydrography Dataset (NHD) (U.S. Geological Survey [USGS] 2013b) 1:24000-scale flow lines, and the 2013 TIGER/Line shapefiles (U.S. Census Bureau 2013) within the three study watersheds.

Ten environmental gradients likely to influence culvert passability were derived from publicly available geographic data sources for use as predictor variables in models to predict culvert passability (Table 1). These eight gradients included Land cover/use types (which we further split into percent open water, forest, shrub/scrub, grassland, pasture, cultivated crops, woody wetlands, and herbaceous wetlands), percent impervious, topographic variation, compound topographic index, stream power, slope position (the position of a culvert relative to surrounding topography), stream reach gradient, upstream watershed size, and estimated discharge for a five year flood. We hypothesized these topographic variables to influence erosional processes in streams and that areas with higher amounts of erosion would increase perch height as a result of scouring at the culvert outflow and therefore decrease the likelihood that a fish could enter a culvert and successfully move to the stream reach upstream of the culvert. Topographic variables were used for selecting survey sites, predictive modelling, or both.

Survey Site Selection

To select sample sites, we first delineated an upstream drainage area polygon for each road-stream intersection using 30m Digital Elevation Models (DEMs) and ArcGIS 10.2 (ESRI 2013). Road-stream crossings that had an upstream drainage area greater than 60 km^2 were assumed to be bridges and removed from further analysis, based on a similar threshold used by Anderson et al. (2012). Each intersection point feature was attributed with percent land cover and percent ownership within the upstream drainage area. We then used cluster analysis to stratify road-stream intersections across the range of land cover and ownership that was present in the three study watersheds using the statistical program R (R Core Team 2013). Intersections were clustered into six groups using a scree plot that displayed the variance of each component (see Everitt and Hothorn 2009 for an analogous case using a scree plot for cluster analysis). This method ensured the sample sites encompassed the range of land cover types and ownerships that were present within each watershed. Approximately 33 points were selected at random from each of the six groups to have an approximate total of 200 potential survey points. Although the goal was to survey 150 sites, this larger pool of survey points allowed for the substitution of an equivalent site when one from the first 150 proved inaccessible in the field. In total 506 sites were measure across all three watersheds in four states (TN, NC, GA, and AL).

Field Measurements

Data were collected at each survey site to determine passability of culverts with respect to the swimming ability of fishes. Field surveys were conducted in the summer, fall, and winter from May 2013 to December 2014. We recorded the construction material of the culvert and general shape (pipe or box) and condition (new, moderately aged, holes present, collapsed, etc.) upon arrival at a site. Diameter, height, and length of each culvert were also recorded. Other data collected at each site include: lower edge of the culvert at the outflow (lip) distance to water surface (perch height) and to the bed sediment, and maximum water depth within 30 cm of culvert lip. These measures are derived from fish swimming abilities and help determine whether a fish is physically able to enter a culvert (Coffman 2005) and are specific for fishes in the families Salmonidae (typically large bodied, with strong swimming/leaping abilities), Cyprinidae (typically small bodied, with moderate swimming/leaping abilities), and Percidae (typically benthic, with limited swimming and low leaping abilities). We measured culvert slope by recording and calculating the difference in elevation at the entrance and outflow of each culvert using a LaserMark^{R} LM800 laser level and dividing by the culvert length. We quantified "embeddedness" by measuring sediment depth and wetted width within the culvert. We evaluated stream morphology upstream and downstream of the culvert by measuring channel width and depth at the thalweg (deepest part of the channel). We measured the control point elevation to help determine whether a culvert is backwatered (Coffman 2005). The control point is identified as the tail water riffle crest, where sediment from the culvert outflow pool is deposited and is the highest point downstream of culvert in the stream channel. The control point determines outflow pool height.

Passability estimation

The term “passability” is used to describe how an installed structure impedes fish movement. Throughout the literature there is a considerable amount of variation in how passability is defined (see Kemp and O’Hanley 2010 for a synthesis of passability definitions). In this study, we use the more simplistic definition of passability where a structure may be passable, impassable, or indeterminate. While passability is a characteristic of a particular structure, it generally needs to be considered in terms of a fish species or swimming guild. Passability of a structure can vary between different species or within a single species based on differing body sizes, swimming abilities, life stages, or simply an individual organism’s motivation to move (Inbid).

Passability of field surveyed culverts was estimated using Coffman’s (2005) static culvert classification model. This system breaks passability into three states: “passable”, “impassable”, or “indeterminate” with respect to the swimming abilities of fishes in the Percidae, Cyprinidae, or Salmonidae families. Classified culverts using this method were used to train models to evaluate the effects of landscape gradients on passability. Because we found very few indeterminate structures during field work, we removed those from our data sets and did not consider the indeterminate classification in future analyses.

To evaluate whether different strategies for passability classification of field surveyed culverts were more effective for predictive modeling, we also used a classification method developed by Anderson et al. (2012). This system used Bayesian belief networks (BBN) to estimate the probability that a surveyed structure was impassable to a generalized, small bodied fish. Probabilistic values from the BBN were converted to 1 (impassable) if the probability of impassability was greater than 50% or to 0 (passable) if the probability of impassability was less than 50% to better compare the BBN classification scheme to the categorical classification used in the Coffman method. Further, we used the Cyprinidae Coffman classification model to allow for a more direct comparison to the BBN that classified passability in terms of a generalized small bodied fish (inclusive of Cyprinidae and Percidae) in this analysis.

We compared performance of passability models using training data classified by the Coffman (2005) method to models that used BBN classified culverts as training data.

Random Forests Modelling

We analyzed relationships between culvert passability and environmental variables and compared classification methods with the randomForest package in R (Liaw and Wiener 2002). Random forest is a decision tree based machine learning algorithm. Random forest is defined by Breiman (2001) as a classifier consisting of a collection of tree structured classifiers comprised of independent identically distributed random vectors where each tree contributes (votes) to a prediction for x. A single tree within a random forest is built using a random subset of the training data.

Parameter selection for the RF models utilized an algorithm developed by Murphy et al. (2010) which minimizes the number of parameters used in the model, mean square error, and maximizes the percentage of variation explained using a model improvement ratio for each metric. This algorithm was performed 100 times and the selected parameters for each iteration were appended into a single data table. The most frequently chosen parameters (i.e. abundant parameters in the data table) were retained and used to build the random forest models.

Random forest models were validated using leave-p-out cross-validation, in which 5% of the data were selected at random to be withheld as a validation set and the remaining 95% of the data were used for training the models. This process was repeated 500 times to find the average error rates and estimate overall model accuracy. Area under the receiver operating characteristic (ROC) curve, AUC, was used as a measure for determining the classification accuracy and predictive performance of a particular model. AUC values that are near 0.50 are no better than random, while AUC values of 1 would indicate perfect classification. We evaluated the performance of models trained with data classified with the Coffman method for Salmonidae, Cyprinidae, and Percidae fishes. We also evaluated the performance of models that used data classified with the BBN classification method.

Important parameters were identified by evaluating the mean decrease of the Gini impurity (which is derived from the Gini index split criterion) implemented from the randomForest package (Liaw and Wiener 2002). The Gini index split criterion attempts to minimize impurity (increase homogenization) of the training subsets after each split in a decision tree (Berzal et al. 2002). Splits in the decision tree are made using the model parameters, therefore, important parameters would better be able to split impassable from passable culverts. Partial dependency plots were graphed for the most important parameters used in the family-specific predictive models using the forestFloor package in R (Welling et al. 2015). This method helped to infer how landscape gradients influenced passability of culverts.

Results

In total, 19,812 road-stream intersections were found across the three study watersheds (1,658 in the Chipola, 4,994 in the Etowah, and 13,210 in the Nolichucky). Of that total, 506 road crossings were visited across all three study watersheds (174 in the Nolichucky, 177 in the Etowah, and 155 in the Chipola River Basin; Figure 1.1). The majority (55.5%) of surveyed road crossings were circular pipe culverts (n=281), followed by bridges (16.2%, n=82), and box culverts (14.2%, n=72). Bridges were more abundant than expected, likely because small bridges were installed on low order streams more frequently in the Nolichucky than in the other two watersheds.

Culvert outlet lips were elevated from the water at 109 (30.8%) structures and elevated from the sediment at 182 (51.5%) structures. Circular culverts had, on average, lower downstream perch heights than box culverts; however the highest perch height observed occurred at a circular pipe culvert (Table 1.2). Box culverts also had a greater mean and median length than circular culverts. The longest culverts were typically found underneath divided state and interstate highways.

The majority of sites were estimated to be passable for each of the three families of fish. The most culverts were passable to salmonids (58%), followed by cyprinids (53%), and 50% were passable to percids (Figure 1.2). Only seven surveyed structures were classified as indeterminate by the Coffman model (2005) and were not considered for further analysis. Likewise, 35 road crossings surveyed were found to be spanning dry stream beds and were removed from the modelling data sets.

Model Performance

Random forest models generated for each of the three families under the Coffman passability classification model varied slightly in their predictive ability (Table 1.3). Models built using the Percidae classification were the poorest performers with AUC of 0.614, Cyprinidae models performed better with AUC of 0.642, and Salmonidae models were the best overall with AUC values of 0.655. Despite a slight difference in average model performance, our results indicate that omission and commission error rates were similar between models for all three families. Median omission error for impassable structures (i.e. impassable culverts that were incorrectly predicted as passable) varied from 0-20% and median commission error for impassable structures (i.e. passable culverts that were incorrectly predicted as impassable) varied from 60-78%. Likewise, the median percent of correctly classified impassable structures varied from 80% for Percidae and Cyprinidae models to 100% for Salmonidae models.

The most important variables included the geomorphic measures (stream power, compound topographic index [CTI], slope position, watershed area, stream reach gradient, and topographic variation at the buffer and watershed scale). Land use parameters that were found to be most important included the percent of forest cover, percent impervious surface, pasture/hay, grassland, shrub/scrub at the watershed level scale and percent impervious at the 100m buffer scale.

Partial contribution plots show, as hypothesized, that with increasing values of stream power, CTI, stream reach gradient, percent impervious, and topographic variation, structures were more likely to be impassable (Figures 1.3,1.4,1.5). Counter to our hypotheses, higher percentages of forest cover corresponded to impassable structures (likely due to topographic variation being correlated with higher amounts of forest cover) and higher percentages of cultivated crops and pasture land corresponded to passable structures.

Predicted vs. Observed comparison

We further analyzed the predictive abilities of the random forests models at a more generalized HUC 10 scale. The percentage of structures predicted as impassable was compared to the percentage of structures observed and classified as impassable using the Coffman methodology and we visualized the results with scatter plots (Figure 1.6). Only HUC 10 watersheds with at least 10 surveyed road crossings were included in this analysis.

If the random forest models were able to perfectly classify structures, we would expect a 1:1 relationship with high correlation among predicted vs. observed impassability percentages per HUC 10. Our results indicate relatively similar performance among models for the three different families. Percidae models were found to have a Pearson's correlation = 0.507, Salmonidae models were found to have a Pearson's correlation = 0.507, and Cyprinidae models resulted in a Pearson's correlation = 0.693.

We generated more plots of this type to compare the percentage of structures correctly classified to the percentage of structures observed and classified as impassable using the Coffman methodology (Figure 1.7). Perfect classification would be seen in these plots as points clustered around a line equivalent to y=1.0, however, a positive 1:1 relationship would suggest that the models performed well in HUC 10 watersheds with the highest percentage of impassable culverts. Our results also showed relative similarity among random forest models for all three families. Percidae models were found to have a Pearson's Correlation = 0.508, Salmonidae models had a Pearson's correlation = 0.508, and Cyprinidae models had a Pearson's correlation = 0.671.

Comparison of classification methodologies

Results found that passability models using training data that were classified with the Coffman (2005) method performed worse (with an AUC of 0.632) than passability models using training data classified with the BBN classification system (with an AUC of 0.697; Table 1.4). A comparison of omission and commission rates for impassable structures between the two methods shows a slight increase in median omission error (impassable structures incorrectly predicted as passable) when using Bayesian classification (35% vs 22% with the Coffman methodology), however a reduced median commission error (passable structures incorrectly predicted as impassable), 35% vs 62% with the Coffman methodology.

We plotted predicted vs. observed impassable sites as another method to evaluate predictive success of models trained with BBN classified data. The percent of structures predicted as impassable were plotted against the percentage of structures observed and classified as impassable and a correlation (Pearson's) of 0.668 was found (Figure 1.8).

Finally, we compared the percentage of structures correctly classified as impassable to the percentage of structures observed and classified as impassable using the Bayesian belief network (Figure 1.9). Perfect classification would be seen as points clustering around the line, y=1.0; however, strong, positively correlated data would suggest that models are performing well in HUC 10 watersheds that have the highest percentage of impassable structures. Pearson's correlation analysis found values of 0.633.

Discussion

In this study we were able to contribute to the growing body of literature that identifies culverts as a significant source of fragmentation in lotic ecosystems (Diebel 2014, Januchowski-Hartley et al. 2014, Januchowski-Hartley et al. 2013, Diebel et al. 2010, Poplar-Jeffers et al.

2009, Park et al. 2008). We used a similar modelling approach to the Boosted Regression Trees used by Januchowski-Hartley et al. (2014) and support their conclusions that culvert passability is influenced by landscape level gradients. We elaborate on this finding by identifying other topographic variables that have a strong correlation with impassable culverts in the Southeast. Further, our findings concur with those of the aforementioned authors in that a machine learning, classification tree modelling approach (i.e. random forest) is a reasonable method to address the abundance of potential passability problems presented by culverts in other regions, however, care needs to be taken to classify the training data with an accurate passability classification method. We also suggest that factors that lead to an impassable culvert will vary across geographic provinces; therefore, it is important to identify potential parameters that are most relevant to culvert passabilty within a region of interest and potentially build predictive passability models for a specific geographic province.

Passability and Landscape Gradients

A suite of environmental variables were found to explain the occurrence of impassable culverts. Similar to Januchowski-Hartley et al. (2014), we found variables that represent gradient and drainage area to be informative in predictive models, such as stream power and stream reach gradient. Relatedly, we also found variables that we hypothesized to relate to erosional processes to be informative in our models.

Most variables used in the RF models support our hypothesis that factors that account for greater amounts of erosion (greater topographic relief, greater stream gradients, more impervious surface, and slope position) lead to impassable structures. Contrary to our initial hypotheses however, more forest cover tends to be associated with impassable structures and higher amounts of agriculture tends to be less associated with impassable structures. It is unclear if this is a true relationship between land use and impassability. Instead, the relationship between impassable culverts and forest cover may be a result of correlation between higher amounts of topographic relief and forest cover.

Other factors are likely to influence passability of culverts. As noted by other researchers, estimates of culvert time since installation and culvert type are likely to be important (Januchowski-Hartley et al. 2014, Park et al. 2008, Poplar-Jeffers et al. 2008). Unfortunately databases maintained by state transportation departments vary in the quantity and type of data that could be used for modelling passability. North Carolina was the only state in our study area that possessed a large database of road crossings with information on installation date and structure type. Januchowski-Hartley et al. (2014) recommend using human density to infer infrastructure expenditures that would correlate with the structure type installed. We would suggest in addition to a density measure, an economic and development age measure be added. Road type has been identified by previous studies as a potential factor that would influence culvert passability. We used FCODE from the TIGER lines shapefile as a rough means to identify road type for use in models and found it provided limited information. A more rigorous identification of road type may be useful. Based on our field studies we found a diversity of installation methods and culvert types that are likely a result of which entity maintains the crossing. For instance, culverts beneath interstates and divided state highways were always box culverts and were quite long (up to 120 m), relative to the typical culvert in our survey, due to the greater width of the roadway, median, and shoulder of these features. In general, it is likely that there are many other anthropogenic and environmental factors that influence culvert passability and can be derived from widely available broad scale datasets that could be used in predictive models. More research in this area will undoubtedly yield better performing models and a greater understanding of fragmentation caused by culverts.

Model Interpretation

The final random forest models developed in this study had an overall modest predictive ability for all three of the families, however Salmonidae and Cyprinidae models appeared to perform better overall than Percidae models. The disparity between these models can be interpreted as reflecting the ability of the RF algorithm to infer impassable conditions from landscape derived variables. Put simply, it is easier for the model to classify a more extreme condition, i.e., an impassable culvert for salmonids, than the less extreme condition of impassability for percids. This is likely a result of the much greater slope and perch height required to make a structure impassable to a salmonid vs. a percid fish. Despite the overall modest performance, our models are comparable to the performance of other models for predicting culvert passability (Januchowski-Hartley et al. 2014).

Ultimately, the models are predicting the conditions that lead to impassability or the tendency to become impassable and are limited in their abilities to definitively predict culvert impassability at a specific point on the landscape. This concept inspired us to use our models to predict impassability at the HUC 10 scale. From this analysis, we found moderate correlation between predicted and observed impassable structures as well as the percentage of correctly classified structures and percent observed impassable structures per HUC 10 watershed (Figure 1.9). This suggests that our models are somewhat better at identifying impassable structures in a watershed with a greater percentage of surveyed impassable structures. In other words, our passability models are able to identify regions that are more likely to have culverts with passability problems. This ability alone can greatly facilitate managers and decision makers in allocating resources for field surveys. We recommend visualizing predictions of impassabilty at a regional scale to help identify areas for monitoring or further attention, rather than trying to identify specific structures. Figure 1.10 displays maps of the three study watersheds with mean culvert passability estimates for each HUC 10 within the watershed symbolized.

We found clear distinctions in model predictive ability between the three study watersheds (Figure 1.7). In general, our models did poorly in the Chipola River watershed and much better in the Etowah and Nolichucky River basins. This would suggest that the parameters chosen for the models are more relevant for determining passability in regions with more topographic relief than in coastal plain regions. Future studies should analyze predictive models for coastal or low gradient river basins separate from river basins with greater topography to avoid spurious relationships between spatial data and impassability estimates and to elucidate what processes may actually influence impassability in lower gradient systems. This result agrees with other studies that suggest variables should be chosen based on regionally unique factors and hypotheses that influence culvert passability variability (Januchowski-Hartley et al. 2014).

Despite the lower predictive abilities for RF models in the Chipola River basin, it is worth clarifying that field surveys have found this (and other coastal plain watersheds) to have relatively low amounts of impassable culverts. RF models seem to support this by consistently predicting the Chipola River basin to have fewer impassable structures (Figures 1.6 and 1.7). Fragmentation at road crossings in the coastal plains may be less of a conservation threat in these watersheds and therefore it may be worth prioritizing barrier assessment on larger streams and rivers that are likely to affect anadromous species (fishes in the *Alosa*, *Acipenser*, and *Morone* genera, for example).

Our results agree with previous studies that a predictive modelling approach can provide enough information to adequately inform decision makers and lead to actionable results (Januchowski-Hartley et al. 2014). A rapid survey protocol may be utilized to obtain the data necessary to train predictive models. When possible, it is suggested to perform a more rigorous passability classification methodology, like that developed by Anderson et al. (2012). Future emphasis should be placed on accurate classification of barriers after field data collection to improve predictive ability of the models trained from the field data. Of the two methods compared, Bayesian belief networks may be preferable to the Coffman passability models in their current state. The methods developed by Coffman may still be useful if the models were created for a more specific taxonomic level, such as by genera, subgenera, or species.

Conservation Implications

The use of random forest models to predict culvert impassability can reduce the problem that the sheer number of culverts on the landscape pose for connectivity assessments. This and similar methods (Januchowski-Hartley et al. 2015) can be transferred to other regions to quantify the number of barriers in a watershed or identify specific regions to focus field efforts. The latter application may be more appropriate based on the modest model performance. Regions to target field work can be identified by finding spatial clusters of impassable structures predicted by the models. Of particular use is the knowledge of the environmental gradients that influence culvert impassability gained from this study. This can be used to identify regions where impassability is likely to occur without needing specific crossing information. Additionally, knowing environmental gradients that tend to lead to impassable structures could help guide government entities to select appropriate and cost effective culvert types based on the surrounding landscape.

This study adds to the growing understanding of the role of culverts in hydrologic connectivity. By providing a greater understanding of landscape gradients that inform culvert passability and building off research presented by Januchowski et al. (2014) we were able to show that modelling approaches are a feasible method to understand the role of culverts on connectivity in a large watershed. Finally, we hope that the information presented here provides managers with a good starting point when attempting comprehensive conservation actions in terms of hydrologic connectivity.

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Table 2.1. Landscape variables used for survey site selection and random forest models

Variable	Data Source	Method	Hypothesis
Percent land cover type*†	National Land Cover Dataset Jin et al. 2013	National Water-Quality (NAWQA) Area-Characterization Toolbox Price et al. 2010	**Forest cover** – more forest cover will be associated with less erosion and less scour at culvert outlets correlating with smaller culvert perches **Grassland and shrub** – this land use may indicate more stable environments than land in cultivation and have lower amounts of erosion **Wetlands and open water** –wetlands and open water will slow stream velocities and decrease erosion, outlet scour, and perch height
Percent land use type*†	National Land Cover Dataset Jin et al. 2013	National Water-Quality (NAWQA) Area-Characterization Toolbox Price et al. 2010	**Pasture/hay and cultivated crops** – more anthropogenic activity may create less stable soils and increase erosion levels that correlate with culvert perch height
Percent impervious surface†	National Land Cover Dataset Jin et al. 2013	National Water-Quality (NAWQA) Area-Characterization Toolbox Price et al. 2010	Greater amounts of impervious surfaces tend to produce flashy flow conditions that are more likely to scour culvert outlets and increase perch heights.
Topographic variation† Grohmann et al. 2010	30 meter DEM USGS 2013a	Roughness tool in the Geomorphemetry and Gradient Toolbox Evans et al. 2014 (mean topographic variation was calculated)	Areas of greater topographic variation would potentially be subjected to a wider range of flows and rapid flow increases that would increase scour downstream of culverts and increase perch heights.
Compound topographic index (CTI)	30 meter DEM USGS 2013a	CTI tool in the Geomorphemetry and Gradient Toolbox Evans et al. 2014	A function of upstream contributing area per unit width orthogonal to flow and slope – essentially a measure of stream power Higher amounts of erosion would occur at points with higher CTI and influence perch height and therefore a fish's ability to enter a culvert.
Stream Power	30 meter DEM USGS 2013a	Raster Calculator LN((Flow Accumulation+0.001) * (Slope/100)+0.001)) ArcGIS	Greater stream power would lead to higher amounts of erosion increasing scour and culvert perch height

Table 2.1. Continued

Variable	Data Source	Method	Hypothesis
Slope position of culvert	30 meter DEM USGS 2013a	Slope position tool in the Geomorphemetry and Gradient Toolbox Evans et al. 2014	The position of a point relative to the elevation of its surroundings. Low slope position generally occurs in valley. Stream crossings at a low slope position (surrounded by higher elevation) would be more prone to scouring as a result of runoff from the higher surrounding elevations thus increasing perch heights.
Stream reach gradient	30 meter DEM USGS 2013a	Calculate stream slope in a 200m buffer around each crossing ArcGIS	Reaches with a higher gradient would be subject to more scour and increase perch heights than reaches with lower gradients.
Ownership (only used to select survey points)	PAD-US 1.1 CBI edition	National Water-Quality (NAWQA) Area-Characterization Toolbox Price et al. 2010	Construction variation and maintenance between county, state, and federally maintained roads may lead to the installation or likelihood of impassability.
Road type	TIGER/Line shapefiles U.S. Census Bureau 2013	Intersection ArcGI	Construction variation and maintenance between county, state, and federally maintained roads may lead to the installation or likelihood of impassability.
Upstream watershed area of culvert*	30 meter DEM USGS 2013a	Watershed delineation, Hydrology toolbox ArcGIS	Upstream watershed size will correlate with culvert passability.
Discharge for a 5 year flood (only used in RF models)	30 meter DEM USGS 2013a	USGS Regional Recurrence Equations Law and Tasker 2003, Gotvald et al. 2009, Verdi and Dixon 2011	Sites that are prone to more frequent, larger floods are more likely to experience scour.

*Variable was used for survey site selection and Random Forest models
†Variable was calculated for the upstream watershed as well as in a 100m buffer

Table 2.2. Summary statistics for important field measurements related to passability of culverts. Culvert type "C" refers to circular culverts and type "B" refers to box culverts.

	Chipola						**Etowah**						**Nolichucky**					
	Mean		Max		Min		Mean		Max		Min		Mean		Max		Min	
Culvert Type	C	B	C	B	C	B	C	B	C	B	C	B	C	B	C	B	C	B
Perch (cm) (to sediment)	9.6	16.4	93.0	67.0	0	0	15.9	36.0	97.0	96.0	0	0	19.12	18.9	300.0	76.0	0	0
Perch (cm) (to water surface)	4.4	7.5	77.0	54.0	0	0	12.6	20.9	100.0	69.0	0	0	15.15	11.0	305.0	86.0	0	0
Length (m)	14.7	19.0	61.5	39.5	3.8	9.9	20.5	29.7	49.0	104.0	1.9	3.0	12.99	28.3	59.5	120.0	4.9	4.9

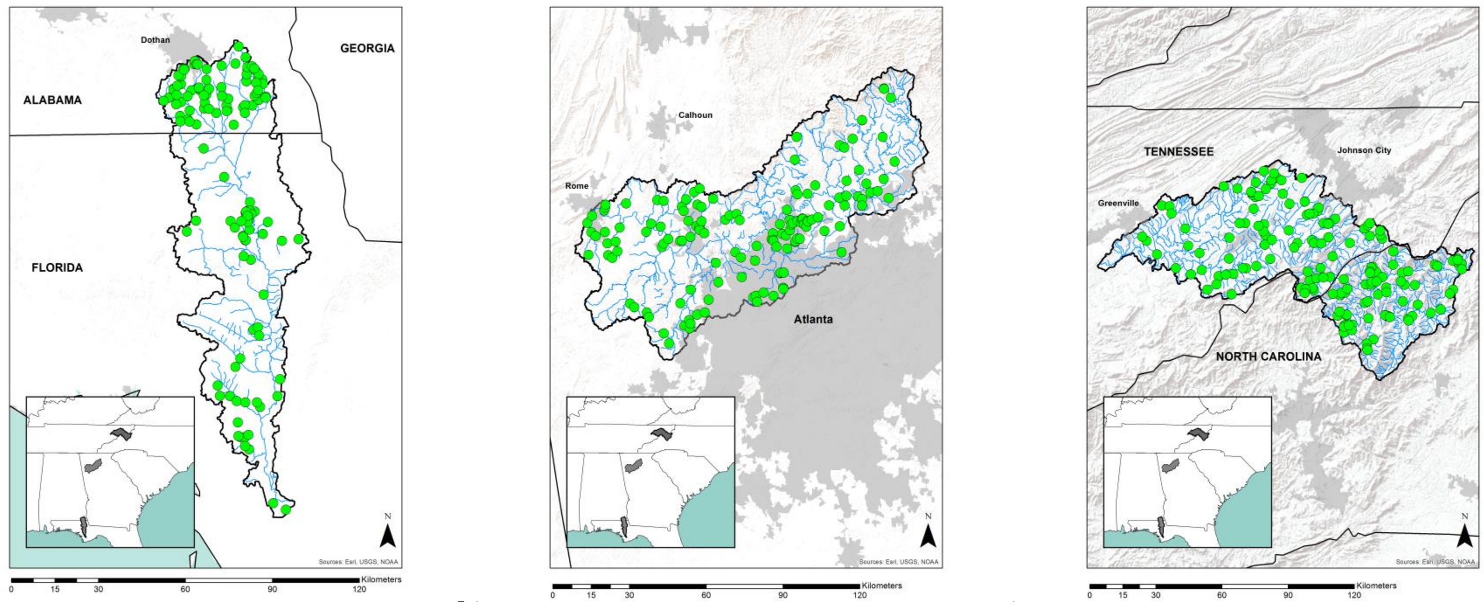
Table 2.3. Family specific models using data trained with the Coffman (2005) classification method

Family Specific Model	Parameters	AUC
Percidae	Mean Topographic Variation (WS)[+]*, % Impervious (WS)[+], Stream Power[+], % Forest (WS) [-], Topographic Variation (BF)[+], Watershed Area [-/+], % Impervious (BF) [+], % Shurb/Scrub (WS) [-], % Grassland (WS) [-], % Pasture (BF) [-], % Woody Wetland (WS) [-], % Cultivated Crops (WS)[-],% Herbaceous Wetland (WS)[-]	0.614
Cyprinidae	Mean Topographic Variation (WS) [+], Topographic Variation (BF) [+], Slope Position [-], CTI [+], % Forest (WS) [-], Watershed Area [-/+], % Impervious (BF) [+], Stream Gradient [+], % Shrub/Scrub (WS) [-], % Grassland (WS), % Woody Wetland (WS) [-], % Cultivated Crops, % Shrub/Scrub (BF) [-],	0.642
Salmonidae	Slope Position [-], % Forest (WS) [-], Watershed Area [-/+], Topographic Variation (BF) [+], % Impervious (WS) [+], % Impervious (BF) [+], Topographic Variation (WS) [+], Stream Gradient [+], % Shrub/Scrub (WS) [-], % Grassland (WS) [+/-], % Pasture (BF) [-], % Woody Wetland (WS) [-], % Cultivated Crops [-]	0.655

* Sign in [ ] indicates relationship with impassability, parameters with -/+ indicate an initial negative relationship with impassability that changes to a positive relationship as that parameters value increases.

Table 2.4. Model performance using training data classified with two different methods

Method of classifying training data	AUC
Static flow chart, Coffman (2005)	0.632
Bayesian Belief Network, Anderson (2012)	0.697



a). **b).** **c).**

Figure 2.1. Road crossings surveyed in the Chipola River (a), Etowah River (b), and Nolichucky River (c)

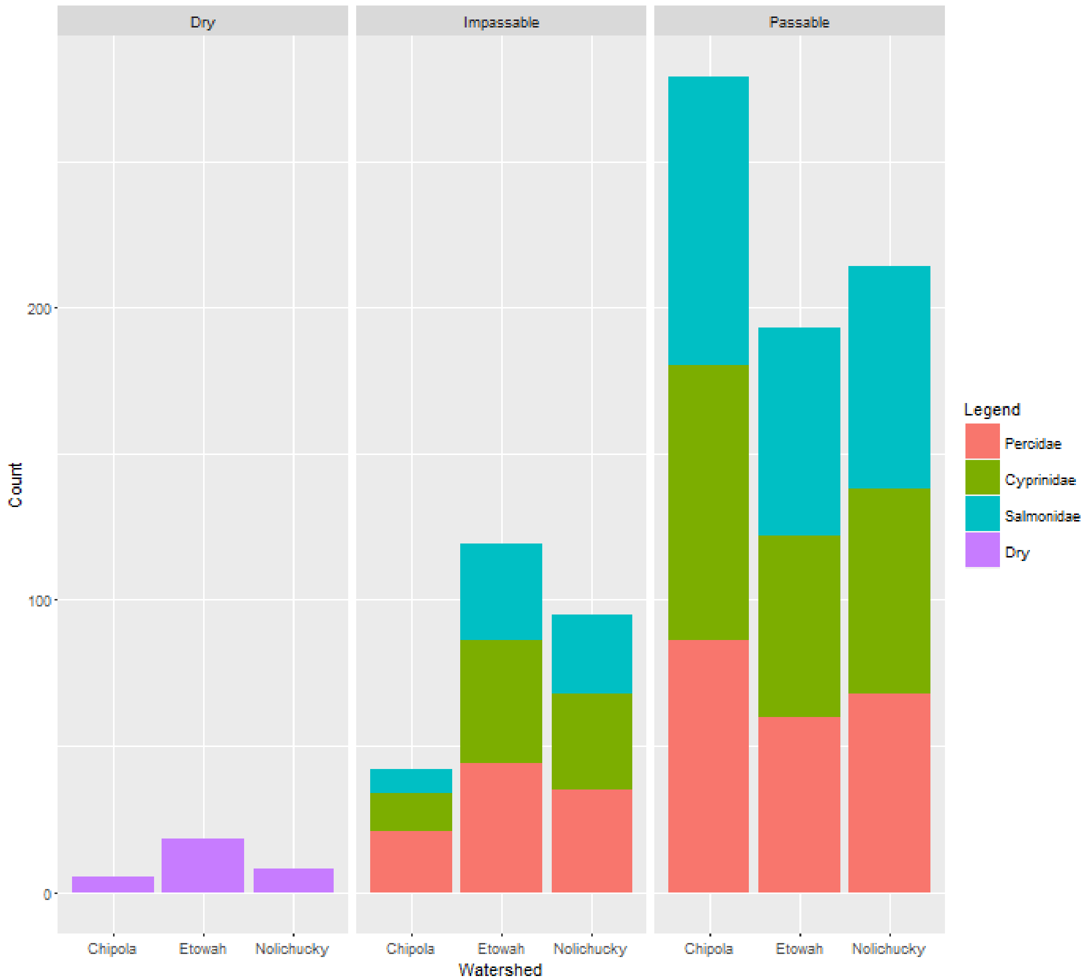


Figure 2.2. Number of passable, impassable and dry structures classified in each watershed with respect to Percidae, Cyprinidae, and Salmonidae swimming abilities according to the Coffman (2005) static classification model

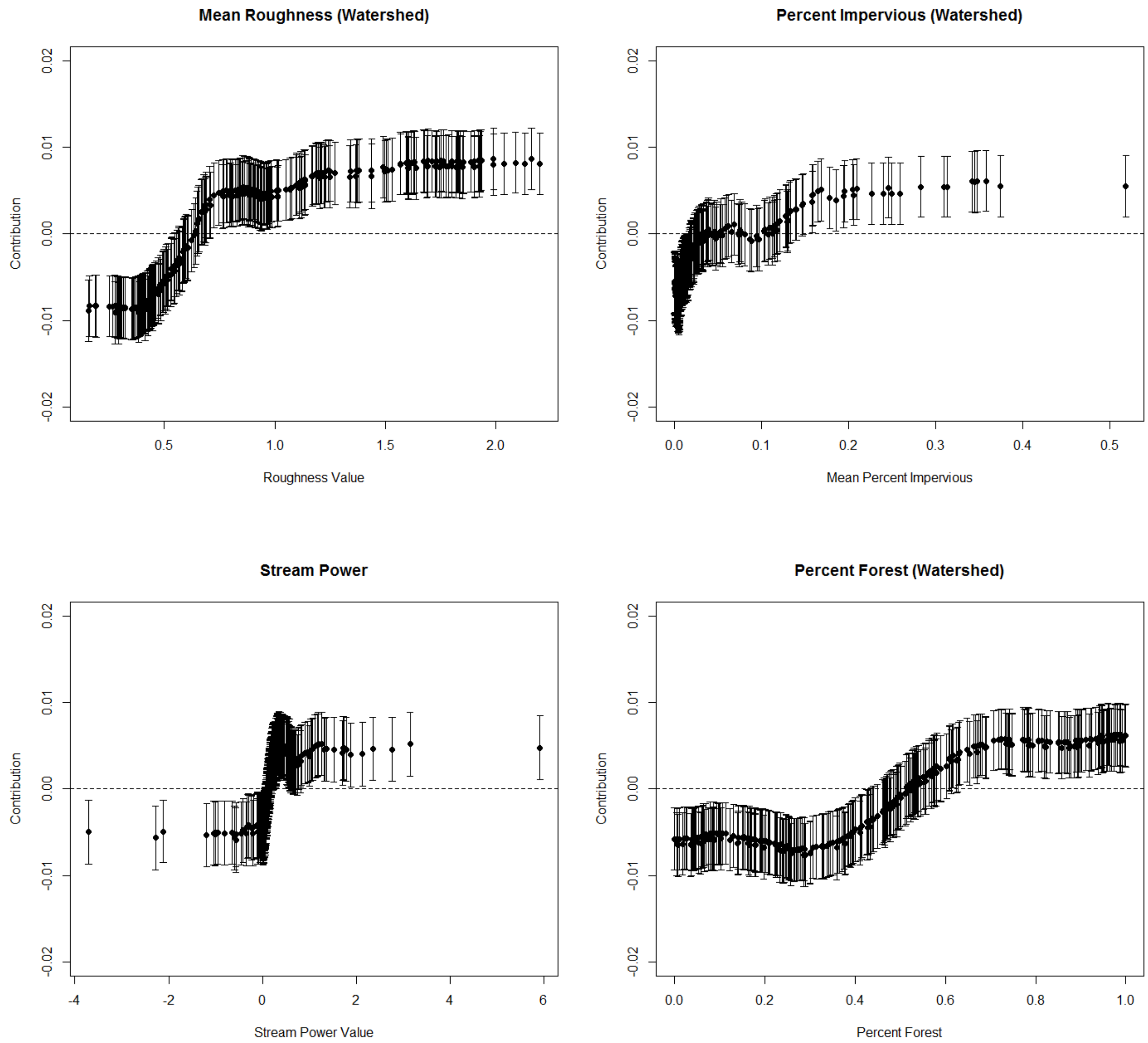


Figure 2.3. Influence of variables on impassability for Percidae models. Increasing values on the y-axis indicate a greater likelihood a culvert is impassable.

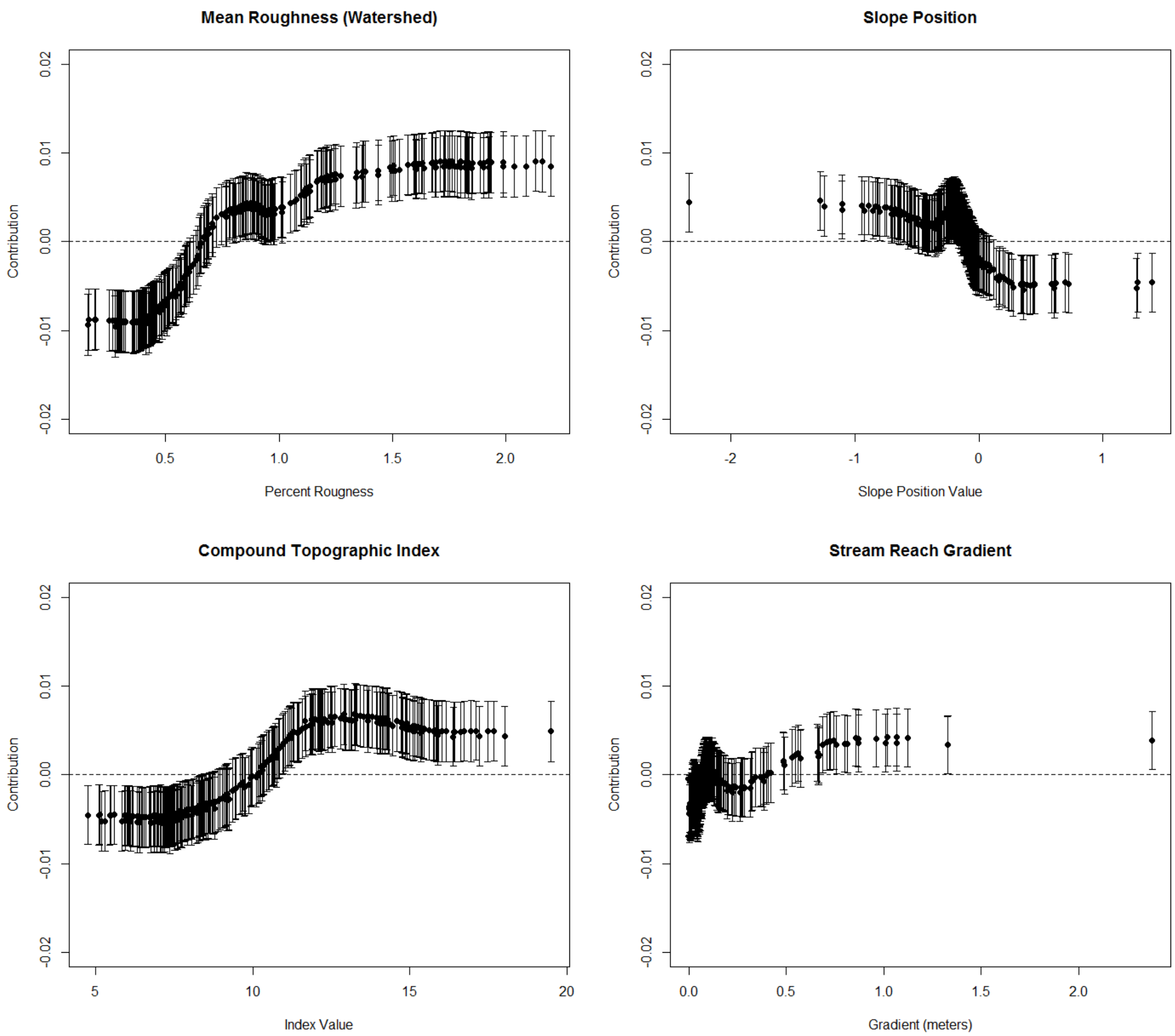


Figure 2.4. Influence of variables on impassability for Cyprinidae models. Increasing values on the y-axis indicate a greater likelihood a culvert is impassable.

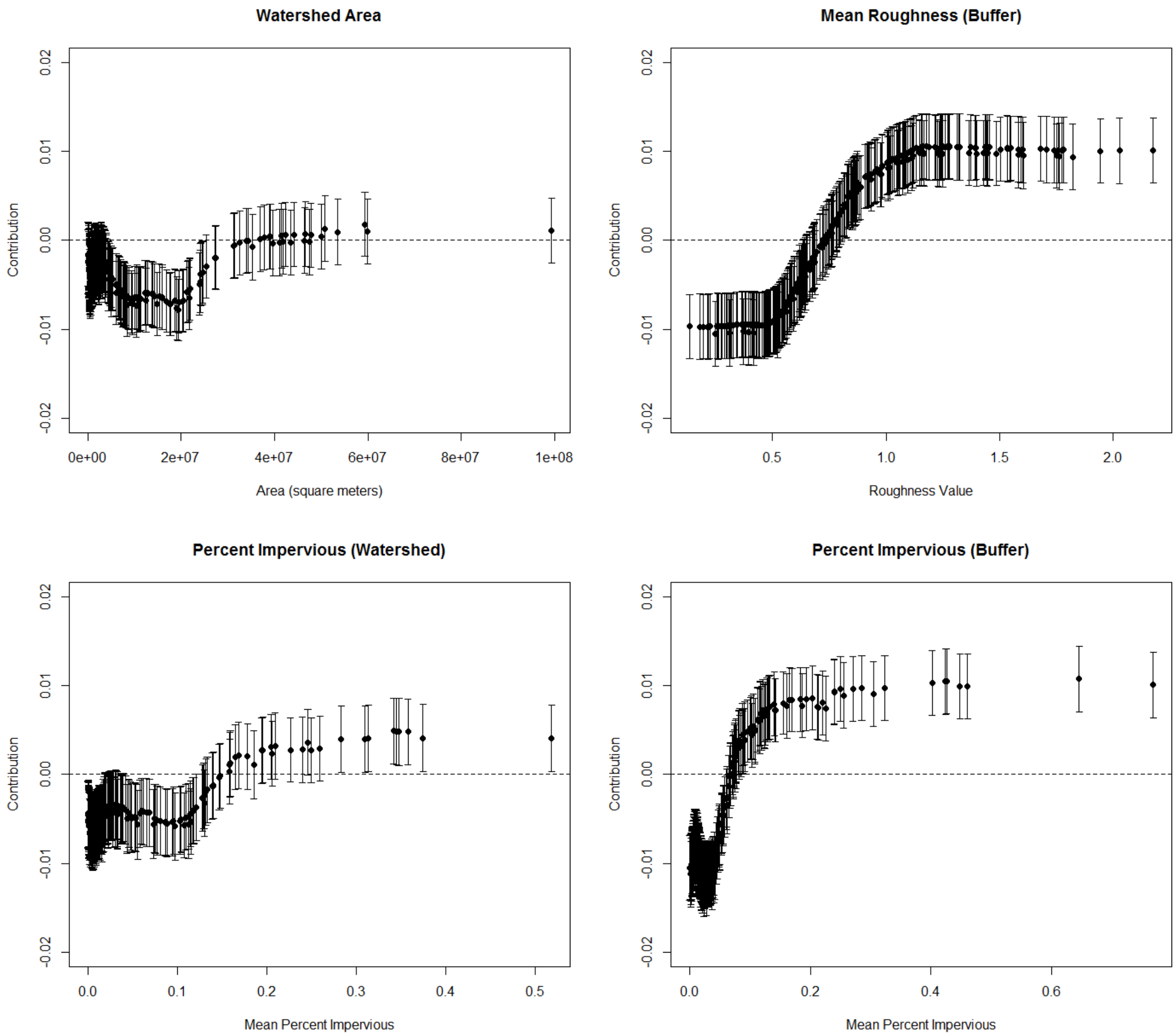


Figure 2.5. Influence of variables on impassability for Salmonidae models. Increasing values on the y-axis indicate a greater likelihood a culvert is impassable.

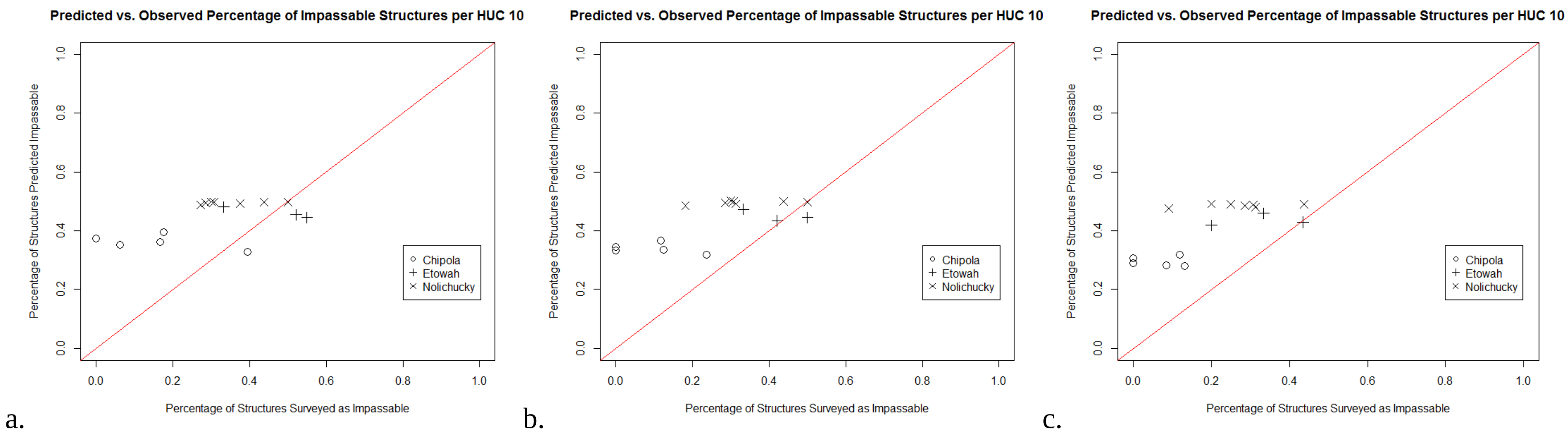
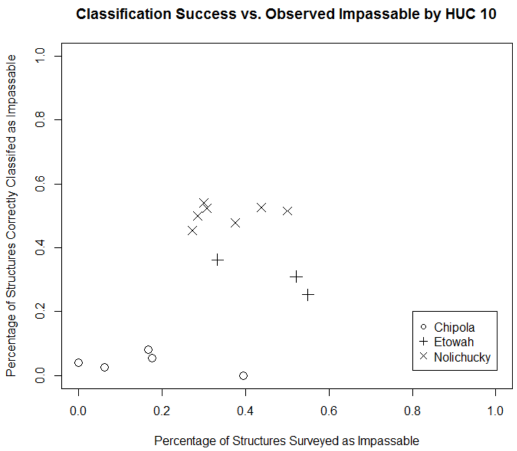
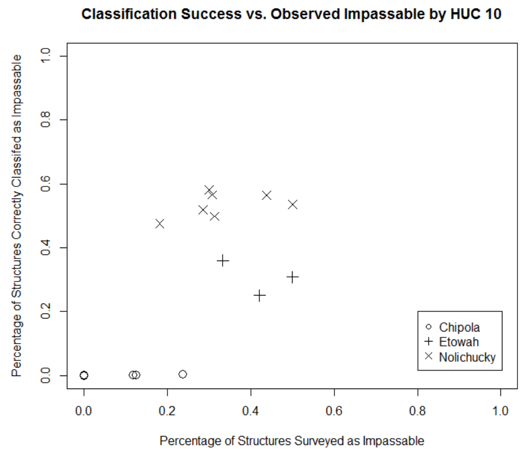


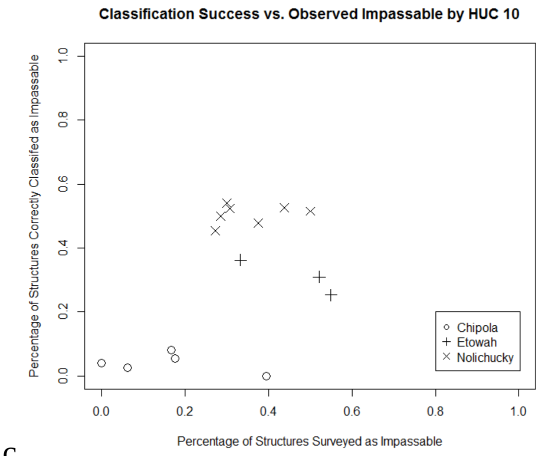
Figure 2.6. Plot of predicted vs. observed impassable culverts. Culvert passability was initially classified using models developed by **Coffman** (2005) in terms of **Percidae (a), Cyprinidae (b),** and **Salmonidae (c)** fishes. The red line represents a 1:1 relationship. Our models tend to over-predict impassability of structures. The plot represents only HUC 10 watersheds in which ≥ 10 culverts were surveyed. Pearson's correlation for **Percidae** = 0.507**, Cyprinidae** = 0.693 , and **Salmonidae** = 0.507



a.



b.



c.

Figure 2.7. Plot showing the percentage of impassable structures correctly classified as impassable using Random Forest models vs percentage of structures surveyed as impassable by HUC 10 watersheds within the larger study watersheds. Culvert passability was initially classified using models developed by **Coffman** 2005 in terms of **Percidae** (a), **Cyprindae** (b), and **Salmonidae** (c) fishes. Our models were better able to classify impassability within the Nolichucky River watershed and could not correctly classify impassability within the Chipola River watershed. The plot represents only HUC 10 watersheds in which ≥ 10 culverts were surveyed. Pearson's correlation for **Percidae** = 0.508, Cyprinidae = 0.671, and Salmonidae = 0.5

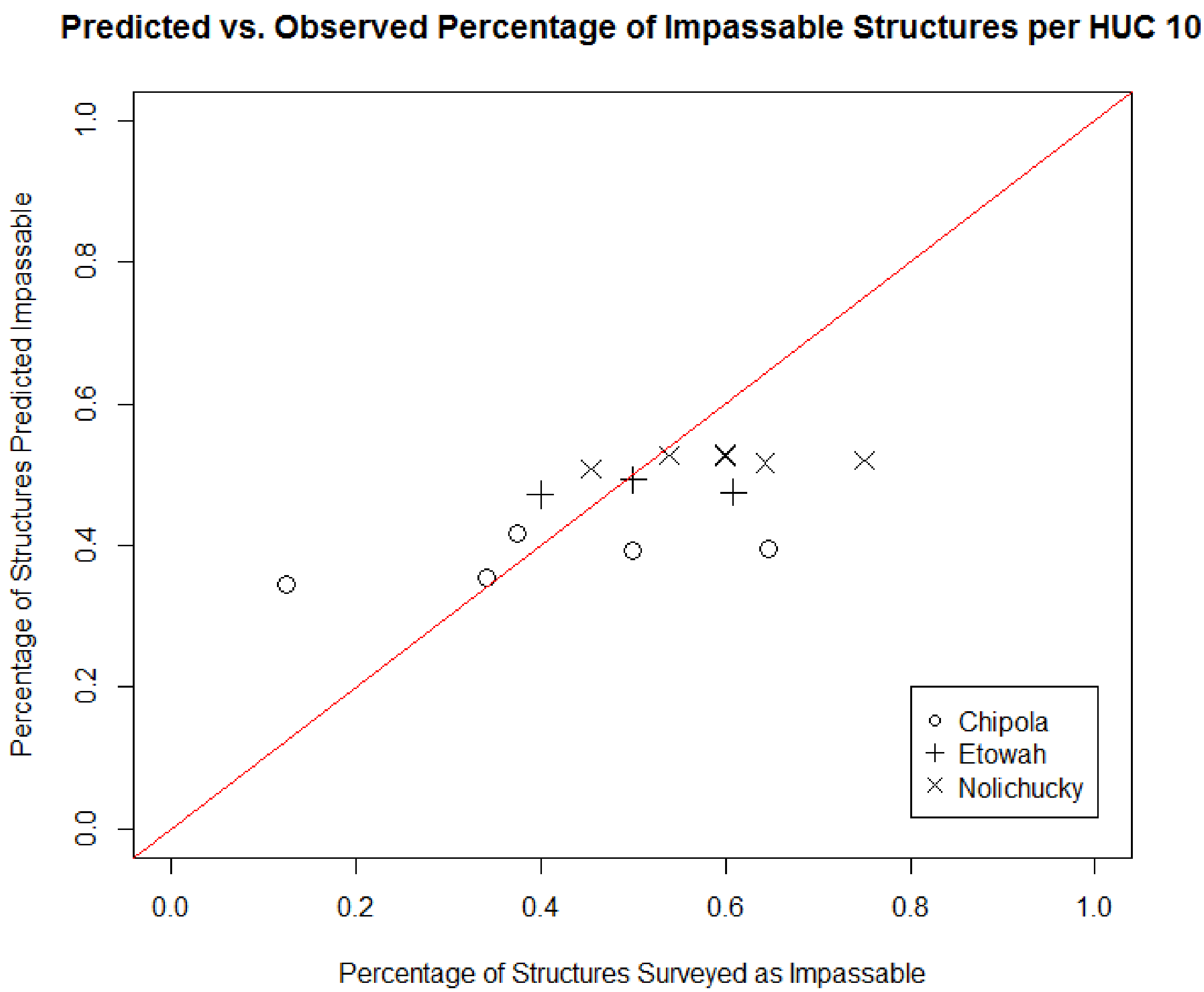


Figure 2.8. Plot of predicted vs. observed impassable culverts. Culvert passability was initially classified using **Bayesian** network models developed by Anderson et al. 2012 in terms of a small bodied fish. The red line represents a 1:1 relationship. The plot represents only HUC 10 watersheds in which ≥ 10 culverts were surveyed. Pearson's correlation = 0.668

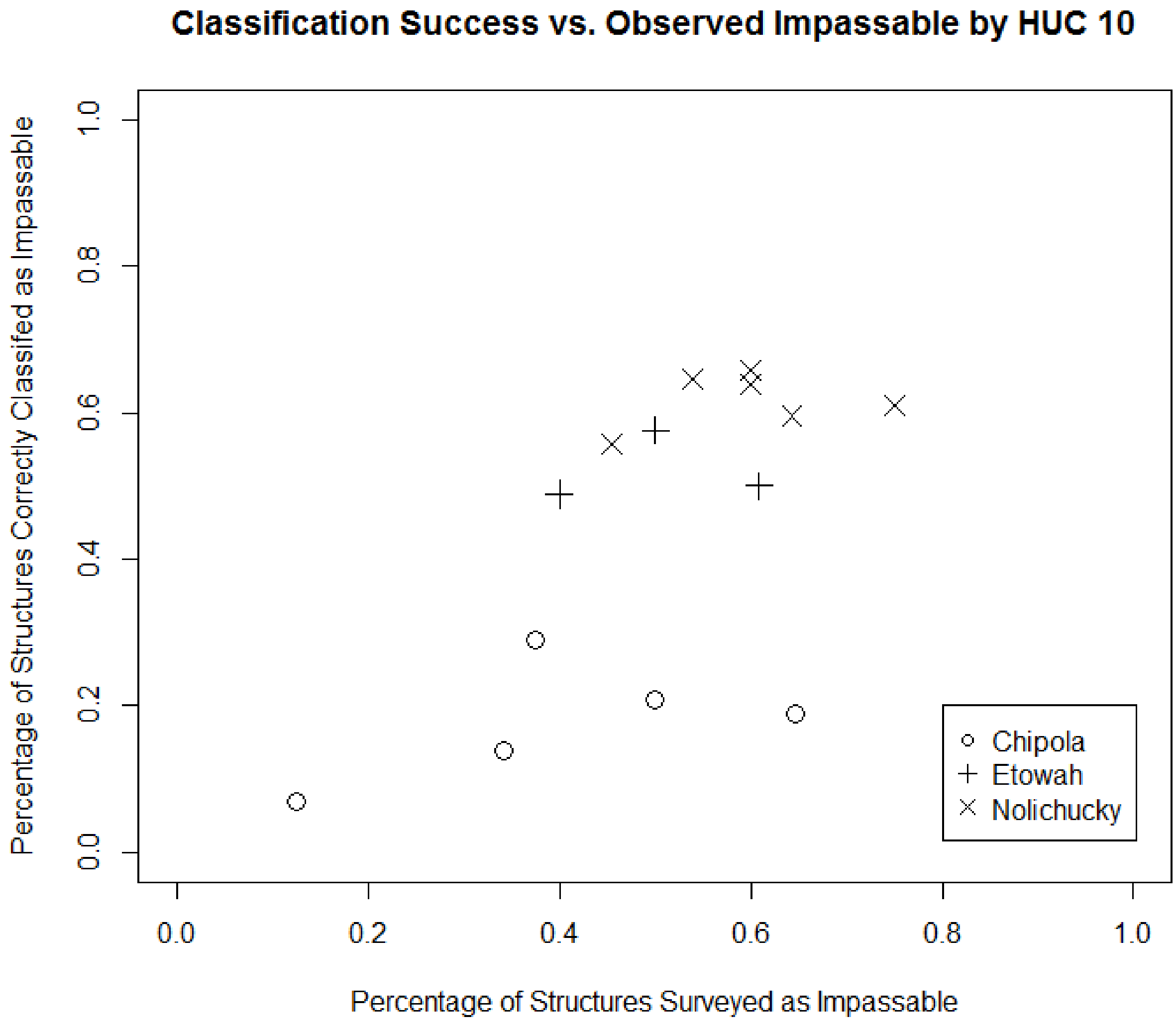
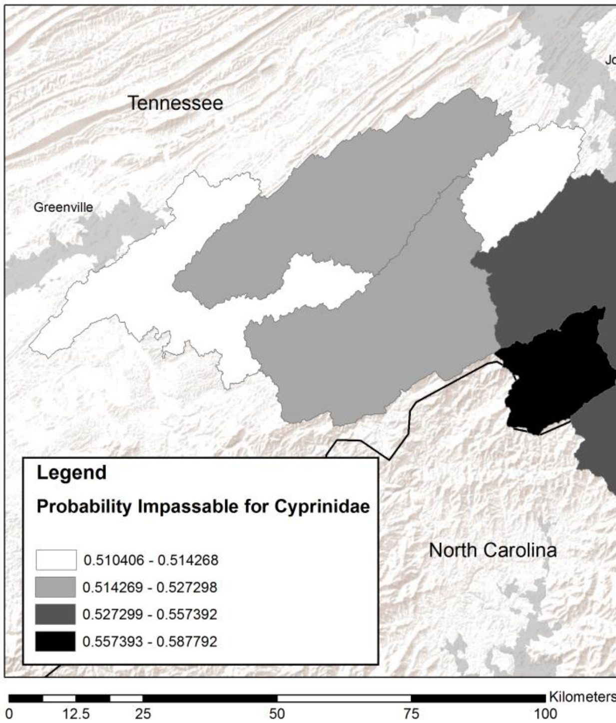
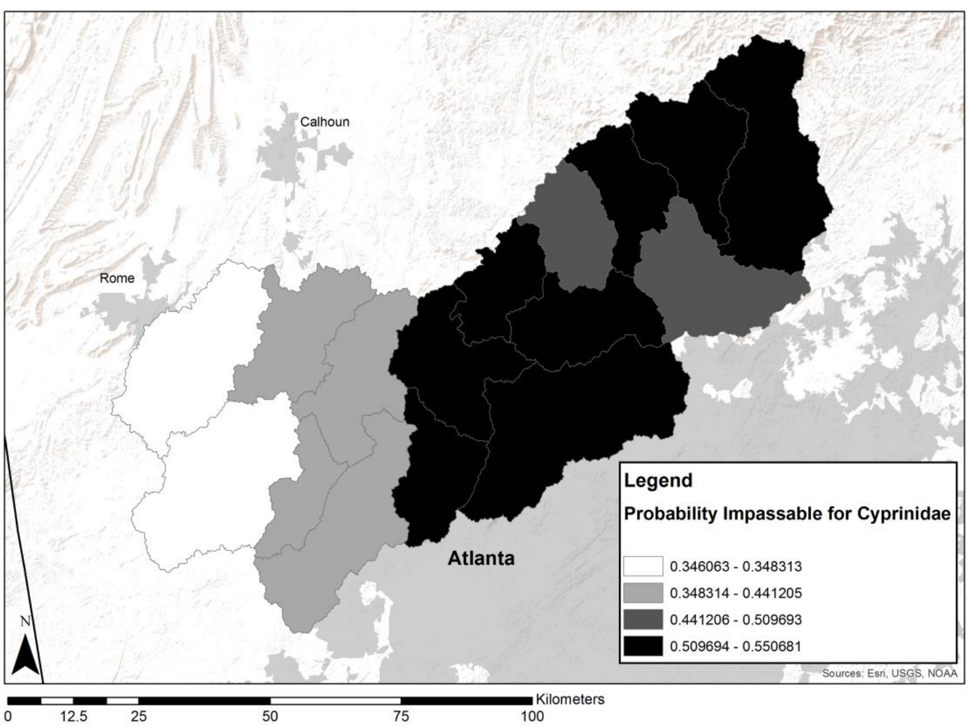


Figure 2.9. Plot showing the percentage of impassable structures correctly classified as impassable using Random Forest models vs percentage of structures surveyed as impassable by HUC 10 watersheds within the larger study watersheds. Culvert passability was initially classified using **Bayesian** network models developed by Anderson et al. 2012 in terms of a small bodies fish. The plot represents only HUC 10 watersheds in which ≥ 10 culverts were surveyed. Pearson's correlation = 0.633

Nolichucky Mean Impassability per HUC 10



Etowah Mean Impassability per HUC 10



Chipola Mean Impassability per HUC 10

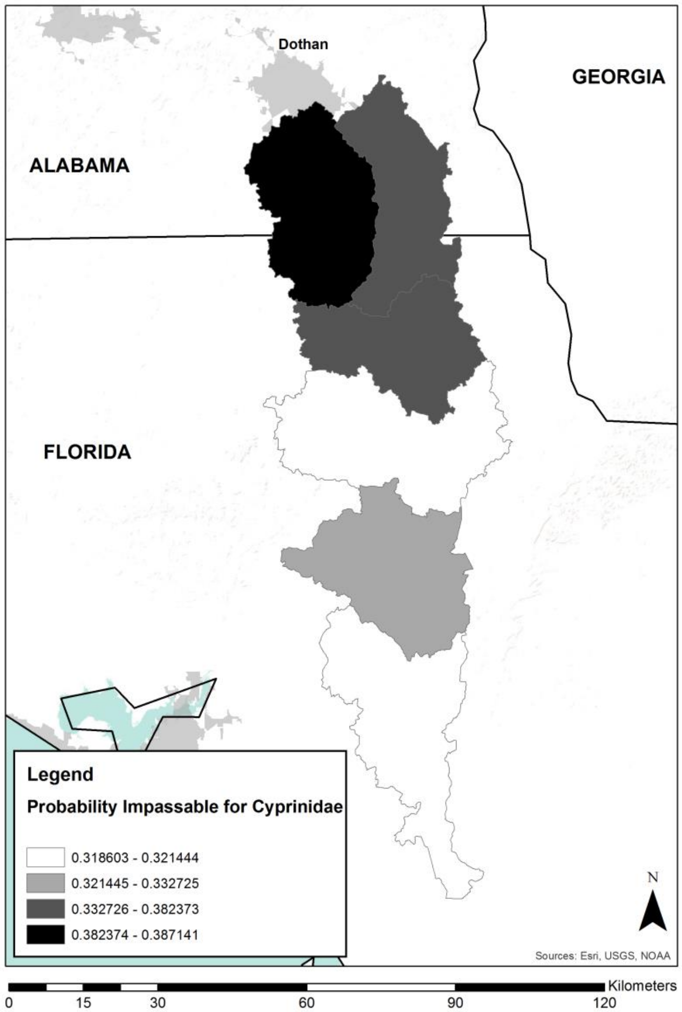


Figure 2.10. Maps show the mean impassability of culverts within HUC 10 watersheds in our three study river basins for fishes with swimming abilities comparable to Cyprinidae. Darker watersheds indicate higher degrees of impassability.

CHAPTER 3

UNDERSTANDING THE CUMULATIVE EFFECTS OF CULVERTS ON STRUCTURAL CONNECTIVITY IN THE ETOWAH RIVER WATERSHED[2]

[2] Collins, E. T. Prebyl, D. Elkins, N. Nibbelink. To be submitted to *Environmental Management*

Abstract

Loss of connectivity (fragmentation) threatens the persistence of freshwater fish faunas worldwide. Fragmentation of lotic ecosystems can be caused by a different types of engineered structures from dams and weirs to culverts and pipelines. In particular, culverts have been identified as significant contributors to fragmentation due to their abundance across the landscape. Past studies have estimated the quantity of passable and impassable culverts across large watersheds; however, little work has contextualized how culverts cumulatively influence connectivity. Here we use random forest modelling to predict impassable and passable culverts to help identify the cumulative effects of culverts on the overall longitudinal connectivity in the Etowah River watershed. We evaluated the effects of culverts using three passability scenarios to reflect the semipermeable passability that culverts likely exhibit. The dendritic connectivity index (DCI) was used to measure overall watershed connectivity. Further, we used the three passability scenarios to gain a better understanding of how culvert prioritization and removal will affect connectivity in a large, species rich, and geographically diverse watershed in the Southeast. Our results show that culverts drastically decrease the DCI by approximately 60 points, however culverts primarily influence low order streams. Finally we found that limited improvements in the DCI were gained from removing high priority culverts or by increasing the quantity of structures removed. These results suggest that connectivity restoration efforts should be focused on smaller watersheds and finer scales.

Introduction

Fragmentation of hydrologic connectivity is a major challenge to conservation of lotic ecosystems and has been identified as a primary threat to freshwater biodiversity (Closs et al. 2016, Gido et al. 2016, Nilsson et al. 2005, Leirman et al. 2005, O'Hanley and Tomberlin 2005). Because of the one-dimensional, dendritic structure of rivers and streams, connectivity is particularly sensitive to relatively few fragmentation events (Fagan 2002). Therefore, it is imperative to fully understand what features fragment lotic systems and to what degree they contribute to overall fragmentation and connectivity in order to effectively conserve and manage freshwater biodiversity.

It is widely known that large structures, like dams, significantly decrease overall connectivity in a watershed (Olden et al. 2016). Dams are essentially complete barriers that often preclude the movement of organisms upstream and alter nutrient and sediment regimes between two points in the watershed (Ibid.). More recently, other elements of human infrastructure and development have been identified as having the ability to decrease overall connectivity in lotic systems (Diebel et al. 2015, Januchowski-Hartley et al. 2013, Diebel et al. 2010, Kemp and O'Hanley 2010). These features generally include linear structures that cross streams and rivers at numerous points, such as pipelines (sewer, oil, gas, and water) and roads (Kemp and O'Hanley 2010). Here, we focus our efforts on road crossings over streams, specifically culverts (tunnel-like, typically modular structures placed into streams to carry water beneath roads).

While dams are a clear source of fragmentation, culverts are far more numerous on the landscape. In the Great Lakes watershed of the United States and Canada, 38 times more culverts exist than dams (Januchowski-Hartley et al. 2013). Dam construction, especially large federal hydropower projects, has declined since the 1960's in the United States (Billington et al. 2005);

however, growing human populations and urbanization prompts a greater need for infrastructure that can accommodate more people on the landscape. Therefore, it can be assumed that we will see a general increase in the number of road-stream crossings and culvert installation with time, especially in regions with the highest levels of predicted growth and urbanization.

Culverts have been found to negatively affect fish population dynamics by increasing the risk of local extirpation and reducing immigration, thus causing decreases in fish abundance and richness, and community structure in a given stream network (Evans et al. 2015, Pépino M et al. 2012, Nislow et al. 2011, Warren and Pardew 1998). These negative effects are often dependent on the structure put in place that allows for the conveyance of water beneath the road (Warren and Pardew 1998). Road engineers are presented with a choice of structures to place in streams that broadly include bridges and culverts. Culverts are often chosen for installation due to their more modular nature, ease of placement in the stream, and their lower cost when compared to bridges (Gibson et al. 2005).

Culverts further complicate analyses of connectivity due to their semi-permeable nature. Although culverts have been found to drastically decrease a fish's ability to move freely between two points in a watershed, they typically still allow for limited movement (Norman et al. 2009, Warren and Pardew 1998). It has been articulated through past studies that culverts can exhibit a range of passability probabilities for various species and guilds of fishes (Norman et al. 2009, Kemp and O'Hanley 2010, Anderson et al. 2012). For instance, road crossings' passability can vary depending on physical characteristics, such as type, length, slope, outlet condition, and flow level or vary depend on species specific traits like swimming ability, life history stage, or simply just an individual animal's motivation to move through a culvert (Kemp and O'Hanley 2010).

Despite understanding that particular culverted road crossings may negatively affect fish movement and population dynamics, the cumulative effects of culverts on longitudinal connectivity are poorly understood. Previous studies have been able to estimate the number of potentially problematic culverts (Januchowski-Hartley et al. 2013, Diebel et al. 2010), but to date, no study has quantified the total effect culverts exert on overall connectivity and fragmentation.

While it is important to be able to identify single culverts that are complete or significant barriers to fish movement, it is also important to understand the cumulative effects that they have on a watershed. By clarifying the influence culverts have on overall connectivity we are better able to articulate the problem they present to managers and decision makers and find solutions. Therefore, our objectives in this study are to understand the level of fragmentation in the Etowah River system, quantify the amount of fragmentation due to culverts vs. dams, and help guide managers by presenting the benefits gained from prioritizing culverts for removal or remediation. We used random forest modelling (Breiman 2001) to predict individual culvert passability as well as percentage of impassable culverts within the entire watershed. Binary predictions (passable and impassable) were assigned to passability probability estimates to reflect three scenarios of passability based on results from Anderson et al. (2012). The dendritic connectivity index (Cote) was used to measure overall watershed connectivity as well as a means to prioritize culverts for removal (Prebyl in prep) under the three passability scenarios.

Methods

Study Area

This study encompasses the Etowah River system. The Etowah River is part of the larger Coosa River system and, ultimately, the Mobile River Basin. It drains an area of about 4,800 km^2

across the Piedmont, Ridge and Valley, and Blue Ridge within Georgia. The Etowah River supports a number of imperiled aquatic species, including three federally listed fish species (Etowah darter, Amber darter, and Cherokee darter) and two federally threatened species (Holiday darter, Bridled darter) (Jelks et al. 2008, NatureServe 2015). Due to the Etowah River's proximity to the Atlanta metropolitan area, urban development continues to be a major threat to the persistence of aquatic species and the overall health of the aquatic ecosystem (Wenger et al. 2010, Burkhead et al. 1997).

Survey Site Selection

To select sample sites, we first delineated an upstream drainage area polygon for each road-stream intersection using 30m Digital Elevation Models (DEMs) and ArcGIS 10.2 (ESRI 2013). Road-stream crossings that had an upstream drainage area greater than 60 km^2 were assumed to be bridges and removed from further analysis, based on a similar threshold used by Anderson et al. (2012). Each intersection point feature was attributed with percent land cover and percent ownership within the upstream drainage area. We then used cluster analysis to stratify road-stream intersections across the range of land cover and ownership that was present in the three study watersheds using the statistical program R (R Core Team 2013). Intersections were clustered into six groups using a scree plot that displayed the variance of each component (see Everitt and Hothorn 2009 for an analogous case using a scree plot for cluster analysis). This method ensured the sample sites encompassed the range of land cover types and ownerships that were present within each watershed. Approximately 33 points were selected at random from each of the six groups to have an approximate total of 200 potential survey points. Although the goal was to survey 150 sites, this larger pool of survey points allowed for the substitution of an equivalent site when one from the first 150 proved inaccessible in the field. In total we surveyed 141 out of over 4,757 road crossing in the Etowah River system.

Random forest models

141 culverts were surveyed in the Etowah River watershed. Passability was estimated for field surveyed culverts using a three-passability-level Bayesian Belief Network developed by Anderson et al. (2012). Culverts classified using this method were used to train random forest models (Breiman 2001) with the randomForest package in R (Liaw and Wiener 2002). We used a classification tree approach within the randomForest, therefore we converted the probabilistic values from the BBN to 1 (impassable) if the probability of impassability was greater than 50% or to 0 (passable) if the probability of impassability was less than 50%. Environmental gradients that are most informative to culvert impassability were identified in an earlier analysis and used as predictor variables in the models (Chapter 2). Random forest models were used to predict whether culverts were impassable or passable for the remaining 4,616 road crossings in the Etowah River watershed. Because final model predictions only reflected two states (impassable and passable), we used passability probabilities from BBNs developed by Anderson et al. (2012) to create three passability scenarios to estimate the potential range of influence culverts have on overall watershed connectivity. These scenarios reflect a range of passability probabilities that culverts could possess under a best, worst, and medium case scenario. Culverts predicted to be passable in the random forest model were assigned passability probabilities of 1, 0.75, or 0.50 under maximum, median, and minimum passable scenarios. Structures that were predicted to be impassable were assigned passability probabilities of 0.49, 0.25, and 0 under maximum, median, and minimum passable scenarios. These three scenarios also allowed us to account for uncertainty surrounding culvert passability predictions and to establish a likely range of

fragmentation effects that culverts place on a watershed. The percent of passible structures was estimated by the mean number of predicted impassable culverts within the watershed after 500 model runs.

We used the Dendritic Connectivity Index (DCI) as a measure of overall watershed connectivity and to prioritize culverts for removal or remediation in the Etowah River watershed.

The DCI provides a means to quantify longitudinal connectivity based on the probability that an organism can move between points in a network (Cote et al. 2008). The equation to calculate the DCI for potamodromous fishes is presented below.

$$DCI_P = \sum_{i=1}^{n} \sum_{j=1}^{n} c_{ij} \frac{l_i}{L}\frac{l_j}{L} * 100$$

The DCI_p evaluates connectivity based on the length of sub-reach i and j (represented by l_i and l_j in the equation) in relation to the total length of the network (represented by L). Passability of barriers between reaches i and j is represented by c_{ij}. This value is calculated by finding the product of the upstream (p_m^u) and downstream (p_m^d) passability for M number of barriers between reaches i and j. For the purpose of this study, upstream passabability probability of a particular culvert was set to the random forest predicted passability under each of the three passability scenarios. Because downstream passability probability of a culvert is not well known, we assumed it to be 0.75 for all three scenarios in our analyses. This assumption reflects that downstream passage through a culvert may be easier for fishes than upstream passage though not always completely passable.

$$c_{ij} = \prod_{m=1}^{M} p_m^u p_m^d$$

To quantify the effects of culverts on overall fragmentation in a watershed, we compared DCI scores for the watershed if dams are the only barriers present vs DCI scores that include both dams and culverts as barriers under the three passability scenarios. For this analysis, we included a fourth passability scenario that assumed culverts were completely passable moving in the downstream direction (downstream passability probability = 1.0) and upstream passability was equivalent to the maximum passability scenario described earlier. This scenario allows for culverts to have the highest probability of passability under our random forest predicted outcomes.

As a second method to measure the effects of culverts on overall connectivity, we compared the distribution of stream reach lengths between barriers when dams were the only cause of fragmentation vs the distribution of fragment lengths when culverts and dams acted as barriers in the system. For this analysis, passable structures were assumed to be completely passable (passability probability = 1) and not considered as barriers, while impassable structures were assumed to be completely impassable (passability probability = 0). Fragment length distributions were generated by simulating different combinations of passable and impassable culverts 100 times to account for prediction uncertainty. For each simulation, random culverts were selected and assigned as impassable such that the overall percentage of impassable structures was equal to the model predicted percentage of impassable structures within the watershed. Reach fragments were sorted into corresponding length classes and the class distribution was visualized for the whole Etowah River watershed, for streams less than 4th order, and streams greater than 3rd order.

Two analyses were undertaken to understand how barrier removal would influence overall connectivity. We evaluated DCI improvement as increasing numbers of culverts were removed under the three passability scenarios to estimate the amount of connectivity improvement that can be expected by addressing culverts for removal and remediation. Because it is not computationally feasible to exhaustively evaluate all possible combinations of culverts, we used a heuristic approach to determine which combination of barriers would result in the largest connectivity gain for a given number of culverts removed (Prebyl, in prep). The heuristic limits the number of barriers considered for removal by first identifying the barriers that fall on stream paths connecting stream fragments with lengths greater than the 75th percentile of all fragment lengths to the stream fragments greater than the 50th percentile. These sets of barriers are then iteratively modified by exchanging barriers for those that connect alternative streams and with each iteration the DCI is evaluated until the heuristic converges on the optimal set of barriers for removal or remediation.

We also evaluated changes in overall connectivity when higher vs. lower priority structures were removed to estimate the overall benefit of prioritizing structures for removal and remediation (see Figure 2.1 for a methods workflow visualization). Culverts were prioritized using a heuristic approach that identified culverts that when removed reconnected the largest fragments (Prebyl, in prep).

Results

The results of our random forests models indicated that approximately 45% of culverts were impassable in the Etowah River watershed, less than the proportion of impassable structures found in other watersheds (Diebel et al. 2015). Model performance was comparable to similar studies that used boosted regression trees to make passability predictions, with the area under the receiver operating characteristic (AUC) equal to 0.697 (Januchowski-Hartley et al. 2014).

Culverts at road crossings are a significant source of fragmentation in the Etowah River watershed. By comparing the DCI of the Etowah River when dams are the only barriers present to when culverts and dams both act as barriers, under our most generous passability scenario, there is a decrease in the DCI of 62.354 (Figure 2.2). Our analysis shows that culverts increase overall fragmentation in the Etowah River predominately in streams less than 4th order (Figure 2.3). This is likely because culverts are rarely placed on streams larger than 3rd order. In the Etowah River watershed 70% of low order streams are fragmented into reaches that are less than 25 km and 58% of low order streams are fragmented into reaches that are less than 10 km. By comparison, if dams are the only barriers present in the system, 80% of stream fragment lengths are greater than 500 km.

Through our comparison of culvert priority ranks and overall DCI improvement, we found that the largest gains in DCI came from structures that are ranked within the top 10, and culverts that are not within the top 10 for removal essentially do not change the DCI from its original state (Figure 2.4b). The amount of improvement gained from removing the top structure, however, is minimal (Figure 2.4a). Finally, we found only small increases in the DCI to occur as more culverts were removed or remediated from the network (Figure 2.5).

Discussion

This further demonstrates that culverts have a major influence on hydrologic connectivity and should not be overlooked as a stressor on lotic ecosystems (Januchowski-Hartley 2013, Januchowski-Hartley et al. 2014, Diebel et al. 2010). In this study, we were able to demonstrate the degree to which culverts affect a watershed and present a plausible “culvert effect” range using maximum, median, and minimum passability scenarios. We were also able to explicitly state that the influence of culverts is restricted to 1^{st}-3^{rd} order streams in the Etowah River watershed. It is likely that this is generalizable across other, similar sized watersheds with similar levels of development. Similar to other studies (Diebel et al. 2015); we found culverts to not only be more numerous on the landscape but also have a larger effect on connectivity. However, contrary to the findings presented by Diebel et al. (2015) we found more minimal improvements on overall connectivity restoration through culvert removal. These findings are likely a result of a differing geographies as well as different amounts of road-stream crossings. The Etowah River basin is approximately twice as large as the Pine-Popple watershed in Wisconsin and contains 26 times as many road-stream crossings. The disparity between the results of these two studies would indicate that connectivity restoration actions through removal and remediation of culverts are more feasible at smaller scales.

Conservation Implications

Culverts have been increasingly identified as presenting problems for fish passage. Recent studies have advocated their inclusion in connectivity assessments and consideration for removal or remediation when undertaking restoration activities (Januchowski-Hartley 2013). In order to maximize improvement from restoration activities, other studies have focused on prioritization algorithms to identify optimal structures for removal and remediation that maximize the amount of connectivity restored for money spent (O'Hanley 2011, Kemp and O'Hanley 2010, O'Hanley and Tomberlin 2005). We agree that culverts need to be included in restoration activities and that the only way to make noticeable improvement in connectivity is through prioritization, however, managers need to be realistic about benefits achieved through addressing culverts in their restoration activities. The results of our prioritization analysis indicate only minimal increases in overall connectivity of a large watershed are achieved by removing the structure found to provide the greatest improvement to DCI. Similarly, the removal of up to 40 culverts only results in slight increases in the DCI likely because culverts are so numerous in the Etowah River system. It is important to consider cost of removal with respect to the latter result. While it is difficult to generalize the cost of culvert replacement, if it is assumed that the cost to replace an impassable culvert with a properly sized arch culvert is approximately $51,000 (a reasonable estimate based on WSDOT 2014), then increasing the number of structures for removal may become cost prohibitive. Alternatively, the cost of multiple culvert removals may be equivalent to the price of a small dam removal and therefore more consideration between the benefits of a single dam removal or multiple culvert removals should be considered. Our results would suggest that culverts are a major stressor to the system that drastically decreases connectivity, particularly in small streams, to the point that large scale restoration of connectivity may be infeasible in the short term. Instead restoration efforts should focus on finer scales and smaller watersheds.

Noticeable improvements in connectivity might be made through removal and remediation of culverts by clarifying objectives and focusing restoration work to a finer scale. For instance, Fullerton and others (2010) identified scale dependence of lotic connectivity to be a challenge to evaluating connectivity, and Schlosser and Angermeir (1995) determined that the study scale needs to relate to taxa of interest. We suggest that identifying smaller watersheds where a species of concern or an assemblage of species that are of conservation concern are present will help focus connectivity restoration to a scale where meaningful actions can occur, this recommendation is similar to that advised by the North Atlantic Aquatic Connectivity Collaborative (NAACC 2015). In a large, developed watershed like the Etowah River the quantity of barriers is so large that the contribution of any single structure is minimal. In contrast, a smaller watershed may have few enough barriers present that an individual barrier may have a larger contribution to overall connectivity. Ultimately, by relating connectivity analyses and restoration activities to species of interest, it is easier to articulate how success can be measured.

Not only do culverts drastically decrease connectivity in terms of the DCI, they also decrease stream fragment lengths. Approximately 60% of fragment lengths fall in the smallest length class (<10 km). Within that length class, approximately 40% of fragments are less than 2 km. Although, there is generally limited understanding of how much movement stream fishes undertake, it is increasingly acknowledged that stream fishes may make larger movements than previously thought (Gowan et al. 1994, Albanese et al. 2001, Fausch et al. 2002, Roberts et al. 2008). For instance, Roberts and others (2008) were able to record a 3.2 km and 2.5 km movement from a darter species (Roanoke darter, *Percina rex*)! Given that even small bodied, benthic fish species are capable of larger movements, it is probably unreasonable to assume that stream fragments less than 2 km are not detrimental to species persistence. Perkin and Gido (2011) further demonstrated this point by showing eventual extinction of certain cyprinid species in fragments less than 136 km. Future work that aims to restore connectivity should address not only connectivity as a whole or as an index, but also ensure that the life history of a species of interest is considered and that appropriately-sized fragments are restored that benefit to species the most.

It is tempting to compare dam removal to culvert removal and remediation when trying to prioritize structures to consider for connectivity restoration. Caution should be used in this exercise, however, because of the disparity in the size of streams that each structure influences. Even if the culverts in consideration restore an equivalent amount of connectivity as would be achieved by removing a dam, the ecological benefit would differ. For instance, a dam removal would not likely benefit fishes that occupy smaller streams (minnows in the genus *Chrosomus* and *Rhynichthys* and darters in the subgenus *Ozarka*, to name a few). Conversely, culvert removal would not likely be as relevant to large-bodied anadromous and potamodromous species (fishes in the genus *Acipenser*, *Alosa*, *Morone*, and *Moxostoma* for instance) in Southeastern rivers. Again, by decreasing the scale of analysis and explicitly defining restoration objectives, the dilemma of culvert vs. dam can be adequately addressed.

In summation, this study joins other lotic connectivity literature in identifying culverts as a significant feature in freshwater fragmentation, but extends from that work to clearly articulate the cumulative effects that culverts have across a large watershed and where those effects are located. While the results may initially seem pessimistic, we hope that a clear understanding of how pervasive and problematic small barriers are in the watershed is presented. Finally, we suggest that large-scale connectivity restoration activities may not be feasible. Instead, it is important to define objectives at a finer scale that is relevant to single species or a species assemblage of interest.

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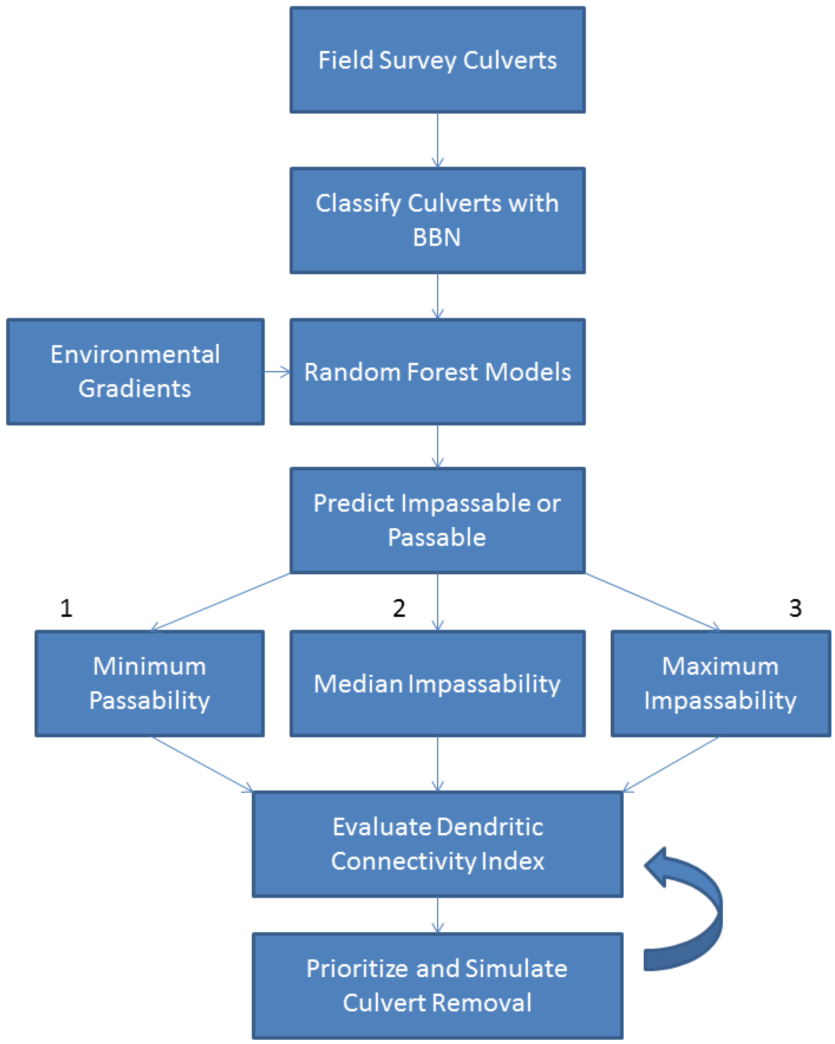


Figure 3.1. Visualization of methods workflow for this study

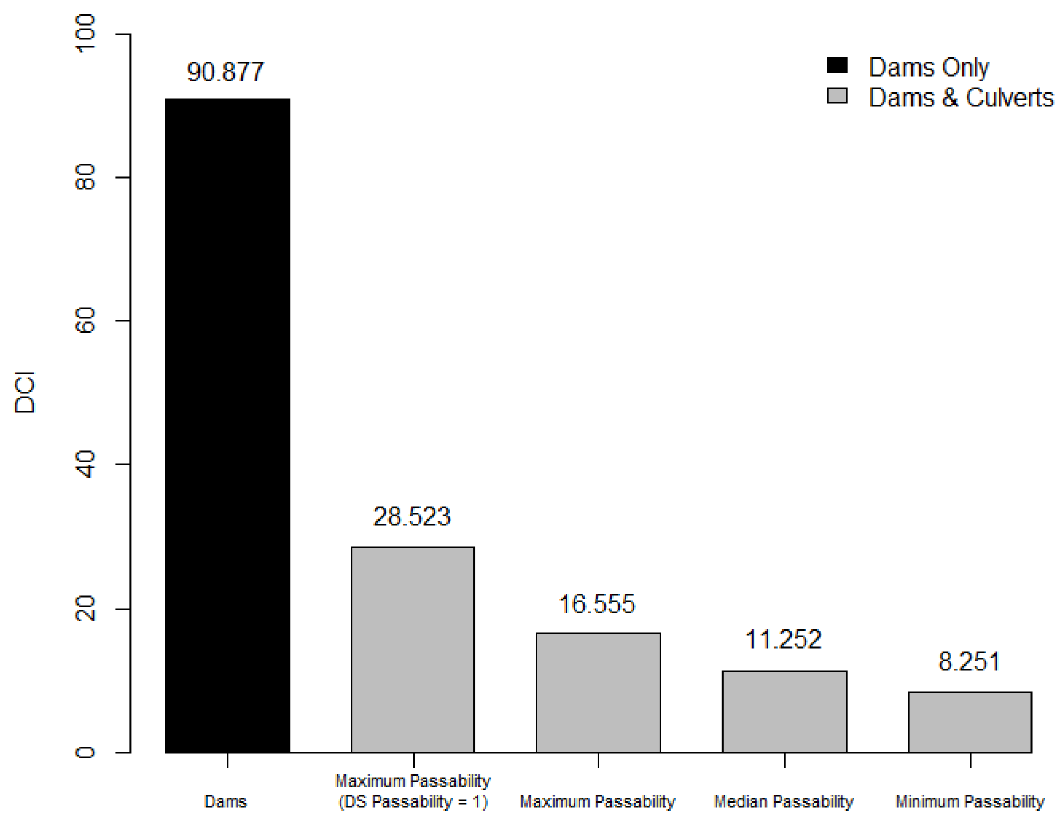


Figure 3.2. DCI scores evaluated when only considering dams as barriers and when both dams and culverts are considered. Four passability scenarios are presented for the dams and culvert DCI calculations. Culverts in the minimum passability scenario were assigned 0.0 probability of being passable for impassable structures and 0.5 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures. Culverts in the median passability scenario were assigned 0.25 probability of being passable for impassable structures and 0.75 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures. Culverts in the maximum passability scenario were assigned 0.49 probability of being passable for impassable structures and 1.0 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures. The scenario "Maximum Passability (DS Passability=1)" indicates the same upstream passability probability as the maximum passability scenario but downstream passability probability was increased to 1.0.

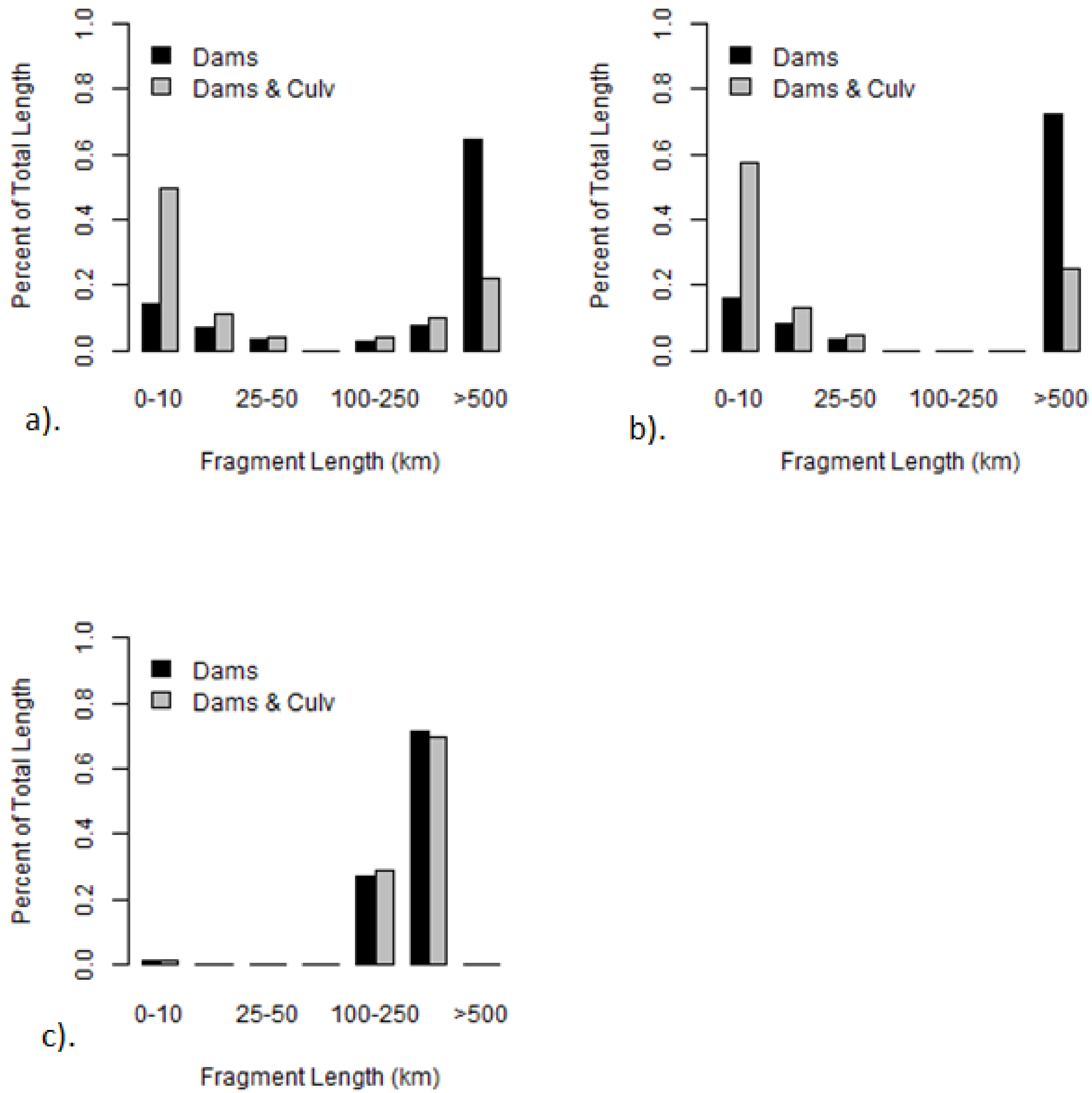
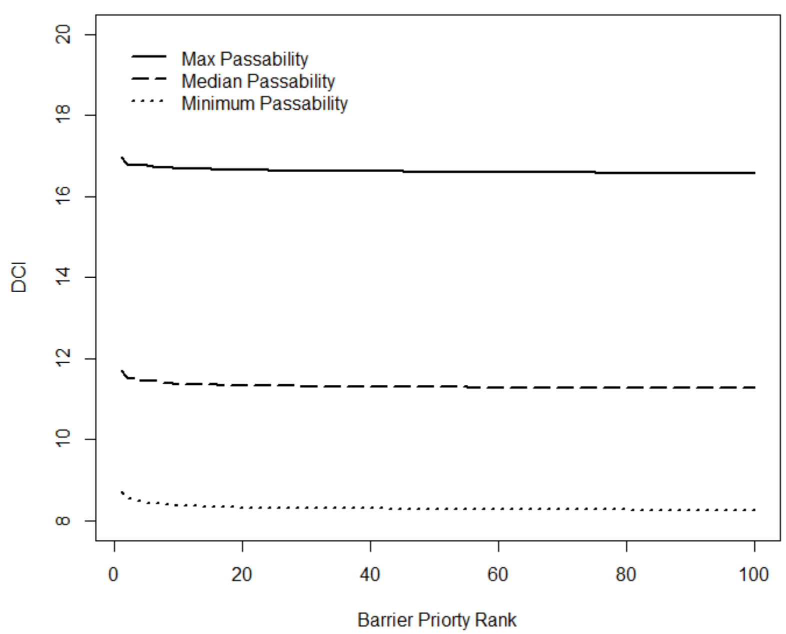
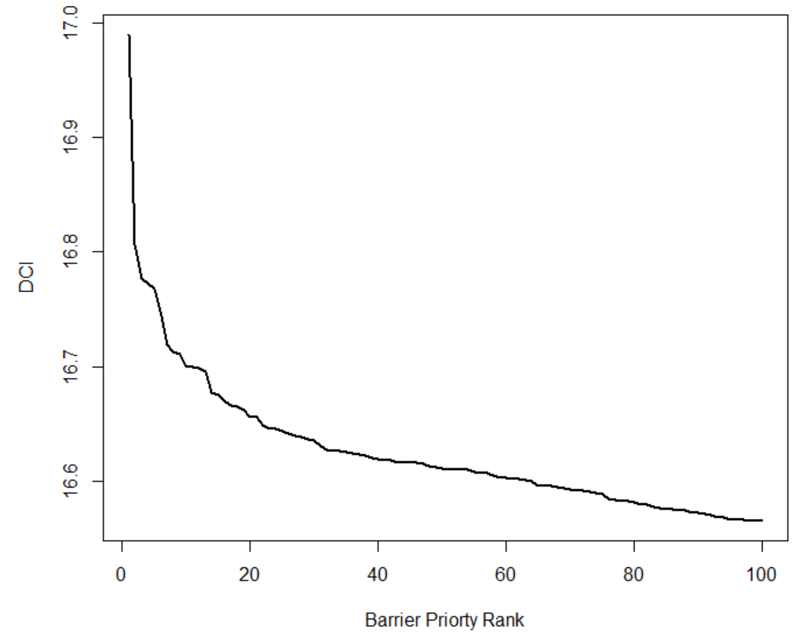


Figure 3.3. The distribution of fragment lengths are compared when dams are the only barriers present and when culverts and dams act as barriers in the Etowah River watershed. A fragment length is defined as a stream reach that exists between two barriers, culvert or dams. Plot **a)** shows the distribution of fragment lengths across the entire watershed. When dams are the only barriers present the majority of fragments are over 500 km. When culverts also act as barrier, the majority of fragment lengths are less than 10 km. Plot **b)** only evaluates streams that are 3rd order (Strahler) and less. Plot **b)** indicates that culverts have a large effect on these smaller streams. Plot **c)** only evaluates streams that are 4th order and larger. In this case, culverts have a negligible effect on fragment length.



a).



b).

Figure 3.4. a) DCI$_P$ score when removing a barrier in order of top priority to least. DCI$_P$ scores are based on the three passability scenarios. Culverts in the minimum passability scenario were assigned 0.0 probability of being passable for impassable structures and 0.5 probability of being passable for passable structures. Culverts in the median passability scenario were assigned 0.25 probability of being passable for impassable structures and 0.75 probability of being passable for passable structures Culverts in the maximum passability scenario were assigned 0.49 probability of being passable for impassable structures and 1.0 probability of being passable for passable structures. Downstream passability scores of 0.75 were assigned for all structures. Plot only show the top 100 barriers for removal. Plot **b** focus DCI$_p$ improvement only for the maximum passability scenario. Removing lower priority culverts only minimally changes the original DCI score for each scenario (see figure 3.2 for DCI scores with no barriers removed).

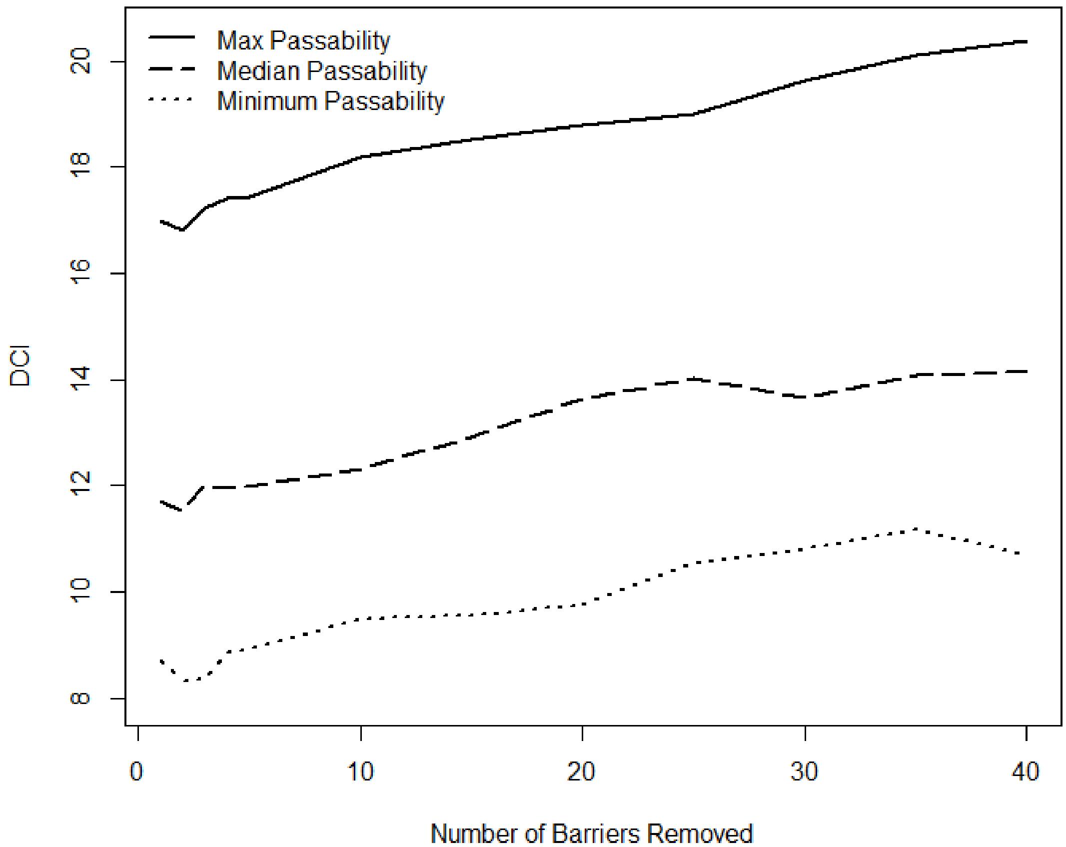


Figure 3.5. Improvement in the DCI_P as increasing numbers of barriers are removed. DCI_P scores are based on the three passability scenarios. Culverts in the minimum passability scenario were assigned 0.0 probability of being passable for impassable structures and 0.5 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures. Culverts in the median passability scenario were assigned 0.25 probability of being passable for impassable structures and 0.75 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures. Culverts in the maximum passability scenario were assigned 0.49 probability of being passable for impassable structures and 1.0 probability of being passable for passable structures; downstream passability scores of 0.75 were assigned for all structures.

CHAPTER 4

DISSCUSSION AND RECOMMENDATIONS

Fragmentation of hydrologic connectivity has been identified as a one of the major threats to freshwater biodiversity (Closs et al. 2016, Gido et al. 2016, Nilsson et al. 2005, Leirman et al. 2005). A variety of human activities can decrease connectivity and fragment aquatic habitats, but the most well-known are examples of human engineering and construction, i.e. dam building. Increasingly, road-stream crossings with installed culverts have been found to have the ability to decrease overall connectivity in lotic ecosystems (Januchowski-Hartley et al. 2013, Diebel et al. 2010). While culverts are physically smaller than dams, and may at least allow some fish movement (Anderson et al. 2012, Norman et al. 2009, Warren and Pardew 1998), they drastically outnumber dams across a watershed. One study found approximately 38 times more culvert than dams in a large watershed (Januchowski-Hartley et al. 2013). In our analyses, we found between 3,000 and 12,000 potential road crossings in watersheds that ranged in size from approximately 3,000 to 4,800 km^2. Because culverts are so numerous, they present a formidable challenge to effective conservation actions that address lotic connectivity. The purpose of this study was to gain a clearer understanding of environmental gradients that influence culvert passability with the hope that these could be used to build effective models that could predict the quantity of impassable structures across a large watershed. To further help managers with building predictive models, we also wanted to understand if differences existed in methods of passability classification of field surveyed culverts. Finally, we aimed to gain a better understanding of the total effect culverts have on connectivity in a large watershed.

Only one previous study evaluated the influence of landscape level variables on culvert passability. In that study, measures of stream gradient and upstream catchment area were found to be informative to culvert passabilty (Januchowski-Hartley 2014). Our study contributes to this previous research by identifying other topographic variables that help inform passabilty. Most variables used in the RF models support our hypothesis that variables that account for greater amounts of erosion (greater topographic relief, greater stream gradients, more impervious surface, and low slope position) lead to impassable structures. Contrary to our initial hypotheses however, more forest cover tends to be associated with impassable structures and higher amounts of agriculture tends to be less associated with impassable structures. Knowledge of these landscape gradients may help transportation agencies identify regions where more effort should be placed to prevent the installation and formation of impassable culverts.

We were able to build random forest models that could predict culvert passability across a large watershed. Final random forest models had a fairly modest performance, although they were comparable to boosted regression tree models developed by Januchowski-Hartey et al. (2014) with AUC scores near 0.70 for the best models. It is likely that as more environmental gradients that influence passability are identified model predictions will improve. These results suggest that machine learning algorithms can effectively be used to understand the degree to which culverts fragment watersheds and target areas for more in-depth field surveys or to target connectivity restoration efforts.

We found that model performance was improved when a field classification method was used that incorporated uncertainty into passability estimates of training data. Therefore we suggest performing a more rigorous passability classification methodology, like that developed by Anderson et al. (2012). Future emphasis should be placed on accurate classification of barriers after field data collection to improve predictive ability of the models trained from the field data. Of the two methods compared, Bayesian belief networks may be preferable to the Coffman passability models in their current state. The methods developed by Coffman may still be useful if the models were created for a more specific taxonomic level, such as by genera, subgenera, or species.

We were able to demonstrate the degree to which culverts affect a watershed and present a plausible "culvert effect" range using maximum, median, and minimum passability scenarios and the dendritic connectivity index (DCI) (Cote 2009). The three passability scenarios were derived from the range of passbility probability that impassable and passable culverts exhibit as determined by Anderson et al. (2012). To our knowledge, this is the first time the cumulative effect of culverts has been clearly articulated.

We were also able to explicitly state that the influence of culverts is restricted to 1^{st}-3^{rd} order streams in the Etowah River watershed. An analysis of fragment lengths of these lower order streams shows that ~60% of stream fragments are <10 km. Future analyses will determine whether these are consistent findings for other watersheds in the southeastern U.S. The implications of these results that small streams are highly fragmented. While it is unclear exactly how far small bodied stream fishes move, it is likely that some species make movement longer than 10km (Roberts et al. 2008, Albanese et al. 2001). Depending on life history traits, these fragments may lead some species into localized extinctions (Perkin and Gido 2011). Fragments of this size may also make populations that occur within them less resilient to droughts or environmental perturbations. Conservation actions should consider how species will benefit the most from connectivity restoration. Clearly increases in fragment size are desirable, but does it make more sense to prioritize increases in linear distance or restoration of a dendritic structure?

Through the course of this study it became clear that fragmentation of culverts is strongly related to spatial scales. For instance, our analysis of culvert removal prioritization and removal number indicated that relatively little improvement can be made by addressing culverts across a large watershed. This result is accurate if our objectives are to restore connectivity across large spatial scales, however, improvement at the site of culvert removal should not be ignored. The latter idea is particularly relevant when we consider that several native fish species occupy fairly small ranges. It will be most effective to assess connectivity and culvert passability in terms of a species of interest. This has the potential to narrow the scope of work to a more realistic spatial scale. Further, the removal of single problem culverts is likely to have a more significant effect at smaller scales. Finally, by tailoring connectivity restoration actions to a species or species assemblage, managers can determine whether culverts or dams are more relevant based on habitat preferences.

Reducing the scale of analysis may also help improve model performance. We found a disparity in the predictive abilities of models within each watershed. Models performed particularly poorly in the Chipola River watershed. It is likely that the landscape variables we selected for use in the random forest models are more relevant to higher gradient streams. Also, some of the variables we selected for use in the models had a relationship with passability that was counter intuitive. Increases in percent forest cover and decreases in percent agriculture were found to be related to impassable culverts. It is unclear if this is a true relationship between land use and impassability. Instead, the models may be using land cover types more common to the Chipola watershed (which has a higher percentage of passable structures) to classify passability.

Future work should attempt to understand what factors lead to impassable structures in lower gradient, coastal systems. By decreasing the scale of analysis, it may be easier to identify landscape gradients most relevant to culvert passability within that region.

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