

TOWSON UNIVERSITY
OFFICE OF GRADUATE STUDIES

THE INFLUENCE OF NETWORK STRUCTURE, HABITAT FRAGMENTATION,
AND FAUNAL SOURCES ON AQUATIC COMMUNITIES IN HEADWATER
STREAMS

by

Sean D. Sipple

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THESIS APPROVAL PAGE

Sean Sipple

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Science)

 _____ Joel W. Snodgrass _____ 12/5/16

Chairperson, Thesis Committee Signature Type Name Date

 _____ Chris J. Salice _____ 12/5/16

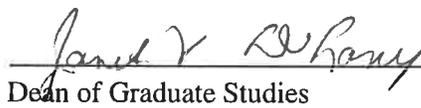
Committee Member Signature Type Name Date

 _____ Scott Stranko _____ 12/5/2016

Committee Member Signature Type Name Date

Committee Member Signature Type Name Date

Committee Member Signature Type Name Date

 _____ Janet V. Delany _____ 12-18-16
Dean of Graduate Studies Type Name Date

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ABSTRACT

Headwater streams comprise the majority of the stream network, providing important ecological functions to the downstream network. Although we are beginning to understand how network structure may influence fish, our understanding of how it influences benthic macroinvertebrate dispersal and population connectivity is limited. We also know little about how these patterns and processes may be disrupted as a result of human-driven landscape change such as stream barriers to movement and creation of artificial habitats such as stormwater and farm ponds. In this study, I investigated the effect of stream network position, stream size, and local habitat on benthic macroinvertebrates, and determined to what degree road crossings and impoundments may be degrading benthic macroinvertebrate and fish communities in headwater streams. These mechanisms were explored using Maryland Department of Natural Resources, (MDNR) Maryland Biological Stream Survey (MBSS) benthic macroinvertebrate, fish, and environmental data from first-order streams in the Piedmont region of Maryland. Using an Information Theoretic Approach (ITA), models were developed based on the hypothesized relationships between benthic macroinvertebrate and fish community structure and several network and anthropogenic impact variables. Based on my results, aquatic community structure was dependent on local habitat conditions and stream network structure. Both assemblages responded negatively to roads, which may suggest an isolation effect. These results also suggest that impoundments are acting as sources for benthic macroinvertebrates and fish, including non-native species.

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CHAPTER 1

LITERATURE REVIEW

1.1 INTRODUCTION

Scientists have long recognized that riverine systems have a hierarchical spatial structure, where stream habitats such as pools, runs, and riffles are combined to form reaches, which come together to form stream networks similar to the branching of a tree (Strahler 1964). The stream network consists of all interconnected streams and floodplains in a watershed, driven by fluvial and biological processes. In stream networks, the flow of material and energy is primarily restricted to the physical network, and the geometry of the branches can affect physical and biological processes and patterns (Campbell Grant et al. 2007). Elements of spatial structure such as basin size, basin shape, network pattern, and size differences between confluent channels can regulate the spatial distribution of physical diversity within river systems (Benda et al. 2004). These natural elements, as well as anthropogenic impacts from habitat fragmentation can also affect the availability of refugia, habitat diversity, and dispersal for aquatic fauna (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Smiley and Dibble 2008). We are also beginning to understand how network structure may influence both physical and biological patterns and processes in fish. However, our understanding of how elements of network structure such as position along a reach, position within the network, and distribution of habitat influence benthic macroinvertebrate dispersal and population connectivity is limited. We also know little about how these patterns and processes may be disrupted as a result of human-driven

landscape change such as stream barriers to movement and creation of artificial habitats such as stormwater and farm ponds.

1.2 DISPERSAL IN STREAM NETWORKS

Two major types of movement in streams include dispersal and migration.

Dispersal is the one-way movement of organisms (or propagules) from their point of origin or release (Lincoln et al. 1998). It is a mechanism by which organisms acquire resources necessary to complete their life-cycle and ultimately increase their fitness, and it plays an important role in determining the distribution of aquatic fauna across stream networks (Ricklefs 1990; Dingle 1996). Dispersal is also important in population dynamics, especially when populations are patchily distributed and demographic rates vary among patches, such as when populations exhibit metapopulation or source-sink dynamics (Dunning et al. 1992). Migration is generally considered to be regular, long-distance movement of organisms among habitat patches in order to exploit new resources or different habitats (Dingle 1996). Migration is an important behavior used by biota with complex life cycles that require multiple habitat types to complete their life cycle. Dispersal and migration in streams can occur within the network (i.e., within the stream corridor) and out of the network (i.e., overland between adjacent streams; Campbell Grant et al. 2007).

Benthic macroinvertebrates primarily disperse through emergence as adults and through a mechanism called drift, but upstream movement of aquatic forms is possible. Drift involves the downstream transport of benthic macroinvertebrates by the force of moving water (Waters 1972; Benson and Pearson 1987). Drifting organisms are typically

transported short distances (McLay 1970; Townsend and Hildrew 1976; Danehy et al. 2011), although Neves et al. (1979) documented drift for hundreds of meters during baseflow and over one kilometer during stormflow. In addition to downstream drift, many aquatic invertebrates will actively move upstream, primarily over short distances, but some will move more than two kilometers as larvae (Vaughan 2002). The more common type of dispersal is found among adult insects with complex life cycles involving metamorphosis and emergence of a terrestrial phase. Although little is known about dispersal distances for most taxa, as adult insects emerge, they typically disperse upstream before reproducing (Hershey et al. 1993; Bilton et al. 2001). Upstream flight may compensate for the downstream drift of larval forms (Waters 1972). Using mark-recapture techniques, Hershey et al. (1993) found that one-third to one-half of the adult mayfly *Baetis* (Ephemeroptera: Baetidae) population traveled 1.6 to 1.9 km upstream. Petersen et al. (2004) found that the majority of adult Ephemeroptera, Plecoptera, and Trichoptera (EPT) dispersed within or very close to the stream channel, although 10% of Plecoptera traveled more than 60 m from the stream channel. Winterbourne et al. (2007) showed similar results, but found that some female Trichoptera dispersed hundreds of meters from their natal stream. These studies suggest that most adult insect dispersal is within the stream corridor rather than laterally, although insects seem to have an inherent dispersal mechanism to colonize new habitats (Winterbourne et al. 2007).

Dispersal of fishes is confined entirely to the wetted stream channel and consists of movements to find suitable habitat for feeding, reproduction, and refugia. Movement can be migratory or more localized in nature, although it is thought that most freshwater fish have some form of migratory behavior over time and space (Brönmark et al. 2014).

Diadromous species (i.e., species that migrate between fresh and saltwater) are known to migrate long distances to complete their life cycle, with migrations ranging from hundreds of meters to thousands of kilometers (Binder et al. 2011). Other species, such as resident fish in streams and lakes, do not usually travel beyond their home range, but will occupy different habitats during different seasons and portions of their life cycle. Although resident species are relatively sedentary, some have been found to travel long distances. For example, Gatz and Adams (1994) studied the movement of redbreast sunfish (*Lepomis auritus*), bluegill (*Lepomis macrochirus*), rock bass (*Ambloplites rupestris*), largemouth bass (*Micropterus salmoides*), and warmouth (*Lepomis gulosus*) over a three-year period in a Tennessee stream. They found that most individuals within the stream traveled less than 100 m along the channel, although several individuals of redbreast sunfish, largemouth bass, and bluegill traveled over 10 kilometers.

1.3 HABITAT CONNECTIVITY

Dispersal of fish and benthic macroinvertebrates in streams is dependent on connectivity, the extent to which populations within a species' range are linked (Palumbi 2003). Connectivity of habitats is an important factor in maintaining biological diversity (Crist et al. 2005), as it can facilitate the movement of genes, individuals, species, and populations among habitat patches (Minor and Urban 2008). In streams with unaltered connectivity, factors such as stream size, position within the stream network, gradient, and distribution of habitat should dictate aquatic diversity and community structure. It is well documented that species richness in fish communities generally increases as stream size increases (Sheldon 1968, Platts 1979, Fairchild et al. 1998). The increase in diversity is due to a general increase in the size and heterogeneity of habitat, as well as

differences in depth from the headwaters to the lower reaches. As described in the Riverine Continuum Concept (RCC; Vannote et al. 1980), aquatic community structure and function also changes with increasing stream size due to changes in geomorphology and physical habitat. The RCC divides rivers into headwaters (1st to 3rd-order streams), mid-reaches (4th to 6th-order streams), and lower reaches (> 6th-order streams).

Headwaters are usually characterized by narrow, highly shaded streams that receive organic input mostly from allochthonous materials in the form of leaves and sticks. The benthic macroinvertebrate community is dominated by shredders, which break down the coarse particulate organic matter. The fish community is low in diversity and largely invertivorous. Mid-reaches are characterized by a higher amount of autochthonous material in the form of periphyton due to their larger size, reduced currents, and more open canopies. However, allochthonous material also plays an important role in mid-reaches due to the surrounding forest. Collectors that collect and consume fine particulate organic matter, and grazers that consume periphyton, dominate the benthic macroinvertebrate community in mid-reaches. However, continued input of allochthonous material supports some shredders in mid-reaches. Mid-reaches are characterized by piscivorous and invertivorous fish species. In the lower reaches, particulate organic matter is common, but there is less primary production due to higher turbidity (Vannote et al. 1980). As a result, benthic macroinvertebrate communities in lower reaches are dominated by collectors, and fish communities are dominated by piscivorous and planktivorous species.

The RCC predicts lowest benthic macroinvertebrate species richness in low-order streams, increasing with stream size until an expected maximum in medium-sized

streams, where environmental variability is highest. Species richness would then decrease again in large-order streams due to the more homogeneous habitat. Thus, plotting the number of species as a function of drainage area should produce a unimodal curve. A study of riffle habitats at ten locations on the Salmon River in Idaho by Minshall et al. (1995) supports this prediction. However, Melo and Froehlich (2001) found no evidence of a unimodal pattern of species richness with increasing stream size in tropical streams. In fact, their study showed that species richness generally decreased along a gradient of stream size from smallest to largest.

Location within the stream network can also influence aquatic diversity and community structure. For example, fish found in headwater streams are more limited by local conditions than fish lower in the watershed, which have access to more of the stream network (Magalhães et al. 2002; Grenouillet et al. 2004; Hitt and Angermeier 2008a). Also, streams connected to larger rivers lower in the network tend to have more species than similarly sized streams connected to smaller streams (Gorman 1986; Osborne and Wiley 1992; Schaefer and Kerfoot 2004; Smith and Kraft 2005; Hitt and Angermeier 2006; Hitt and Angermeier 2011). For example, Osborne and Wiley (1992) found a significant and positive relationship between fish species richness and downstream link (d-link), an index of the spatial location of a stream within a stream network. In their study, d-link explained the greatest portion of variance in diversity, which suggests that downstream processes affect fish community structure in tributary streams more than in similar sized streams further up the drainage. First to third order streams connected to rivers that are at least three orders of magnitude larger are described as adventitious. These tributaries produce unique conditions for aquatic fauna due to

their proximity to the relatively species rich main channel, which facilitates greater dispersal compared to the headwaters of the mainstem (Gorman 1986). Thus, the downstream portions of adventitious streams near the confluence with the main channel tend to be higher in diversity and more variable over time. For example, Thomas and Hayes (2006) found that fish species richness was higher in adventitious streams than in the headwaters of the mainstem, and that fish species composition of adventitious streams was more similar to the mainstem than the headwaters.

The relationship between stream position and benthic macroinvertebrate diversity and community structure is far less studied, although some studies have produced results similar to those for fish communities. Two studies highlight the current knowledge of aquatic invertebrate communities relative to stream position (Harrel and Dorris 1968; Brown and Swan 2010). Brown and Swan (2010) found that benthic macroinvertebrate communities are dictated by environmental factors in the headwaters of streams and by dispersal in the mainstem. Similarly, Harrel and Dorris (1968) showed that benthic macroinvertebrate community structure on a 3rd order adventitious stream was more similar to the mainstem than on a similar size stream further upstream in the watershed, which also suggests dispersal-driven processes in streams more connected to the mainstem. However, no studies have explored the relationship between benthic macroinvertebrate community structure and d-link, a metric that has been utilized for studies on fish. Although, based on the unimodal species distribution predicted by the RCC, one would expect a similar distribution for a plot of benthic macroinvertebrate species richness as a function of d-link. For example, if small streams are predicted to have a low number of macroinvertebrate species, then 1st order streams connected to such

streams should have a relatively low number of species due to the lack of a diverse source population from the small stream. However, since medium-sized streams should have the highest species richness, you would expect that 1st order streams connected to medium-sized streams would have a relatively high number of species. Furthermore, due to the low predicted species diversity in large streams, small streams connected to these streams would likely have low diversity due to the low number of source species in the large mainstem.

It has been well documented that stream habitat has an influence on species diversity and composition (Reid 1961; Vannote et al. 1980; Benda et al. 2004). Habitat in streams is mediated by fluvial processes, which drive the distribution of benthic substrate, woody debris, and other habitat-forming materials that can affect benthic macroinvertebrate and fish community structure (Reice 1980; Duan et al. 2009; Martin et al. 2013). Stream confluences can provide distinct physical conditions that may create high quality habitat (Benda et al. 2004). Stream confluences can enhance diversity by increasing habitat heterogeneity, providing refugia, and allowing access to the mainstem for dispersal and migration (Campbell Grant et al. 2007). The increase in heterogeneity is due to the size difference between confluent channels, which has an effect on reaches immediately upstream and downstream of the confluence (Benda et al. 2004). Upstream of confluences, there are lower gradients, wider channels and floodplains, increased wood recruitment, finer substrates, and greater lateral connectivity. Downstream of confluences, there are higher gradients, larger substrate sizes, deeper pools, and more bars. Hitt and Angermier (2008b, 2011) found that stream confluences could influence fish communities up to several kilometers within both main channels and tributaries.

Similarly, Schaefer and Kerfoot (2004) found that mean fish diversity decreased as distance from the mouth of the stream increased. Confluences can also effect the composition of benthic macroinvertebrates. Downstream of confluences there is a unique composition of taxa that are distinct from the mainstem and tributaries that feed them (Knispel and Castella 2003; Hellmann et al. 2015). Knispel and Castella (2003) found that benthic macroinvertebrate diversity increased downstream of the confluence of a small tributary and a large glacier-fed stream. They concluded that the influence of the tributary on the main channel resulted in greater habitat heterogeneity through increased organic matter inputs and sediment supply, which may have resulted in a more diverse fauna. In contrast, some studies have shown no change in benthic macroinvertebrate density, taxa richness or functional feeding group composition downstream of confluences relative to upstream, despite distinct assemblages in both (MacNally et al. 2011). The above studies have focused on differences in benthic macroinvertebrate communities in the mainstem upstream and downstream of confluences, but very few have studied the effect of the confluence on the tributary stream. There is strong evidence that species composition in small streams is distinct from species composition in medium to large-sized streams (Vannote et al. 1980; Minshall et al. 1995; Melo and Froehlich 2001), thus one would expect that taxa richness and other measures of community structure would change with proximity to a confluence. In a recent study, Wilson and McTammany (2014) found less similarity in benthic macroinvertebrate community structure between a tributary stream and the mainstem, as the distance from the confluence increased on the tributary.

1.4 HABITAT FRAGMENTATION

Alteration of stream hydrology and physical structure by humans can affect habitat connectivity by creating physical barriers to the movement of organisms, which can have negative effects on biological communities (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Neville et al. 2006; Smiley and Dibble 2008). As barriers limit or eliminate upstream movement, remnant populations above the barriers become fragmented and isolated, and can go locally extinct (Kruse et al. 2001), decreasing species diversity (Siligato and Böhmer 2002). Due to their linear nature and extent in the landscape, streams are particularly vulnerable to fragmentation, especially from road crossings and impoundments.

The United States (U.S.) road network covers approximately 2% of the continental U.S. (Cerulean 2002). As a result, the construction of roads can cause fragmentation of watersheds due to the placement of culverts at stream crossings. The severity of the impact depends on the type of road crossing and size and installation of culverts (Jackson 2003). Physical impacts of road crossings include increasing the detention time of water upstream of the crossing; altering the sediment transport and scouring of the channel during storm events; restricting the ability of woody debris to pass downstream; and impeding the movement of aquatic fauna by acting as a physical barrier (Jackson 2003). Physical barriers to movement are caused by elevation drops at the inlet or outlet of culverts; blocked or collapsed culverts; excessive water velocities within and around culverts; lack of bank edge areas above and below culverts; insufficient water depth within culverts; and discontinuity of channel substrate (Jackson 2003). These impacts can have a negative effect on benthic macroinvertebrate (Resh

2004; Khan and Colbo 2007; Peterson 2010) and fish (Benton et al. 2008; Burford et al. 2009) communities. For example, Peterson (2010) found that culverts cause a greater proportion of stressor-tolerant benthic macroinvertebrate taxa and an alteration of dominant feeding groups in streams below culverts. Resh (2004) found that culverts decrease the ability of non-insect macroinvertebrates to disperse upstream. For fish, culverts also limit upstream movement. Burford et al. (2009) found that upstream movement of cutthroat trout averaged 2.45 times lower through culverts than through natural channels. In Burford's study, outlet drop was the most important factor reducing fish passage.

Impoundments (e.g., lakes and ponds), which also cause habitat fragmentation, are present along streams throughout much of the U.S. In Maryland, there are over 400 dams, ranging from 6 to 296 feet in height (Maryland Department of the Environment 2014). Busch and Larry (1996) estimated that 15,167 dams that prevent fish movement are present along the Atlantic coast. Dahl (2011) estimated that there are 2,980,000 agricultural ponds, 410,000 industrial ponds, and 963,000 urban ponds in the U.S., many of which are likely connected to stream systems. In addition, Liermann et al. (2012) found that nearly 50% of global ecoregions are obstructed by large and medium size dams. Impoundments can affect the physical, chemical, and biological characteristics of streams by altering substrate, sediment load, dissolved oxygen, and water temperature, and impeding the movement of aquatic fauna (Kittrell et al. 1959; Baxter 1977; Lessard and Hayes 2003; Falke and Gido 2006). Dams are a sink for sediment that would normally be transported downstream. Immediately upstream of the impoundment, coarse substrate can be embedded with sand and silt. In contrast, immediately downstream of

impoundments, streams are often dominated by larger substrata due to the retention of fine sediment by the impoundment. These alterations to the stream can have a negative effect on both the upstream and downstream benthic macroinvertebrate (Ward and Stanford 1979; Lessard and Hayes 2003; Stranko et al. 2014) and fish (Lessard and Hayes 2003; Falke and Gido 2006; Katano et al. 2006; Lasne et al. 2007; Franssen and Tobler 2013; Stranko et al. 2014) communities. For example, Ward and Stanford (1979) found that impoundments cause a shift in the trophic status of the downstream benthic macroinvertebrate community. This downstream shift was due to less leaf litter for shredders, more periphyton for scrapers, and more organic particles for collectors. Similarly, Lessard and Hayes (2003) showed that impoundments that increase summer temperature could cause a change in the composition of the macroinvertebrate community downstream. Upstream of large impoundments that block American eel (*Anguilla rostrata*) passage, benthic macroinvertebrate densities can decrease due to a greater abundance of benthic fish that eels would normally prey on (Stranko et al. 2014).

For fish, impoundments are usually a barrier to movement, causing isolation of upstream populations (Falke and Gido 2006). As a result, isolated populations are at risk of extinction if the system is degraded and subject to frequent stressors. For migratory species, connectivity is imperative for successful reproduction (Brönmark et al. 2014), and impoundments can block migratory fish from moving upstream. Katano et al. (2006), for example, found that the density and biomass of diadromous species was higher below impoundments than above impoundments. Impoundments can also affect the species richness and composition of the streams that feed them. Kashiwagi and Miranda (2009) found that streams that feed small impoundments supported a higher

percentage of sunfish in upstream and downstream reaches than non-impounded streams. Franssen and Tobler (2013) found higher species richness, diversity and evenness above an impoundment than below the impoundment. This may have been due to the introduction of fish species from the pond to the stream, which increased the diversity at the stream-pond interface; although, it may have also been due to more degraded habitat downstream of the pond. Furthermore, in coldwater systems, densities of coldwater fish may decrease downstream of ponds due to higher water temperatures in ponds feeding streams (Lessard and Hayes 2003).

1.5 PURPOSE AND NEED

Although numerous studies have shown that species diversity and community structure increase with greater measures of stream network structure, most of these studies have focused on fish or stream salamanders and were conducted at a small geographic scale (Lowe and Bolger 2002; Magalhães et al. 2002; Grenouillet et al. 2004; Campbell Grant et al. 2007). Some large-scale studies of fish communities in the Mid-Atlantic Region have been conducted in recent years by Hitt and Angermeier (2006, 2008a, 2008b, 2011), but no large-scale study has been conducted comparing benthic macroinvertebrate communities to natural stream network structure. In addition, the current knowledge of the influence of stream size, position in the stream network, and distance to the confluence on benthic macroinvertebrate communities is limited.

Although some have studied benthic macroinvertebrate species richness as a function of stream size (Minshall et al. 1995; Melo and Froehlich 2001), most studies have been conducted on a small number of streams and have produced inconsistent results. There has also been very little research on the influence of stream position on benthic

macroinvertebrate communities, although current information suggests that these communities are dictated by environmental factors in headwaters streams and by dispersal in the mainstem, which is similar to our knowledge of fish communities. It has been well documented that stream habitat has an influence on benthic macroinvertebrate community structure, especially downstream of stream confluences, where habitat conditions abruptly change. However, there have been very few studies of the effect of stream confluences on the upstream communities in the tributary streams, due to dispersal from the mainstem. Because species richness and composition is predicted to change based on stream size, one would expect that taxa richness and other measures of community structure would change with proximity to a confluence. Furthermore, although numerous studies have looked at the effect of stream blockages (via road culverts and man-made impoundments) and sources (via man-made impoundments) on aquatic biota, most have been at a small scale and none have combined both fish and benthic macroinvertebrate community data.

In this study, I investigated the effect of stream network position, stream size, and local habitat on benthic macroinvertebrates, and determined to what degree road crossings and man-made impoundments (i.e., ponds and lakes) may be degrading benthic macroinvertebrate and fish communities in headwater streams through disruption of network structure. The study is based on the idea that fish and benthic macroinvertebrate diversity and community structure is dependent on the structure of the stream network, and that anthropogenic structures such as road culverts and man-made impoundments will alter the natural network effects and ultimately the benthic macroinvertebrate and fish communities. I explore these mechanisms using existing Maryland Department of

Natural Resources (MDNR), Maryland Biological Stream Survey (MBSS) benthic macroinvertebrate, fish, and environmental data collected from first-order streams in the Piedmont Plateau Physiographic Province of Maryland (Figure 1.1). To my knowledge, no study has used a large, state-wide data set to investigate the influence of natural network structure and habitat fragmentation on both benthic macroinvertebrate and fish communities.

The study consists of two additional chapters. Chapter 2 explores the effect of stream network structure, stream size, and local habitat on benthic macroinvertebrate community structure. Chapter 3 explores the direct effects of blockages (via road culverts and man-made impoundments) and sources (via man-made impoundments) on benthic macroinvertebrate and fish community structure, including the potential indirect effects on benthic macroinvertebrates through effects on fish communities.

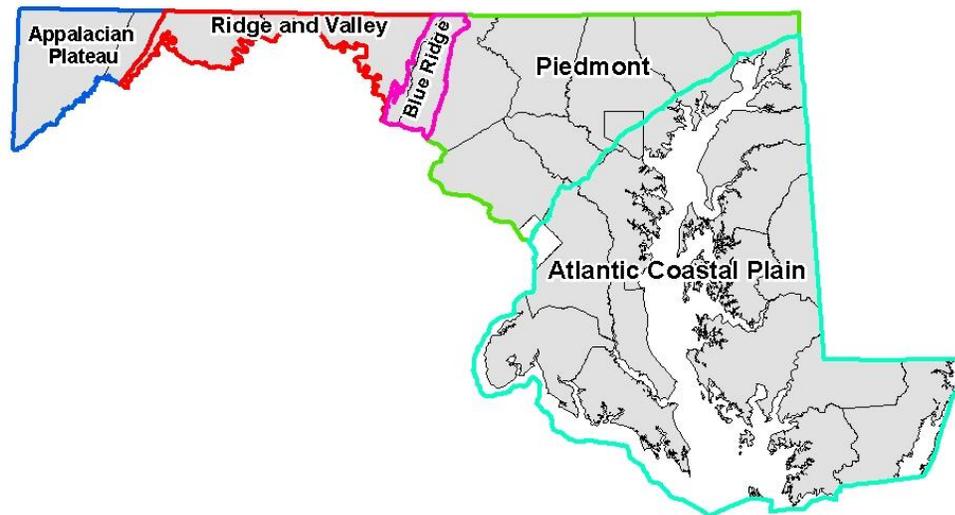


Figure 1.1. Physiographic province map of Maryland.

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CHAPTER 2

**INFLUENCE OF NETWORK STRUCTURE, STREAM SIZE, AND LOCAL
HABITAT ON BENTHIC MACROINVERTEBRATE COMMUNITY
STRUCTURE IN HEADWATER STREAMS**

2.1 INTRODUCTION

Lotic systems are highly connected ecological networks, and scientists have long recognized that they have a hierarchical spatial structure (Strahler 1964). Elements of spatial structure such as basin size, basin shape, network pattern, and size differences between confluent channels can regulate the spatial distribution of physical diversity within these systems (Benda et al 2004). These natural elements can affect the availability of refugia, habitat diversity, and dispersal for aquatic fauna (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Smiley and Dibble 2008). We are also beginning to understand how network structure may influence both physical and biological patterns and processes. However, we have a limited understanding of how elements of network structure such as position in the stream network, proximity to confluences, and habitat contrasts at confluences influence benthic macroinvertebrate movement and population connectivity in headwater streams.

In flowing streams, aquatic fauna primarily move through dispersal and migration. Dispersal is the one-way movement of organisms (or propagules) from their point of origin or release (Lincoln et al. 1998). It is a mechanism by which organisms acquire resources necessary to complete their life-cycle and ultimately increase their fitness, and it plays an important role in determining the distribution of aquatic fauna

across stream networks (Ricklefs 1990; Dingle 1996). Dispersal is also important in population dynamics, especially when populations are patchily distributed and demographic rates vary among patches, such as when populations exhibit metapopulation or source-sink dynamics (Dunning et al. 1992). Migration is generally considered to be regular, long-distance movement of organisms among habitat patches in order to exploit new resources or different habitats (Dingle 1996). Migration is an important behavior used by biota with complex life cycles that require multiple habitat types to complete their life cycle. Dispersal and migration in streams can occur within the network (i.e., within the stream corridor) and out of the network (i.e., overland between adjacent streams; Campbell Grant et al. 2007).

Benthic macroinvertebrates primarily disperse through emergence as adults and through a mechanism called drift, but upstream movement in aquatic forms is possible. Drift involves the downstream transport of benthic macroinvertebrates by the force of moving water (Waters 1972; Benson and Pearson 1987). Drifting organisms are typically transported short distances (McLay 1970; Townsend and Hildrew 1976; Danehy et al. 2011), although Neves et al. (1979) documented drift for hundred of meters during baseflow and over one kilometer during stormflow. In addition to downstream drift, many aquatic invertebrates will actively move upstream, primarily over short distances, but some will move more than two kilometers as larvae (Vaughan 2002). The more common type of dispersal is found among adult insects with complex life cycles involving metamorphosis and emergence of a flying terrestrial phase. Although little is known about dispersal distances for most taxa, as adult insects emerge, they typically disperse upstream where they reproduce (Hershey et al. 1993; Bilton et al. 2001).

Upstream flight may compensate for the downstream drift of larval forms (Waters 1972). Using mark-recapture techniques, Hershey et al. (1993) found that one-third to one-half of the adult mayfly *Baetis* (Ephemeroptera: Baetidae) population traveled 1.6 to 1.9 km upstream. Petersen et al. (2004) found that the majority of adult Ephemeroptera, Plecoptera, and Trichoptera (EPT) dispersed within or very close to the stream channel, although 10% of Plecoptera traveled more than 60 m from the stream channel. Winterbourn et al. (2007) documented similar patterns, but found that some female Trichoptera dispersed hundreds of meters from their natal stream. These studies suggest that most adult insect dispersal is within the stream corridor rather than laterally, although insects seem to have an inherent dispersal mechanism to colonize new habitats (Winterbourn et al. 2007).

Dispersal of benthic macroinvertebrates in streams is dependent on connectivity, defined as the extent to which populations within a species' range are linked (Palumbi 2003). Connectivity of habitats is an important factor in maintaining biological diversity (Crist et al. 2005), as it can facilitate the movement of genes, individuals, species, and populations among habitat patches (Minor and Urban 2008). In streams with unaltered connectivity, factors such as stream size (Vannote et al. 1980), network position (Hitt and Angermeier 2008a; Brown and Swann 2010), and distribution of habitat (Benda et al. 2004) should dictate aquatic diversity and community structure.

As described in the Riverine Continuum Concept (RCC; Vannote et al., 1980), aquatic community structure and function should change with increasing stream size due to changes in geomorphology and physical habitat. The RCC divides rivers into headwaters (1st to 3rd-order streams), mid-reaches (4th to 6th-order streams), and lower

reaches (> 6th-order streams). Headwaters are usually characterized by narrow, highly shaded streams that receive organic input mostly from allochthonous materials in the form of leaves and sticks. The benthic macroinvertebrate community is dominated by shredders, which break down the coarse particulate organic matter. Mid-reaches are characterized by a higher amount of autochthonous material in the form of periphyton due to their larger size, reduced currents, and more open canopies. However, allochthonous material also plays an important role in mid-reaches due to the surrounding forest. Collectors, which collect and consume fine particulate organic matter, and grazers that consume periphyton, dominate the benthic macroinvertebrate community in mid-reaches. However, shredders are still present due to allochthonous input. In the lower reaches, particulate organic matter is common, but there is less primary production due to higher turbidity (Vannote et al. 1980). As a result, benthic macroinvertebrate communities in lower reaches are dominated by collectors.

The RCC predicts that species richness will be the lowest in low-order streams, increasing with stream size until an expected maximum in medium-sized streams, where environmental variability is highest. Species richness would then decrease again in large-order streams due to the largely homogeneous habitat. Thus, plotting the number of species as a function of drainage area should produce a unimodal curve. A study of riffle habitats at 10 locations on the Salmon River in Idaho by Minshall et al. (1995) supports this prediction, where species diversity peaked at sites in mid-reaches of streams. However, Melo and Froehlich (2001) found no evidence of a unimodal pattern of species richness with increasing stream size. In fact, their study showed that species richness generally decreased along a gradient of stream size. Thus, headwater streams can still

support a diverse array of benthic macroinvertebrates, even in their upper reaches. For example, in a review of taxa dependent on headwaters, Meyer et al. (2007) found that three unmapped headwater streams supported over 290 aquatic fauna. Dieterich and Anderson (2000) found 202 aquatic or semiaquatic insect species in intermittent streams in western Oregon, some of which were unique to these types of streams. Although benthic macroinvertebrate taxa richness tends to be higher in perennial streams than intermittent streams (Williams 1996), some studies have shown similar diversity in both stream types (Miller and Gallaway 1996; Price et al. 2003).

The high diversity of benthic macroinvertebrates in headwater streams may be partly due to the low abundance of fish. Low-order streams are typically dominated by small-bodied insectivorous and invertivorous fish (Vannote et al. 1980) such as minnows (Family Cyprinidae), madtom catfishes (*Noturus* spp), darters (Family Percidae), and sculpins (Family Cottidae) (Schlosser 1987). Insectivores feed exclusively on aquatic insects, although invertivorous fish feed on all benthic macroinvertebrates, including aquatic insects, crustaceans, and worms. Although non-insect taxa may make up a portion of their diet, invertivores prefer to prey on aquatic insects (Lotrich 1973; Trial et al. 1983; Todd and Stewart 1985; Tófoli et al. 2013). Due to their small size, shallow depths, and high gradient, headwater streams often cannot support self-sustaining fish populations and are typically low in diversity (Schlosser 1987; Gomi et al. 2002; Richardson and Denehy 2007). Schlosser (1987) described such streams as “colonizing” due to their uniform conditions and shallow depths. These conditions support populations dominated by juvenile minnows and typically lack larger predatory fishes. Even intermittent portions of these streams can support some fish during portions of the

year. When such streams dry, small pools often remain and will be used by young fish as shelter due to the lack of larger predatory fish (McDonough et al. 2011). As habitat heterogeneity and pool volume increase with stream size, species richness and fish density also increase due to the addition of larger minnows and younger sunfish (Family Centrarchidae) and suckers (Family Catostomidae) (Schlosser 1987). Based on Schlosser's framework, streams with the largest pool depth and volume are considered "stable". In these large streams, there are major shifts in fish size, composition, and trophic structure. Due to increased predation and competition, fish communities in larger systems support less small insectivores, invertivores and omnivores and fewer large piscivores.

Stream position can also influence aquatic diversity and community structure, especially for aquatic species such as fish and stream salamanders. For fishes, the species found in headwater streams are more limited by local conditions than those found lower in the watershed, which have access to more of the stream network (Magalhães et al. 2002; Grenouillet et al. 2004; Hitt and Angermeier 2008a). Streams connected to larger rivers lower in the network tend to have more fish species than similarly sized streams connected to other small streams (Gorman 1986; Osborne and Wiley 1992; Schaefer and Kerfoot 2004; Smith and Kraft 2005; Hitt and Angermeier 2006; Thomas and Hayes 2006; Hitt and Angermeier 2011). The relationship between stream position and benthic macroinvertebrate diversity and community structure has been far less studied, although some studies have produced results similar to those for fish communities. Two studies highlight the current knowledge of aquatic invertebrate communities relative to stream position (Harrel and Dorris 1968; Brown and Swan 2010). Brown and Swan (2010)

found that benthic macroinvertebrate communities are dictated by environmental factors in a stream's headwaters and by dispersal in the mainstem. Similarly, Harrel and Dorris (1968) showed that the benthic macroinvertebrate community structure on a 3rd-order adventitious stream was more similar to the mainstem than on a similar size stream further upstream in the watershed, which also suggests dispersal-driven processes in streams more connected to the mainstem. However, no studies have explored the relationship between benthic macroinvertebrate community structure and d-link, a metric that has been utilized for studies of fish.

It has been well documented that stream habitat has an influence on species diversity and composition (Reid 1961; Vannote et al. 1980; Benda et al. 2004). Habitat in streams is mediated by fluvial processes, which drive the distribution of benthic substrate, woody debris, and other habitat-forming materials that can affect benthic macroinvertebrate community structure (Reice 1980; Duan et al. 2009; Martin et al. 2013). Stream confluences can provide distinct physical conditions that may create high quality habitat (Benda et al. 2004). Stream confluences can enhance diversity by increasing habitat heterogeneity, providing refugia, and allowing access to the mainstem for dispersal and migration (Campbell Grant et al. 2007). The increase in heterogeneity is due to the size difference between confluent channels, which has an effect on reaches immediately upstream and downstream of the confluence (Benda et al. 2004). Upstream of confluences there are lower gradients, wider channels and floodplains, increased wood recruitment, finer substrata, and greater lateral connectivity. Downstream of confluences there are higher gradients, larger substrate, deeper pools, and more cobble and sand bars. Confluences can also affect the composition of benthic macroinvertebrates. Downstream

of confluences there is a unique composition of taxa that are distinct from the mainstem and tributaries that feed them (Knispel and Castella 2003; Hellmann et al. 2015). Knispel and Castella (2003) found that benthic macroinvertebrate diversity increased downstream of the confluence of a small tributary and a large glacier-fed stream. They concluded that the influence of the tributary on the main channel resulted in greater habitat heterogeneity through increased organic matter inputs and sediment supply, which may have resulted in a more diverse fauna. In contrast, some studies have shown no change in benthic macroinvertebrate density, taxa richness or functional feeding group composition downstream of confluences relative to upstream, despite distinct assemblages in both (MacNally et al. 2011). The above studies have focused on differences in benthic macroinvertebrate communities in the mainstem, downstream of confluences, but very few studies address the effects of confluences on tributary streams. There is strong evidence that species composition in small streams is distinct from medium to large-sized streams (Vannote et al. 1980; Minshall et al. 1995; Melo and Froehlich 2001), thus one would expect that taxa richness and other measures of community structure would change with proximity to a confluence. In a recent study, Wilson and McTammany (2014) found less similarity in community structure between a tributary stream and the mainstem, as the distance from the confluence increased on the tributary.

Although numerous studies have shown that species diversity and community structure are related to measures of stream network structure, most have studied fish or stream salamanders considered a relatively small geographic scale (Magalhães et al. 2002; Lowe and Bolger 2002; Grenouillet et al. 2004; Campbell Grant et al. 2007). Some large-scale studies of fish communities in the Mid-Atlantic Region have been conducted

in recent years (Hitt and Angermeier 2006, 2008a, 2008b, 2011), but no large-scale study has been conducted exploring the relationship between benthic macroinvertebrate communities and natural stream network structure. In addition, the current knowledge of the effect of stream size, stream network position, and distance to the confluence on macroinvertebrate assemblages is limited. Although some have studied benthic macroinvertebrate species richness as a function of stream size (Minshall et al. 1995; Melo and Froehlich 2001), most studies have been conducted on a small number of streams and have produced inconsistent results. There has also been very little research on the influence of stream position on benthic macroinvertebrate communities, although current information suggests that communities are dictated by environmental factors in headwaters streams and by dispersal in the mainstem, which is similar to our knowledge of fish communities. It has also been well documented that stream habitat has an influence on benthic macroinvertebrate community structure, especially downstream of stream confluences, where habitat conditions abruptly change. Yet, there have been very few studies of the effect of stream confluences on the upstream communities in the tributary streams.

Lastly, it is currently unclear how predation from fish impact benthic macroinvertebrate density and community structure in freshwater streams. Although many species of fish feed on benthic macroinvertebrates in streams and some studies suggest direct (Gilinsky 1984; Gilliam et al. 1989; Winckler-Sosinski 2008; Shelton et al. 2014) and indirect (Power 1992; Stranko et al. 2014a) effects of fish on benthic macroinvertebrates, other studies have shown no effects (Ruetz et al. 2006; Nicola et al. 2010). Additionally, very few studies have documented the effects of fish predation on

benthic macroinvertebrate taxa richness, although one study showed a reduction in richness during certain times of the year (Gilinsky 1984). The inconsistencies of predator-prey studies in streams were explored by Wooster (1994), who suggests that the lack of consistent observed predator effects in scientific studies may be due to small replicate numbers, which would result in poor statistical power.

In this chapter, I investigate the effect of stream network position, stream size, distance to confluence, and local habitat on benthic macroinvertebrates in headwater streams, which is based on the idea that benthic macroinvertebrate diversity and community structure is dependent on the structure of the stream network. I also considered whether any changes in benthic macroinvertebrate community structure could be indirectly attributed to fish predation. For example, benthic macroinvertebrate taxa richness should be highest higher in the network where fish abundance is low. As network complexity increases, invertebrate diversity should decrease due to the presence of predatory fish. However, streams lower in the network that are connected to larger streams should show an increase in benthic macroinvertebrate diversity due to the presence of another trophic level in the form of piscivorous fish, which would release the predation pressure on benthic macroinvertebrates (Figure 2.1). These mechanisms were explored using statistical analysis of the Maryland Department of Natural Resources (MDNR), Maryland Biological Stream Survey (MBSS) data for benthic macroinvertebrates and several environmental variables collected from first-order streams in the Piedmont Plateau Physiographic Province of Maryland.

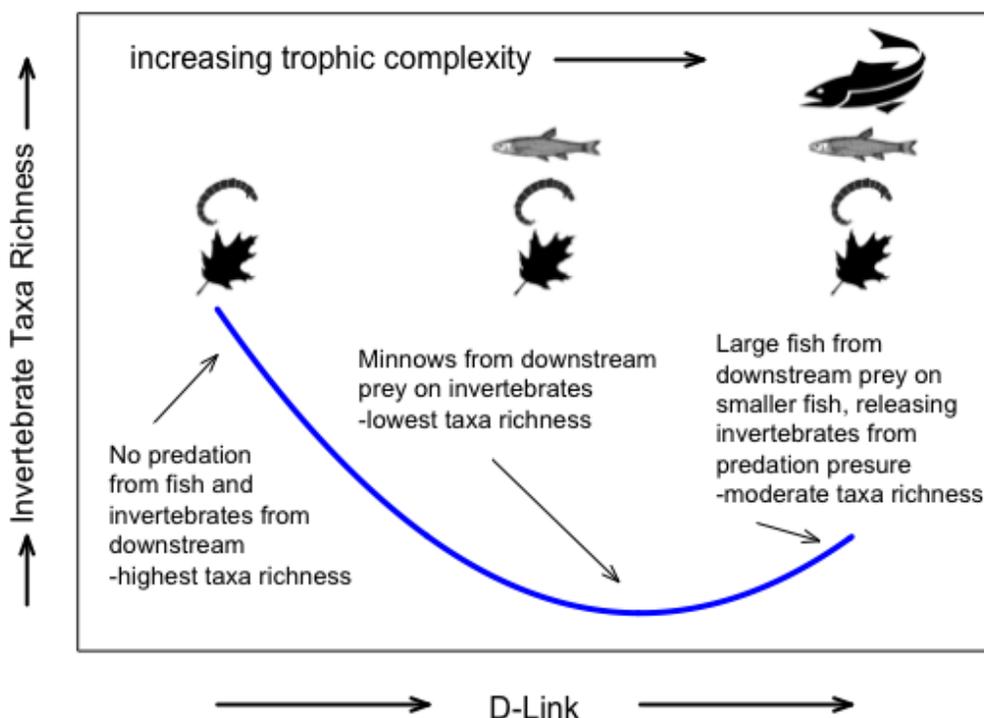


Figure 2.1. Conceptual model showing trophic level interactions among benthic macroinvertebrates, small predatory fish, and top predators in relation to stream network structure.

2.2 METHODS AND MATERIALS

2.2.1 Study Streams

The MBSS was established in 1993 to assess the ecological condition of Maryland's 1st through 4th-order non-tidal streams by measuring chemical, physical, and biological parameters. The MBSS is a probability-based stream sampling program designed to assess stream conditions with known precision at various spatial scales. The program predominately includes random (probabilistic) sites, although some targeted sites are sampled each year (e.g. Sentinel sites; Becker et al. 2010). Probabilistic

sampling sites were established by the MBSS using a random sampling approach, stratified by year, basin, and stream order.

This study used the MBSS probabilistic and targeted monitoring data collected on first-order streams in the lowlands and highlands of the Piedmont Plateau Physiographic Province of Maryland, from 1995 to 2014. Data were not used for streams west of the Piedmont to limit the influence of higher-gradient, geomorphologically different streams in the western part of the State. Similarly, sites were not chosen in Maryland's Coastal Plain region due to differences in geomorphology and fauna. First-order streams were chosen for this study because they make up the majority of stream miles (and MBSS sites) in stream networks and provide important ecological functions to the downstream network (Meyer et al. 2003). Additionally, a focus on first-order streams limited the influence of differences in stream size and upstream confluences on macroinvertebrate communities.

All first-order MBSS sampling sites from 1995 through 2014 were overlaid onto the National Hydrography Dataset Plus (NHD; McKay et al. 2012) in ArcMap 10.2.1 (ESRI 2013). This stream layer was chosen due to its wide use and extensive coverage across Maryland and surrounding states. Other hydrography data were explored for the counties covered by the Piedmont, but were not used due to differences in methods of derivation and inconsistencies among coordinate systems. Similarly, because watersheds do not stop at state boundaries, it was important to have a dataset that extended outside of Maryland.

For MBSS sites that occurred above the terminus of NHD streams, streams were extended to sites based on USGS 7.5 minute topographic quadrangle maps. The MBSS dataset includes multiple sites in each watershed, as well as multiple years of data for some sites. If more than one site was present in a given first-order watershed, one site was randomly chosen for inclusion in the study. Similarly, for sites with multiple years of data, one year of data was randomly chosen for inclusion in the study. As discussed further below, sites with less than 60 organisms were also removed from the dataset. The resultant dataset used for this study included 346 total sites (Figure 2.2).

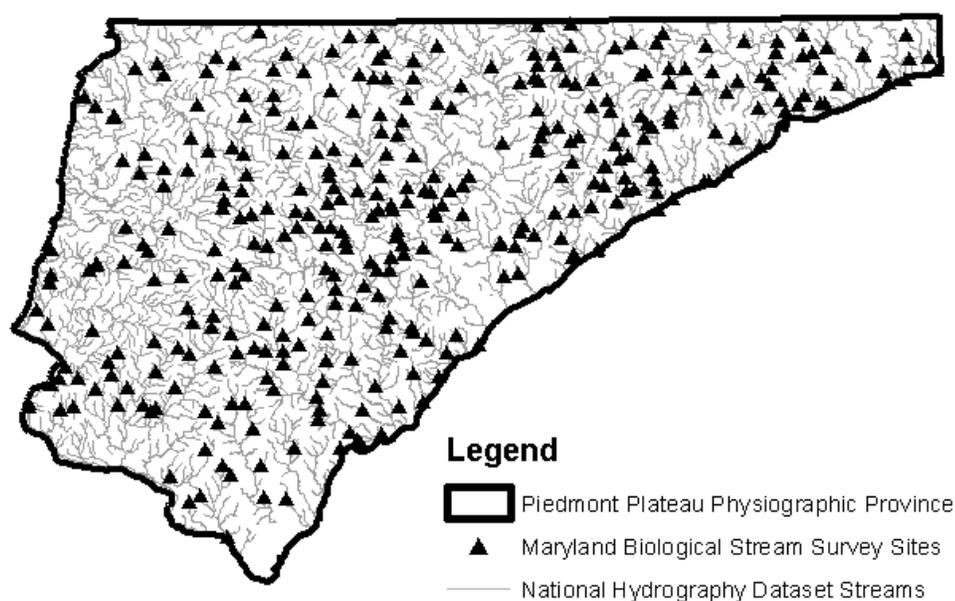


Figure 2.2. Map of Maryland's Piedmont Plateau physiographic province showing 346 MBSS sampling sites on first-order streams used in this study, sampled from 1995-2014.

2.2.2 Data Collection

Five dependent variables were used to characterize benthic macroinvertebrate community structure, including rarified taxa richness, percent Chironomidae, percent

clingers, percent shredders, and percent flying invertebrates (Table 2.1). These variables were chosen to provide a variety of community structure attributes based on taxonomy (rarified taxa richness), tolerance of anthropogenic stressors (percent Chironomidae), habitat preference (percent clingers), trophic classification (percent shredders), and mode of movement (percent flying invertebrates). Two explanatory variables were used to measure network structure, including d-link and distance to nearest confluence (Table 2.2). D-link is a measure of adjacent habitat characteristics and downstream processes, and distance to downstream confluence is a measure of isolation of sample reaches from downstream confluences. In addition to these variables, three covariates were included to account for effects of local habitat and stream size on macroinvertebrate community structure (Table 2.2). These covariates included stream gradient, drainage area, and epifaunal substrate score. Other covariates such as imperviousness and conductivity, which could account for variation from human disturbance, were not incorporated into this analysis. It was felt that these measures might be highly correlated with each other and with epifaunal substrate, making it difficult to include them in models together. Percent Chironomidae, percent shredders, percent clingers, drainage area, gradient, and epifaunal substrate were obtained from the MBSS master database. Rarified taxa richness, percent flying invertebrates, distance to nearest confluence, and d-link were measured as part of this study.

Benthic Macroinvertebrate Community Variables

Benthic macroinvertebrate samples were previously collected at each site by the MBSS using protocols for spring sampling (Kazyak 1995; Kazyak 1997; Kazyak 2000; Stranko et al. 2007; Stranko et al. 2014b). Samples were collected during the Spring

Table 2.1. Benthic macroinvertebrate community variables explored in Chapter 2 and their associated community structure attributes. The code used in the analysis for each variable is listed parenthetically.

Benthic Macroinvertebrate Community Variables	Type
Rarified Taxa Richness (NTAXA_RAR)	Taxonomy
Percent Flying Invertebrates (PFLYING)	Mode of Movement
Percent Chironomidae (PCHIRON)	Anthropogenic Tolerance
Percent Shredders (PSHRED)	Trophic Classification
Percent Clingers (PCLING)	Habitat Preference

Table 2.2. Explanatory variables and covariates used in Chapter 2 to measure the effect of habitat adjacency and downstream processes, natural isolation, stream size, and local habitat on benthic macroinvertebrate community structure. The code used in the analysis for each variable is listed parenthetically.

Explanatory Variables	Type
Downstream Link (DLINK)	Habitat Adjacency and Downstream Processes
Distance to Nearest Confluence (DIST_CON)	Natural Isolation
Epifaunal Substrate Score (EPI_SUB)	Local Habitat
Stream Gradient (ST_GRAD)	Local Habitat
Drainage Area (AREA)	Stream Size

Index Period, from March 1 through April 30. Field collections included sampling 1.85 m² of best available benthic macroinvertebrate habitat at each site using a 540- μ m mesh d-framed dipnet. Habitat types sampled included cobble/gravel, snags/leafpacks, undercut banks, rootwads, and submerged vegetation. Beginning at the downstream end of the 75 m site, the D-net was placed firmly in the substrate of the riffle area or other habitat feature while organisms were dislodged by rubbing or kicking of the substrate in a 0.09 m² area in front of the net. Large woody debris and rootwads were jabbed with the d-net, while the surface of the debris or rootwad was agitated by the lower frame of the net in an attempt to dislodge benthic macroinvertebrates clinging to the surface. This process was

repeated until 1.85 m² of substrate was sampled throughout the reach. The sample was washed into a 540 µm sieve bucket and placed in a labelled sample container with 90% ethanol solution for transported to the DNR benthic processing laboratory.

Benthic macroinvertebrate samples were processed, subsampled, and identified by MBSS taxonomists using protocols detailed in Boward and Friedman (2000). In the laboratory, samples were transferred to a gridded tray and subsampled using a fixed-count method. Trays contained 100, 5 cm by 5 cm square grids. Grids were randomly selected and organisms were picked until a total of 120 organisms were counted; after 120 organisms were picked, the grid containing the 120th organism was picked in its entirety and any additional organisms in the cell were included in the sample. Organisms were identified to genus, or the lowest taxonomic level possible. Chironomidae larvae and Oligochaeta were slide-mounted and identified using MBSS methods (Boward and Friedman 2000). Data were entered into a Microsoft Access database and checked by the MBSS staff, where several benthic macroinvertebrate variables were calculated for use in the Maryland Benthic Index of Biotic Integrity (BIBI; Stribling et al. 1998). Where available, benthic macroinvertebrate variables were obtained from the MBSS for use in this study.

Due to differences in sample size, the actual number of organisms identified ranged from 0 to greater than 120. Thus, to reduce any bias associated with differences in subsample size, benthic macroinvertebrate data from each site were rarified to the minimum subsample size used by the MBSS to calculate the BIBI (60; Michael Kashiwagi, personal communication), prior to calculation of taxa richness. Rarification was performed using the Vegan Package in R (Oksanen et al. 2013).

Percent Chironomidae is the percent of the sample comprised of non-biting midge larvae and pupae (Family Chironomidae) (Stribling et al. 1998). Percent clingers is the percent of the sample comprised of individuals primarily adapted to riffle habitats. Percent shredders is the percent of the sample comprised of individuals adapted to utilize (i.e., shred) coarse particulate organic matter as a food source. Percent flying invertebrates was defined as the percent of the sample comprised of individuals that emerges from the stream as a flying adult to disperse. Using the U.S. Environmental Protection Agency's Functional Traits Database (USEPA 2012), Merritt and Cumins (2008), and the MBSS master taxa list, each benthic macroinvertebrate taxon was classified as a flying invertebrate or a non-flying invertebrate.

Network Variables and Covariates

Catchments for the calculation of drainage area were created for each MBSS stream sampling location. Catchments were generated in ArcMap 10.1.3 (ESRI 2012) using sampling point locations collected by MBSS, digital images of USGS topographic maps with 20-foot contour lines, Maryland Department of the Environment's (MDE) 12-digit watershed boundary polygons, and the 1:100,000 scale stream reach file from the NHDPlus. All input and output geospatial data were projected in North American Datum of 1983 (NAD83), Maryland State Plane, meters.

One polygon for each catchment was created by drawing a polygon starting just downstream of the sampling point to ensure that the point fell inside of the resulting polygon. Catchment polygons were snapped to MDE's 12-digit watershed polygons when the catchment polygon shared a ridgeline with the 12-digit watershed. Snapping to the 12-digit watershed ensured consistent watershed boundaries to reduce the chance of

overlapping adjacent watersheds and other topological errors. The drainage area was determined using the Calculate Geometry function.

Several quality control (QC) checks were completed on the catchment polygon dataset. Catchments were visually checked to ensure that each catchment only intersected the NHDPlus stream reach file at one location, and that catchments were drawn for the stream reaches upstream of the sampling location. For the sites located close to a confluence, stream order from the NHDPlus was compared to stream order from the MBSS dataset to ensure that catchments included the correct stream reaches. The Repair Geometry tool in ArcMap was used to identify and repair catchment polygons that had null geometry, self-intersections, or other geometry errors. A log of repaired geometries was kept with the original files. Topology rules were created for the polygon dataset and identified topology errors were corrected in the final catchment polygon dataset.

Distance to nearest confluence was also measured in ArcMap (ESRI 2013). Using the Trace tool, a polyline was created and traced from the MBSS point to the nearest downstream confluence using the NHD layer. The distance was determined by creating a field in the attributes table, and using the Calculate Geometry function to determine the segment length (m) for each site.

D-link was first described by Osborne and Wiley (1992) as the magnitude of the link of a channel below the next downstream confluence (Figure 2.3) and is a measure of the spatial position of a tributary within the drainage network. D-link was measured using the Stream Order tool in the Spatial Analyst extension in ArcMap (ESRI 2013). One meter DEM data were obtained from the U.S. Geologic Survey and the Fill tool was

used to fill any holes or “sinks” in the DEM. The filled DEM was input into the Flow Direction tool to determine the direction water moved across the surface. The flow direction raster was then used to create the flow accumulation raster and a conditional statement was used to generate a raster stream network from the flow accumulation raster. The resulting stream network was compared to the NHD stream network in the study area to confirm accuracy. The raster stream network was assigned stream order values using the Stream Order tool and choosing the Shreve method of ordering. The Shreve stream order is the link magnitude of a given stream (Shreve 1966). The link magnitude of the downstream link was determined by intersecting the polylines created for the distance to the nearest downstream confluence with the Shreve raster stream network.

Stream gradient was measured by MBSS at each site during the Spring Index Period, from March 1 through April 30. From 1995 through 1997, stream gradient was measured over the length of each site using an inclinometer (Kazyak 1995; Kazyak 1997). After 1997, stream gradient was measured over the length of each site using a levelometer (Kazyak 2000; Stranko et al. 2007; Stranko et al. 2014b). Gradient was determined by recording the difference in water surface height from the 0 m to the 75 m locations of the MBSS site as compared to a level plane.

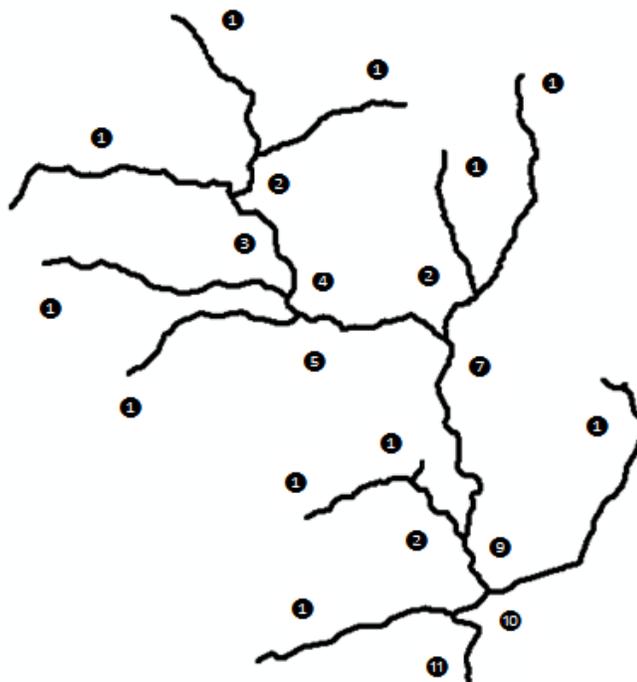


Figure 2.3. Determination of the d-link of a monitoring site. The d-link is the magnitude of the link of a channel below the next downstream confluence. After Osborne and Wiley (1992).

Epifaunal substrate data were collected by the MBSS during the Summer Index Period, from June 1 through September 30, as part of their summer habitat assessment (Kazyak 1995; Kazyak 1997; Stranko et al. 2007; Stranko et al. 2014b). The epifaunal substrate metric is a scaled score meant to rate the suitability of habitat for benthic macroinvertebrates at each site. This habitat parameter was visually estimated at each site in the field using a scale of 0 to 20 based on standard criteria on the MBSS Habitat Assessment Guidance Sheet (Table 2.3).

Table 2.3. The MBSS criteria for determining epifaunal substrate score.

Optimal (16-20)	Suboptimal (11-15)	Marginal (6-10)	Poor (0-5)
Preferred substrate abundant, stable, and at full colonization potential (riffles well developed and dominated by cobble; and/or woody debris prevalent, not new, and not transient)	Abund. of cobble with gravel &/or boulders common; or woody debris, aquatic veg., undercut banks, or other productive surfaces common but not prevalent /suited for full colonization	Large boulders and/or bedrock prevalent; cobble, woody debris, or other preferred surfaces uncommon	Stable substrate lacking; or particles are over 75% surrounded by fine sediment or flocculent material

2.3 STATISTICAL ANALYSIS

The relationship of the benthic metrics of community structure (Table 2.1) to the natural network variables and other covariates (Table 2.2) was investigated using an Information Theoretic Approach (ITA). The ITA uses the principle of parsimony, multiple working hypotheses, and strength of evidence to select the best fitting model for the data at hand (Burnham and Anderson 2002). Using this approach, models were developed based on the hypothesized relationships between benthic macroinvertebrate community structure and the natural network structure variables and covariates. All possible models derived from the full model were considered, including all explanatory variables and covariates and their second-order interactions.

Each model was fit using R statistical software (R Core Team 2014) and the *glmulti* package (Calcagno 2013). Prior to fitting each model, correlations between explanatory variables and covariates were examined to determine whether variables were highly correlated and needed to be removed from the dataset to avoid co-linearity among independent variables. As discussed in the Results section and illustrated in Table 2.4, no

strong correlations were observed, although drainage area was slightly negatively correlated with stream gradient ($R^2 = -0.32$). Because no strong correlations were observed, all explanatory variables and other covariates were included in the analysis. However, because I was interested in the relative influence of the network structure variables and other covariates, these variables were standardized before fitting models. Variables were standardized using the scale function in R, which subtracts the mean and divides it by the standard deviation so the parameter estimates are all on the same scale and can be compared to assess importance. In addition, because d-link data were strongly right-skewed, these data were log-transformed prior to fitting models. Although rarified taxa richness was normally distributed, I used a log-linear model, which produced better results than using a simple linear model. However, I used logistic regression for dependent variables reported as percentages, such as percent Chironomidae, percent clingers, percent shredders, and percent flying invertebrates. Because residual deviances and degrees of freedom suggested the data were over-dispersed, logistic regression models included a scale parameter to correct for the over-dispersed nature of the data.

Model comparisons were made using Akaike's information criterion corrected for small sample size (AICc) and its associated measures (Burnham and Anderson 2002). The best-fit model was identified as the model with the smallest AICc value. The weight of evidence for the best fitting model was determined by calculating Akaike weights (w_i), which indicate the probability that the model is the best among the set of candidate models, and the evidence ratio, which determines how well the best model fits compared to the rest. For logistic regressions I calculated pseudo- R^2 value as the null deviance minus residual deviance divided by the null deviance. Model parameter estimates and

95% confidence intervals were calculated using parameter profiles and the `confint` function in R (Venables and Ripley 2002). The R code for the statistical analysis for Chapter 2 is included in Appendix B.

2.4 RESULTS

2.4.1 Relationship between Independent Variables

D-link, the network structure variable used as a measure of adjacent habitat and downstream processes, ranged from 2 to 20,317 and was highly skewed to the right ($\mu = 350.5$; $SD = 2333.1$). The distance to the nearest confluence, which was used as a measure of isolation of the site from the downstream confluence, ranged from 0 m to 9096 m ($\mu = 1548.0$ m; $SD = 1353.5$ m). Drainage area, one of the covariates used to represent local habitat conditions, ranged from 8.5 ha to 1704.5 ha ($\mu = 243.9$ ha; $SD = 235.4$ ha). The other two local habitat covariates, stream gradient and epifaunal substrate score, ranged from 0 to 10 ($\mu = 1.5$; $SD = 1.1$) and 1 to 19 ($\mu = 11.7$; $SD = 4.1$), respectively.

There were no strong correlations among any of the independent variables ($|r| < 0.33$ in all cases) and no relationship between the network measures of d-link and distance to the confluence (Table 2.4). There were weak correlations among the local-scale variables that appeared to be driven by stream size. As watershed area (and stream size) increased, gradient decreased and epifaunal substrate scores increased. Although these relationships were significant (Table 2.4), because they were weak I included all local-scale variables in the full models of benthic macroinvertebrate response to local and network structure variables.

Table 2.4. Correlation matrix for independent variables included in models of benthic invertebrate community characteristics. Pearson correlation coefficients are in the top half of the matrix and their respective *p*-values are in the lower half of the matrix.

Dependent Variable	Independent Variable				
	ST_GRAD	EPI_SUB	AREA	DIST_CON	DLINK
ST_GRAD		0.13	-0.32	-0.03	0.05
EPI_SUB	0.017		0.19	-0.07	0.06
AREA	< 0.001	< 0.001		-0.14	-0.02
DIST_CON	0.587	0.210	0.009		0.03
DLINK	0.382	0.285	0.735	0.540	

2.4.2 Overall Model Results

Modeling of macroinvertebrate community characteristics resulted in from 5 to 24 models falling within 2 AICc units of the top model, depending on the dependent variable modelled (Table 2.5). Although the sum of weights ($\sum w_i | \Delta AICc < 2$) for models within 2 AICc units of the top model and the weight of the top model ranged from 0.27 to 0.41 and 0.03 to 0.09, respectively, I focused on the top models here as they capture the more important relationships. When the importance of an independent variable is measured by the number of models in which the variable appeared out of those within 2 AICc units of the top model, variables not included in the top model appeared in 58% or less of the models, while variables that appeared in the top model appeared in 62% to 100% of the models (Table 2.6). Moreover, all 95% confidence intervals for parameter estimates for top models did not contain zero (Table 2.7), while all estimates for parameters not included in the top models but appearing in model-averaged models did include zero.

2.4.3 Effects of stream size and local habitat variables

Of the three covariates (epifaunal substrate score, stream gradient, and drainage area), the most common variable observed in the top models was epifaunal substrate

score. It was the most important variable explaining rarefied taxa richness, percent shredders, percent clingers, and percent flying invertebrates (Table 2.7). For models of percent Chironomidae, epifaunal substrate score was included in four of the ten models within 2 AICc units of the top model (Appendix A). Epifaunal substrate score was positively associated with percent clingers. However, for percent shredders and percent flying invertebrates the effects of epifaunal substrate score depended on stream gradient and size, respectively (Table 2.7). In the case of percent shredders, as stream gradients decreased the effects of epifaunal substrate scores shifted from positive to negative (Figure 2.4). In the case of percent flying invertebrates, the effect of epifaunal substrate score was generally positive in relatively medium to large streams, but negative in relatively small streams (Figure 2.5; top panel).

Drainage area was the second most common local habitat variable observed in the top models. Drainage area was positively associated with percent Chironomidae (Table 2.7). For percent flying invertebrates the effects of drainage area depended on stream degradation such that percent flying invertebrates increased with drainage size in degraded streams with low epifaunal substrate scores, but decreased in streams with moderate to good habitat conditions as indicated by moderate to high epifaunal substrate scores (Figure 2.5; top panel). The effects of drainage area on rarefied taxa richness dependent on both stream gradient and epifaunal substrate scores. Only when gradients were relatively high or epifaunal substrate scores low did drainage area have a positive effect on rarefied taxa richness (Figure 2.6; top and middle panels).

Table 2.5. Summary of best fit models and model statistics for benthic macroinvertebrate community variables for 347 sampling sites in the Piedmont of Maryland. Model statistics include those for the best model as well as across all models within 2 AICc units of the best model (i.e., sum of w_i). For quasibinomial models pseudo- R^2 values are reported.

Dependent variable	Best-fit Model	K	R^2 or Pseudo- R^2	w_i	Models		Model Type
					Within 2 AICc	Sum of w_i	
NTAXA_RAR	EPI_SUB + ST_GRAD + AREA + DLINK + AREA:EPI_SUB + AREA:ST_GRAD + DLINK:AREA	9	0.12	0.05	10	0.29	Log-linear
PCHIRON	AREA + DIST_CON + DLINK	5	0.05	0.03	24	0.41	Quasibinomial
PCLING	EPI_SUB + DIST_CON	4	0.07	0.05	9	0.28	Quasibinomial
PSHRED	EPI_SUB + ST_GRAD + ST_GRAD:EPI_SUB	5	0.04	0.05	9	0.32	Quasibinomial
PFLYING	EPI_SUB + AREA + DLINK + AREA:EPI_SUB + DLINK:EPI_SUB + DLINK:AREA	8	0.17	0.09	5	0.27	Quasibinomial

Table 2.6. Importance of explanatory variables included in models of benthic macroinvertebrate community structure as estimated by percentage of models within two AICc units of the top model that contained the variable of interest.

Independent Variable	Dependent Variables				
	NTAXA_RAR	PCHIRON	PCLING	PSHRED	PFLYING
EPI_SUB	1	0.4	1	1	1
ST_GRAD	1	0.58	0.23	1	0.14
AREA	1	0.62	0.16	0.4	1
DIST_CON	0.53	0.97	1	0.74	0.3
DLINK	1	1	0.51		1
EPI_SUB:ST_GRAD	0.07	0.12	0.23	1	
EPI_SUB:AREA	1			0.1	1
ST_GRAD:AREA	1				
EPI_SUB:DIST_CON	0.07	0.03	0.18	0.16	
EPI_SUB:DLINK	0.21	0.07			
ST_GRAD:DIST_CON	0.07	0.07		0.17	
ST_GRAD:DLINK	0.18	0.08			
AREA:DIST_CON		0.03		0.25	0.17
AREA:DLINK	1	0.07			0.78
DIST_CON:DLINK	0.45	0.13	0.09		1

Stream gradient was included in the top models of rarefied taxa richness and percent shredders (Table 2.7). The effect on rarefied taxa richness was the strongest and depended on drainage area, while effects on percent shredders were weaker and dependent on epifaunal substrate scores. When drainage areas were large, increasing stream gradient had large negative effects on rarefied taxa richness, but when drainage areas were medium to small the effects of stream gradient were weaker and positive, respectively (Figure 2.6; middle panel). In the case of percent shredders, when epifaunal substrate scores were high, increases in stream gradient resulted in increases in rarefied taxa richness, but when epifaunal substrate scores were lower the effect of increases in stream gradient was negative.

Table 2.7. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing invertebrate assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of local habitat (epifauna substrate score and stream gradient), stream size (drainage area), adjacent habitat and downstream processes (d-link), and natural isolation (distance to nearest downstream confluence).

Independent Variable	DEPENDENT VARIABLE				
	NTAXA_RAR	PCHIRON	PCLING	PSHRED	PFLYING
Intercept	2.73 (2.69 to 2.77)	-0.32 (-0.34 to -0.30)	0.10 (0.08 to 0.12)	-1.58 (-1.61 to -1.56)	2.68 (2.63 to 2.72)
EPI_SUB	0.11 (0.07 to 0.15)		0.28 (0.26 to 0.30)	0.07 (0.04 to 0.10)	0.64 (0.60 to 0.68)
ST_GRAD	-0.10 (-0.15 to -0.05)			0.05 (0.03 to 0.08)	
AREA	-0.07 (-0.13 to -0.01)	0.11 (0.09 to 0.13)			0.42 (0.35 to 0.48)
DLINK	-0.04 (-0.08 to < 0.00)	-0.20 (-0.22 to -0.18)			-0.20 (-0.23 to -0.16)
DIST_CON		0.14 (0.12 to 0.16)	-0.12 (-0.14 to -0.10)		
EPI_SUB:ST_GRAD				0.17 (0.14 to 0.20)	
EPI_SUB:AREA	0.05 (0.01 to 0.09)				0.34 (0.28 to 0.39)
ST_GRAD:AREA	-0.08 (-0.13 to -0.02)				
EPI_SUB:DLINK					-0.18 (-0.21 to -0.14)
AREA:DLINK	0.06 (0.01 to 0.11)				0.24 (0.18 to 0.30)

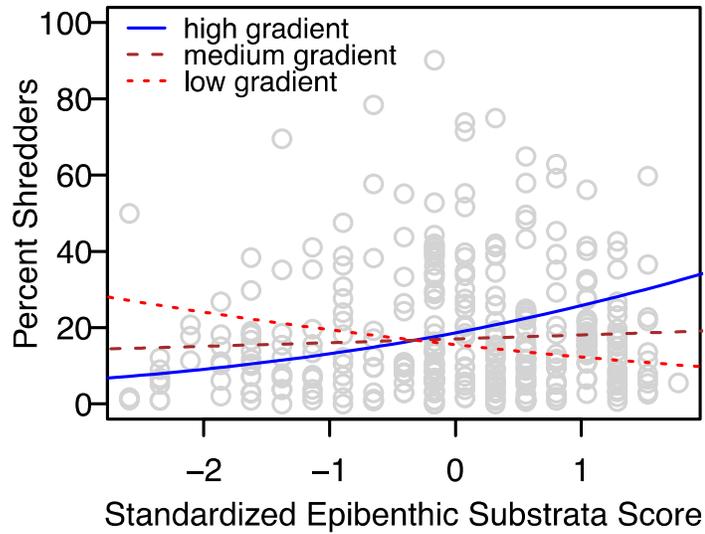


Figure 2.4. Illustration of interactions among local habitat (measured as stream gradient and epifaunal substrate score) in a model of percent shredders for benthic macroinvertebrates in first-order, Piedmont streams of Maryland.

2.4.4 Effect of Network structure variables

One or both of the network structure variables of d-link and distance to the confluence were included in models of macroinvertebrate community structure with the exception of the model for percent shredders. The effects of network structure variables depended on local habitat conditions in some cases, but there were no interaction terms between d-link and distance to confluence included in the top models of macroinvertebrate community structure (Table 2.7).

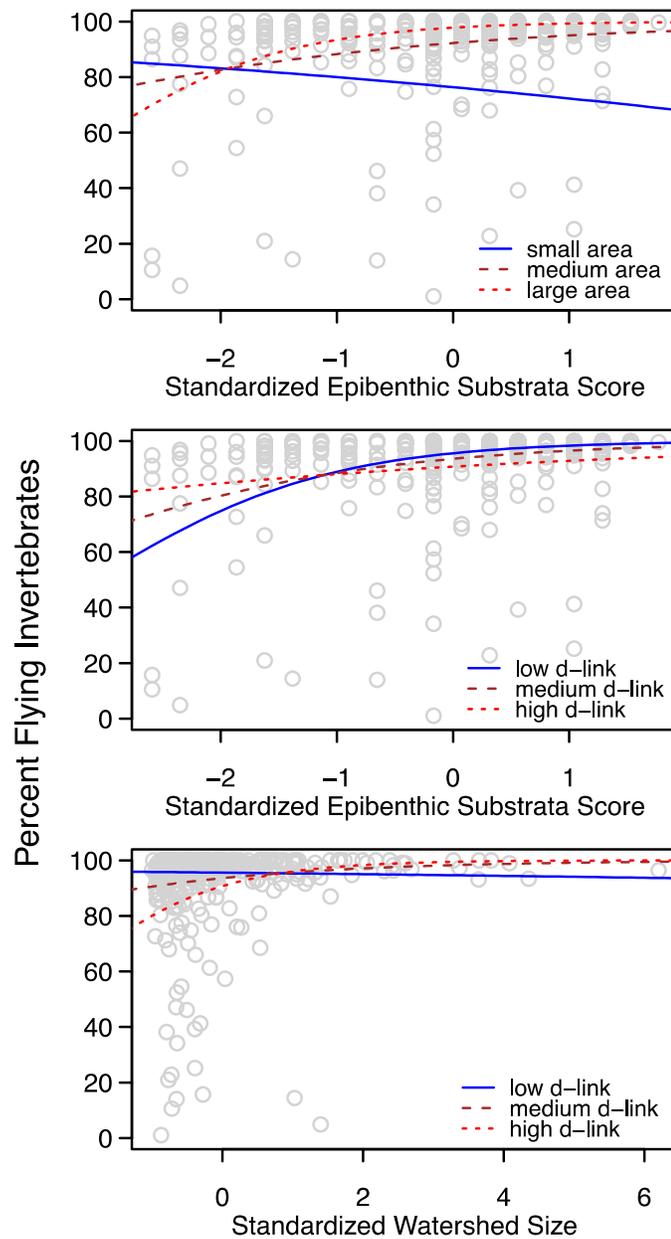


Figure 2.5. Illustrations of interactions among local habitat (measured as epifaunal substrate score), stream size (measured as drainage area), and adjacent habitat and downstream conditions (measured as d-link), in models of percent flying invertebrates in first-order, Piedmont streams of Maryland.

Between the two network structure variables (i.e., distance to nearest confluence and d-link), the most common variable observed in the top models was d-link. It was the most important variable explaining percent Chironomidae and was involved in two interactions in the models for rarefied taxa richness and percent flying invertebrates. For percent Chironomidae the effect of increasing d-link values was negative. There was an interaction between epifaunal substrate score and d-link for percent flying invertebrates. When stream habitat was degraded as indicated by low epifaunal substrate scores, d-link had a positive effect on percent flying invertebrates. However, this increase only occurred when epifaunal substrate values were lower and was not apparent in the higher range of values of epifaunal substrate scores (Figure 2.5; middle panel). There were also interactions between drainage area and d-link for both rarefied taxa richness and percent flying invertebrates. In the drainage area by d-link interaction, rarefied taxa richness increased as d-link increased in streams with large watersheds, but decreased with increasing d-link in small to medium-sized watersheds (Figure 2.6; bottom panel). In the interaction between drainage area and d-link for percent flying invertebrates, increasing d-link values had very moderate effects on percent flying invertebrates when streams were relatively small and no effects in moderate to larger streams with large drainage areas (Figure 2.5; bottom panel).

The other local habitat variable, distance to nearest confluence, was observed in two of the top models, percent Chironomidae and percent clingers. It was the second most important variable explaining percent Chironomidae and percent clingers, but was not involved in any interactions.

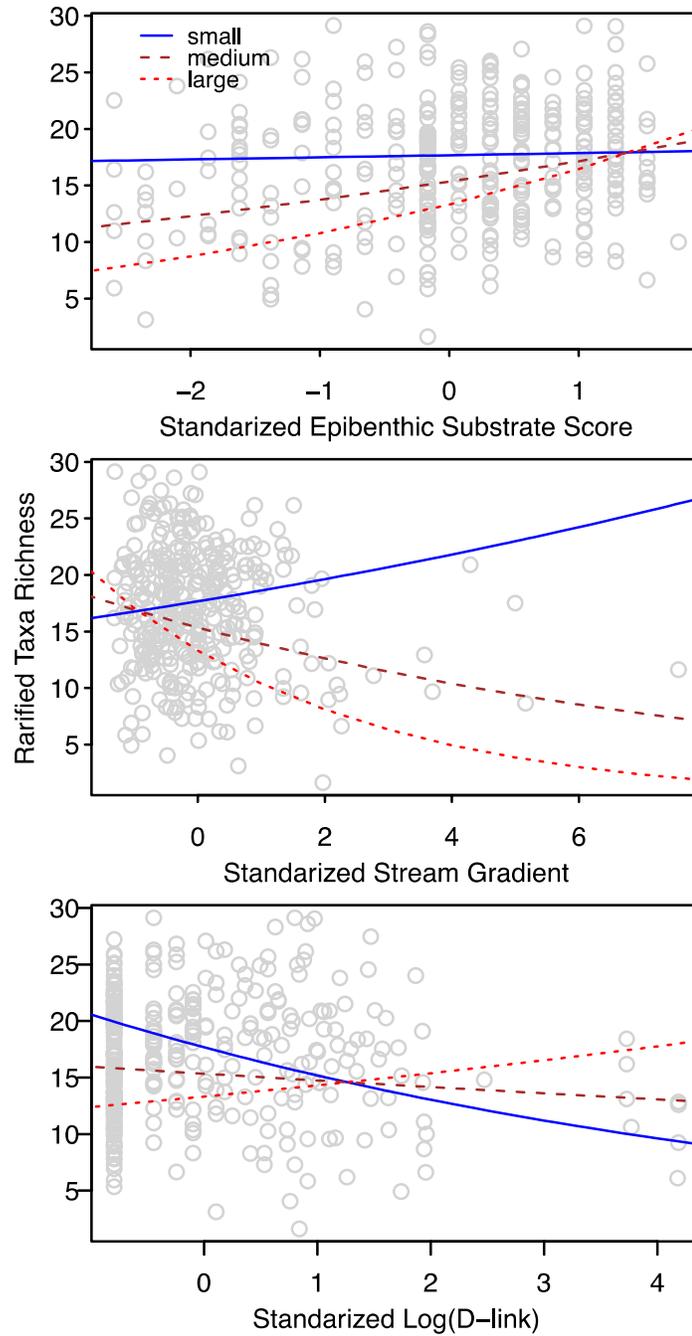


Figure 2.6. Illustrations of interactions among local habitat (measured as epifaunal substrate score and gradient), stream size (measured as drainage area), and adjacent habitat and downstream processes (measured as d-link), in models of rarified taxa richness in first-order, Piedmont streams of Maryland.

2.5 DISCUSSION

The results of this study suggest that local habitat, stream size, habitat adjacency, and natural isolation are indeed important factors for structuring benthic macroinvertebrate communities in first order streams in Maryland's Piedmont region. Some of these results corroborate previous research, although my study also provides new insight on how network structure affects benthic macroinvertebrate communities. More interestingly, the majority of the variables explored in this study were dependent on others, which may be due to the influence of higher trophic levels, suggesting top-down effects, as well as habitat supplementation.

2.5.1 Local Habitat Quality

It is well known that substrate quality can have a positive effect on benthic macroinvertebrate colonization. Studies of rapid habitat assessment methodologies such as the MBSS (Kazyak 1995; Kazyak 1997; Stranko et al. 2007; Stranko et al. 2014b) and U.S. Environmental Protection Agency's Rapid Bioassessment Protocols (Barbour et al. 1999) have shown significant positive relationships between epifaunal substrate score and benthic macroinvertebrate community structure (Roth et al. 1999; Sullivan et al. 2004; Cook et al. 2015). In my study, I show similar results, as epifaunal substrate score was the most common explanatory variable observed in the top benthic macroinvertebrate models. For example, there was a positive correlation between percent clingers and substrate quality, which was expected, considering that the highest epifaunal substrate scores are assigned to streams that provide optimal conditions for benthic macroinvertebrate taxa that are adapted to clinging to stable substrates.

Substrate quality was also associated with several other benthic macroinvertebrate community variables through interaction effects, some of which may involve other trophic levels. For example, in medium and large streams, rarified taxa richness was positively associated with epifaunal substrate, although there was no effect from substrate quality on the smallest streams. Because there is typically low fish diversity in the upper reaches of headwater systems (Schlosser 1987; Richardson and Denehy 2007), there may have been less predation pressure on benthic macroinvertebrates, making substrate quality a less important variable for explaining rarified taxa richness in small streams. Similarly, there was a positive correlation between percent flying invertebrates and epifaunal substrate for medium and large streams, but substrate was negatively correlated with percent flying invertebrates for small streams. This negative relationship could be due to the substrate quality and invertebrate composition in the smallest streams. In the smallest-sized streams, substrate quality may not be an important factor in determining the percent flying invertebrates due to low discharge, which would limit the substrate size to particles such as mud, sand, or gravel. These substrates may be more suitable for non-insect invertebrates such as scuds (Order Amphipoda), sowbugs (Order Isopoda), crayfish (Order Decapoda), and aquatic worms (Class Oligochaeta), which can be very abundant in the smallest streams (Meyer et al. 2007). In medium to large watersheds, the benthic macroinvertebrate taxa composition may have shifted to more flying invertebrates due to the increase in flow and substrate heterogeneity.

Stream gradient was the least important explanatory variable in the analysis, but was most important in explaining rarified taxa richness and percent shredders. The positive relationship between benthic macroinvertebrate taxa richness and stream

gradient for small watersheds may be due to the limitations of fish movement as gradient increases, as headwater streams are often too steep, too shallow, or too isolated to support fish (Gomi et al. 2002; Richardson and Denehy 2007). As stream size increased, gradient had an opposite effect, which may be due to the presence of predatory fish in these larger streams. For percent shredders, epifaunal substrate score depended on stream gradient. For high gradient streams with good substrate quality, percent shredders and epifaunal substrate were positively correlated, which may have been due to the limitations on fish presence in higher-gradient first order streams (Gomi et al. 2002; Richardson and Denehy 2007) and increasing shredder habitat as substrate quality increased. Hawkins et al. (1982) found more shredder taxa in higher gradient reaches than in lower gradient reaches in Cascade Range Streams in Oregon, although canopy closure had no effect on taxa richness. They concluded that taxa designated as shredders may be restricted to higher gradient reaches for other reasons than food quality. In my study, there was less of an effect from epifaunal substrate as gradient decreased, which may have been due to the introduction of fish, which would be more expected to occur in lower gradient first order streams. On the other hand, it could also be due to the effects of urbanization on stream conditions. In many lower gradient first order streams from the Piedmont region, higher substrate quality may not necessarily equate to an increase in percent shredders due to the effects of urbanization on stream hydrology. The Piedmont physiographic province contains the highly urbanized Washington D.C. – Baltimore, Maryland metropolitan region. Streams with watersheds containing high imperviousness in such areas are characterized by a higher variability in discharge; an increase in channel width, pool depth, and scour; a higher sediment load; and a decrease in organic matter retention

(Walsh et al. 2005). Thus, many of the lower gradient streams in my study could have been shaped by urban hydrology, which could have artificially increased substrate quality, but lowered the percent shredders, which are considered a specialist feeding group that is sensitive to urbanization.

2.5.2 Stream Size

In this study, drainage area was used as a proxy for stream size, which is predicted to influence benthic macroinvertebrate community structure through changes in geomorphology and physical habitat (Vannote et al. 1980). The RCC predicts that species richness will increase with stream size, until an expected maximum in medium-sized streams. This theory was tested by Minshall et al. (1995), who showed a unimodal distribution of richness along a gradient of stream size. However, more recent studies have shown that benthic macroinvertebrate diversity decreases with stream size (Melo and Froehlich 2001), and in many instances my study showed similar results. For example, streams with poor or average substrate quality, streams with the highest gradient, and streams with low d-link all showed a decrease in rarified taxa richness with stream size. The smallest headwater streams have been shown to support a diversity of benthic macroinvertebrates (Dieterich and Anderson 2000; Meyer et al 2007), which may be partially due to the low diversity of fish in the upper reaches of headwater systems (Schlosser 1987). Thus, as fish become more abundant as stream size increases, benthic macroinvertebrate richness may decrease, since fish have been shown to reduce benthic macroinvertebrate taxa richness during certain times of the year (Gilinsky 1984). The only substantial increase in taxa richness observed with increasing stream size was for high d-link streams, which may have been due to the introduction of more piscivorous

fish from the larger streams, which could release the predation pressure on the benthic macroinvertebrate prey. These types of indirect effects were documented by Stranko et al. (2014), who found that benthic-feeding fish were significantly lower at sites containing American eel (*Anguilla rostrata*) in comparison to sites where American eel have been blocked by the presence of large dams. However, benthic macroinvertebrate densities were significantly higher at sites containing American eel, suggesting that top predatory fish may have an influence on lower trophic levels.

Although benthic macroinvertebrate richness tended to decrease with stream size, the percent of the community comprised of Chironomidae and flying invertebrates increased. The increase in percent flying invertebrates with stream size was especially true for streams with good substrate quality (as discussed previously) and streams with a high d-link. For high d-link streams, the increase in percent flying invertebrates with stream size may be due to the presence of piscivorous fish. It is possible that these larger predatory fish, could have released the predation pressure on aquatic insects, which are fed on by smaller fish that may prefer aquatic insects over non-insect invertebrates (Lotrich 1973; Trial et al. 1983; Todd and Stewart 1985; Tófoli et al. 2013). On the other hand, the relationship between percent Chironomidae and stream size may be due to a decrease in organic particle size with increasing stream size, as Chironomidae are for the most part classified as collectors (Merritt and Cummins 2008). Chironomidae diversity has also been shown to increase with stream size in other systems (Heino and Paasivirta 2008).

2.5.3 Habitat Adjacency and Downstream Processes

In addition to local habitat, benthic macroinvertebrate community structure was explained by d-link, a measure of the spatial position of a tributary within the drainage network. First order streams with the lowest d-link value (i.e., d-link = 2) are connected to other first order streams. In contrast, streams with high d-link values are connected to large streams or rivers, which are drastically different in size and support very different aquatic communities. Osborne and Wiley (1992) found a significant and positive relationship between d-link and fish species richness, which suggests that downstream processes affect fish community structure in tributary streams more than in similar sized streams further up the drainage. There has not been a similar study using d-link to determine the importance of downstream processes on benthic macroinvertebrate community structure, and the affect of d-link on fish described by Osborne and Wiley could have top-down effects on benthic macroinvertebrates. In my study, d-link was the most important network scale variable explaining benthic macroinvertebrate community structure. The negative effect observed between d-link and percent Chironomidae could be the result of predation from fish in higher d-link streams. It has been well documented that streams connected to larger rivers lower in the network tend to have more fish species than similarly sized streams connected to other small streams (Gorman 1986; Osborne and Wiley 1992; Schaefer and Kerfoot 2004; Smith and Kraft 2005; Hitt and Angermeier 2006; Thomas and Hayes 2006 Hitt and Angermeier 2011). Thus, if higher d-link streams are expected to have more fish species, there should be more species that feed on invertebrates, some of which selectively feed on midges (Lotrich 1973; Todd and Stewart 1985). Although this may explain the decrease in percent Chironomidae as d-

link increases, it is not consistent with the observed positive relationship between drainage area and percent Chironomidae.

The importance of d-link for explaining rarified taxa richness and percent flying invertebrates may also be related to the presence of fish or habitat supplementation. When two very small streams come together (i.e., d-link = 2), both streams are unlikely to support high numbers of fish that would feed on benthic macroinvertebrates. As a result, there would be less predatory pressure on the benthic community, which may be why the smallest streams with low d-link values had high benthic macroinvertebrate taxa richness. Habitat supplementation could also be occurring, where organisms move between patches in the landscape to make use of substitutable resources (Dunning et al. 1992). In this case, two headwaters streams that come together each represents a similar patch of habitat. As a result, a disturbance in one stream may not have a big effect on the other, as colonist from the similar less disturbed stream may reduce the impacts to the more disturbed stream through rescue effects (Brown et al. 1977; Eriksson 2014), which could have resulted in the higher taxa richness observed in my study. However, as d-link increased in small streams, benthic macroinvertebrate taxa richness decreased, which may be attributed to the introduction of more predatory fish from the larger streams. Similarly, as stream size increased in low d-link streams, taxa richness decreased, which may have also been due to the introduction of similar types of fish. In the largest first order streams, as d-link increased, an additional trophic level may have been introduced into the system in the form of piscivorous fish, which could release the predation pressure on the benthic macroinvertebrate prey. As a result, this may have caused taxa richness to increase with higher d-link values. Although they did not examine predator-prey

interactions, Harrel and Dorris (1968) found that the benthic macroinvertebrate community structure on a large adventitious stream was more similar to the mainstem than on a similar size stream further upstream in the watershed.

A similar pattern was observed for percent flying invertebrates. In low d-link streams draining small watersheds, the percent flying invertebrates was high, which may have been due to the low numbers of fish, many of which prefer aquatic insects over non-insect invertebrates (Lotrich 1973; Trial et al. 1983; Todd and Stewart 1985; Tófoli et al. 2013). Percent flying invertebrates only slightly decreased with increasing stream size, which could be attributed to the introduction of slightly more fish. As d-link increased in small streams, the streams may have been able to support more fish, which could have caused the reduction in percent flying invertebrates through predation. However, as stream size increased in medium to large d-link streams, the addition of another trophic level could have released the predation pressure on aquatic insects, which may be why I saw an increase in percent flying invertebrates.

2.5.4 Natural Isolation

Due to the change in substrate characteristics and flow, the connection to the stream network at the confluence, and rescue effects, it was expected that measures of benthic macroinvertebrate community structure would change in relation to the nearest downstream confluence. Sites closer to a confluence should have more access to the stream network and other source populations, whereas sites further from the confluence should be more isolated. However, the only associations observed with distance to nearest downstream confluence were for percent Chironomidae and percent clingers. The

increase in Chironomidae may be due to isolation from predatory fish, such as blacknose dace (*Rhinichthys atratulus*), further from the confluence. First order streams are often dominated by pioneer fish species such as blacknose dace, which actively select Chironomidae as a food source (Triall et al. 1983). Sites farthest from their confluence would be located in the headwaters of the stream, which would be expected to have low abundance of fish due to the limitations of fish movement.

Due to the finer substrate that is usually present immediately upstream of confluences (Benda et al. 2004), you would expect an increase in percent clingers as distance to the downstream confluence increases, which was not the case in my study. The negative effect of distance to nearest confluence on percent clingers may be due to the increase in percent Chironomidae. Because Chironomidae are mostly classified as sprawler and burrowers (Merritt and Cummins 2008), the percent of other groups at each site such as the clingers would increase.

2.6 DATA LIMITATIONS

The results of this study suggest that benthic macroinvertebrate community structure can be partially explained by local habitat and stream network structure. The best-fit models for this study only explained between 4% and 17% of the variation in benthic macroinvertebrate community structure in first order streams from Maryland's Piedmont region (Table 2.5). The low variation explained was likely due to several factors, including the field sampling methodology, laboratory subsampling, and use of rarefaction prior to the analysis. The MBSS utilizes a rapid, semi-quantitative method for sampling benthic macroinvertebrates in streams. Using a D-framed dipnet, 20 jabs or

kicks (totalling 1.85 m²) were collected from best available habitats chosen by the field crew and spread across a 75 meter reach in order to obtain a representative sample. Samples were also only collected once during the spring index period (March 1 – April 30), which doesn't account for seasonal variation in community composition. Variation is also introduced through the laboratory methods. Organisms from field samples were randomly picked in the laboratory from a gridded tray until a targeted 120 organisms were obtained. Prior to identification, midges (Family Chironomidae) and aquatic worms (Class Oligochaeta) were further subsampled if they exceeded 10 individuals from any family/subfamily (Boward and Friedman 2000). Because the methodology requires the last grid to be picked in its entirety, and some samples may consist of very few organisms due to poor stream quality, the actual number of organisms identified ranged from 0 to greater than 120. As a result, benthic macroinvertebrate data from each site were rarified to 60 organisms, which is the minimum subsample size used by the MBSS to calculate the BIBI. If other biomonitoring programs exist at a similar scale that use more quantitative methods, these data could be used for future studies to better explain the variation in benthic macroinvertebrate community structure based on network position and local habitat.

2.7 IMPLICATIONS

Headwater streams comprise at least 80 percent of the stream network in the United States (Meyer et al. 2003). They provide important ecological functions to the downstream network, including flood control, maintenance of water quantity and quality, and provide habitat for a diverse flora and fauna, even in the upper reaches. Stream restoration is commonly used to try to ameliorate losses to headwater stream functions

due to urbanization and other land use practices that contribute to stream degradation. Many resource agencies are now requiring restoration projects to prove that a restoration has achieved ecological improvement, although this is not well defined and can be quite difficult to quantify. Many practitioners also believe that restoring habitat in a degraded stream will improve aquatic communities (i.e., the Field of Dreams Hypothesis; Palmer et al. 1997). This paradigm is due to the fact that stream habitat is linked to biological conditions in streams (Reice 1980; Duan et al. 2009; Martin et al. 2013), which my results have also corroborated.

For example, both medium and large first order streams with good epifaunal substrate had higher rarified taxa richness than similar sized streams with poor substrate. The greatest difference in richness was observed between large streams with poor epifaunal substrate verses large streams with good epifaunal substrate, but no matter the habitat quality, small first order streams had relatively high taxa richness. Thus, if the goal of a stream restoration project is to recover the loss in benthic macroinvertebrate diversity from an impact to a headwater stream, these results would suggest that restoring medium to larger first order streams with degraded habitat could provide ecological improvement. The fact that taxa richness did not change with increasing epifaunal substrate score in small streams does not necessarily mean these streams may not be suitable for ecological improvement. Rather, the lack of an effect could be due to the applicability of the substrate scoring methodology in very small streams, which may be characterized by different substrate conditions than larger first order streams due to low discharge.

Nevertheless, these results still support the paradigm that increasing habitat heterogeneity promotes the restoration of biological diversity. Yet, the fact is that most studies of stream restoration projects have shown little to no recovery in diversity of fish or benthic macroinvertebrates, even when habitat or biological improvement was a goal (Palmer et al. 2010; Stranko et al. 2012). For example, Stranko et al. (2012) found no significant difference between benthic macroinvertebrate and fish diversity in restored versus unrestored streams in Maryland's Piedmont region. Similarly, in a study of 78 independent stream restoration projects, Palmer et al. (2010) found no evidence that habitat heterogeneity was the primary factor controlling benthic macroinvertebrate diversity. Given the current approaches for stream restoration in this region, the lack of increased biological diversity following stream restorations may be due to the irreversible effects of urbanizations and other land uses. Thus, some argue that it is more effective to invest in protecting watersheds rather than restoring urban streams to re-establish biological diversity (Stranko et al. 2012). Even so, there could be other reasons that restoration projects haven't shown an improvement in diversity, such as limiting sites to the reach scale, the absence of close source populations to support ecological recovery, or that the position of the project within the stream network is not conducive to recovery (Thomas 2014).

Source populations are important for biological recovery of habitats following disturbances (Brown et al. 1977; Eriksson 2014), especially from stream restoration activities (Lake et al. 2007). The two main mechanisms for the reestablishment of a benthic macroinvertebrate community are drift and reproduction from flying adults. However, in order for these two mechanisms to be the most effective at a stream

restoration project, there must be source populations nearby. When deciding on an approach for stream restoration, considering network scale factors could aid in the development of design goals and improve the chances of species recovery. For example, my results showed that first order streams with large watersheds and a high d-link were more specious than small watersheds with a high d-link, which could be attributed to piscivorous fish releasing predation pressure on the benthic macroinvertebrate prey in the larger highly connected streams. Additionally, small streams connected to streams with a low link magnitude were shown to have high taxa richness, which may be attributed to low numbers of fish, as well as rescue effects through habitat supplementation. Thus, if increased benthic macroinvertebrate diversity is a project goal, the chance of species recovery would be greater if the headwater stream restoration project was adjacent to a similar sized stream with complementary suitable habitat and the restoration stream lacked an effective fish population. Similarly, restoring larger first-order streams lower in the drainage network may also improve benthic macroinvertebrate diversity, although adjacent habitat would have to be suitable in order to facilitate recovery, which may not necessarily be a common occurrence in degraded systems.

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**APPENDIX A: MEAN PARAMETER ESTIMATES FOR MODELS WITHIN TWO
AIC UNITS FOR BENTHIC MACROINVERTEBRATE MODELS**

Table A-1. Mean parameter estimates for models within two AIC units for benthic macroinvertebrate base models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
Rarified Taxa							
Richness							
EPI_SUB:ST_GRAD	0	0	1	0.065	-0.004	0.004	0.004
DIST_CON:EPI_SUB	-0.001	0	1	0.067	-0.007	0.005	0.006
DIST_CON:ST_GRAD	0.002	0	1	0.074	-0.005	0.009	0.007
DLINK:ST_GRAD	-0.003	0	2	0.182	-0.018	0.012	0.015
DLINK:EPI_SUB	-0.005	0	2	0.212	-0.024	0.014	0.019
DIST_CON:DLINK	-0.015	0	5	0.446	-0.055	0.025	0.04
DIST_CON	-0.009	0	6	0.532	-0.04	0.022	0.031
(Intercept)	2.73	0.001	10	1	2.685	2.775	0.045
EPI_SUB	0.112	0	10	1	0.071	0.153	0.041
ST_GRAD	-0.099	0.001	10	1	-0.15	-0.048	0.051
AREA	-0.074	0.001	10	1	-0.132	-0.016	0.058
DLINK	-0.038	0	10	1	-0.078	0.002	0.04
AREA:EPI_SUB	0.051	0.001	10	1	0.007	0.095	0.044
AREA:ST_GRAD	-0.078	0.001	10	1	-0.137	-0.019	0.059
AREA:DLINK	0.056	0.001	10	1	0.005	0.107	0.051
Percent							
Chironomidae							
DIST_CON:EPI_SUB	-0.001	0	1	0.0289	-0.0049	0.0029	0.0039
AREA:DIST_CON	0.0006	0	1	0.0297	-0.0018	0.003	0.0024
DLINK:EPI_SUB	-0.0041	0.0003	2	0.0651	-0.0194	0.0112	0.0153
AREA:DLINK	0.0033	0.0002	2	0.0654	-0.0091	0.0157	0.0124
DIST_CON:ST_GRAD	-0.0042	0.0003	2	0.0668	-0.0198	0.0114	0.0156

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
DLINK:ST_GRAD	0.0055	0.0003	2	0.0822	-0.0144	0.0254	0.0199
EPI_SUB:ST_GRAD	0.0144	0.0015	3	0.1223	-0.0355	0.0643	0.0499
DIST_CON:DLINK	-0.0063	0.0003	4	0.1337	-0.0282	0.0156	0.0219
EPI_SUB	-0.0286	0.0014	10	0.4014	-0.0972	0.04	0.0686
ST_GRAD	-0.0663	0.0035	14	0.583	-0.177	0.0444	0.1107
AREA	0.0676	0.0031	15	0.6182	-0.0357	0.1709	0.1033
DIST_CON	0.1242	0.0007	23	0.9701	0.0905	0.1579	0.0337
(Intercept)	-0.3229	0.0001	24	1	-0.3453	-0.3005	0.0224
DLINK	-0.184	0.0002	24	1	-0.2104	-0.1576	0.0264
Percent Clingers							
DIST_CON:DLINK	0.0053	0.0003	1	0.0898	-0.0137	0.0243	0.019
AREA	-0.0066	0.0003	2	0.1569	-0.0289	0.0157	0.0223
DIST_CON:EPI_SUB	0.0103	0.0005	2	0.1765	-0.0235	0.0441	0.0338
ST_GRAD	0.0088	0.0003	2	0.2286	-0.0187	0.0363	0.0275
EPI_SUB:ST_GRAD	-0.0301	0.0031	2	0.2286	-0.1216	0.0614	0.0915
DLINK	0.0402	0.0016	5	0.5069	-0.0388	0.1192	0.079
(Intercept)	0.1009	0.0001	9	1	0.078	0.1238	0.0229
EPI_SUB	0.2744	0.0002	9	1	0.2479	0.3009	0.0265
DIST_CON	-0.1267	0.0001	9	1	-0.1476	-0.1058	0.0209
Percent Shredders							
AREA:EPI_SUB	-0.0077	0.0006	1	0.0964	-0.0353	0.0199	0.0276
DIST_CON:EPI_SUB	0.0101	0.0006	2	0.1575	-0.0239	0.0441	0.034
DIST_CON:ST_GRAD	-0.0119	0.0007	2	0.1672	-0.0513	0.0275	0.0394
AREA:DIST_CON	0.0219	0.0015	2	0.248	-0.043	0.0868	0.0649
AREA	-0.0156	0.0005	4	0.4011	-0.0567	0.0255	0.0411

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
DIST_CON	0.0497	0.0011	7	0.7429	-0.0082	0.1076	0.0579
(Intercept)	-1.5822	0.0002	9	1	-1.6114	-1.553	0.0292
EPI_SUB	0.0764	0.0002	9	1	0.0468	0.106	0.0296
ST_GRAD	0.0517	0.0002	9	1	0.021	0.0824	0.0307
EPI_SUB:ST_GRAD	0.1735	0.0003	9	1	0.1415	0.2055	0.032
Percent Flying Insects							
ST_GRAD	-0.0065	0.0003	1	0.1373	-0.0298	0.0168	0.0233
AREA:DIST_CON	0.0512	0.0127	1	0.1746	-0.1155	0.2179	0.1667
DIST_CON	0.0321	0.0038	2	0.301	-0.062	0.1262	0.0941
AREA:DLINK	0.1881	0.011	4	0.7773	0.0105	0.3657	0.1776
(Intercept)	2.691	0.0011	5	1	2.6293	2.7527	0.0617
EPI_SUB	0.6348	0.0004	5	1	0.5943	0.6753	0.0405
AREA	0.4359	0.0023	5	1	0.3438	0.528	0.0921
DLINK	-0.2094	0.001	5	1	-0.2683	-0.1505	0.0589
AREA:EPI_SUB	0.3321	0.0008	5	1	0.277	0.3872	0.0551
DLINK:EPI_SUB	-0.176	0.0004	5	1	-0.2143	-0.1377	0.0383

APPENDIX B: R CODE USED FOR DATA ANALYSIS

```

setwd("~/Grad School/Thesis/Data Analysis/Benthics")
data.invert.taxa<-read.csv("Benthic_Variables.csv",header=T)
library(Hmisc)
rcorr(as.matrix(data.invert.taxa[,3:7]))
library(rJava)
library(glmulti)
library(MASS)

# creating data sets with standardized variables. Note that we include only those variable
# that we need. Scale function here takes columns 2 through 7 of the data.fish.taxa.R data
# set and centers the values (ie subtracts the mean) and scales them (ie divides by the
# standard deviation). The reason for this is so the parameter estimates are all on the same
# scale and can be compared to assess importance.

data.invert.taxal<-
  as.data.frame(cbind(data.invert.taxa[17:21],
    data.invert.taxa[23],
    scale(data.invert.taxa[2:6],center=T,scale=T),
    scale(log(data.invert.taxa[7]),center=T,scale=T)
  ))
data.invert.taxal[1:3,]

install.packages('pastecs')
library(pastecs)
stat.desc(data.invert.taxa[2:7])
stat.desc(data.invert.taxa[17:23])
-----

# Running the base model using rarified taxa richness

with(data.invert.taxal,hist(NTAXA_RAR,seq(0,30,1)))
g.rich.base <- glmulti(log(NTAXA_RAR)~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+DLINK,
  fitfunction="lm",
  data=data.invert.taxal,
  level=2,
  marginality=T)

print(g.rich.base)
sum(summary(g.rich.base)$modelweights[1:10]) # weight of model within 2 AICc of best model
summary(g.rich.base)$modelweights[1] # weight for best model
summary(g.rich.base@objects[[1]])$r.squared # produce r-squared for best model
round(coef(g.rich.base,select=2,
  icmethod="Burnham",
  varweighting="Johnson"), 3) # mean parameter estimate and unconditional
# variances over models within 2 AICc units
# of the best model
summary(g.rich.base@objects[[1]])$coef
extractAIC(g.rich.base@objects[[1]])[1]+1 # k for the best model (note 1 has been added)
extractAIC(g.rich.base@objects[[1]])[2] # AIC for best modle
confint(g.rich.base@objects[[1]]) # 95% CI for paramter estimates
summary(g.rich.base@objects[[1]])$r.squared # produce r-squared for best model

#Looking at interaction between epibenthic substrate and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-12,12,.1),
  ST_GRAD=rep(0,1),ACREAGE=rep(-2,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is small
par(oma=c(0,0,1,0),fig=c(.25,.75,.65,1),mar=c(3,3,0,0),mgp=c(1,0.25,0))
with(data.invert.taxal,plot(EPI_SUB,(NTAXA_RAR),
  cex.axis=.7,cex.lab=.7,pch=1,
  xlim=c(with(data.invert.taxal,min(EPI_SUB)),
    with(data.invert.taxal,max(EPI_SUB))),
  col="lightgray",
  xlab="Standarized Epibenthic Substrate Score",
  ylab="",las=1,tck=-0.02,cex=.8))
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-5,6,1),
  ST_GRAD=rep(0,1),ACREAGE=rep(0,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is average
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-5,6,1),
  ST_GRAD=rep(0,1),ACREAGE=rep(2,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is high
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  col="red",lty=3))

```

```

legend(-0.75,18,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

#Looking at interaction between stream gradient and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-12,12,.1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(-2,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is low
par(fig=c(.25,.75,.325,.675),new=T)
with(data.invert.taxal,plot(ST_GRAD, (NTAXA_RAR),
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(ST_GRAD)),
                                   with(data.invert.taxal,max(ST_GRAD))),
                           col="lightgray",pch=1,
                           xlab="Standarized Stream Gradient",
                           ylab="Rarified Taxa Richness",las=1,tck=-0.02,cex=.8))
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-5,8,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(0,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is average
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-5,8,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(2,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is high
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="red",lty=3))
legend(2,41,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

#Looking at interaction between D-link and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(DLINK=seq(-12,12,.1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(-2,1),
                                  ST_GRAD=rep(0,1)))
par(fig=c(.25,.75,0,.35),new=T)
with(data.invert.taxal,plot(DLINK, (NTAXA_RAR),
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(DLINK)),
                                   with(data.invert.taxal,max(DLINK))),
                           col="lightgray",pch=1,
                           xlab="Standarized Log D-link",
                           ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(DLINK=seq(-5,5,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(0,1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of d-link on rarified taxa richness when
# drainage area habitat is average
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(DLINK=seq(-5,5,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(2,1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of d-link on rarified taxa richness when
# drainage area is high
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="red",lty=3))
legend(1.9,40,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

# Running the base model using percent chironomidae
with(data.invert.taxal,hist(PCHIRON,seq(0,100,5)))

```

```

x<-with(data.invert.taxal,round((PCHIRON/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCHIRON/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=11468/314)
g.pchiron <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                    data=data.invert.taxal,
                    fitfunc="glm",
                    family="binomial",
                    crit="qaicc",
                    level=2,
                    marginality=T)

print(g.pchiron)
sum(summary(g.pchiron)$modelweights[1:22])
summary(g.pchiron)$modelweights[1]
round(coef(g.pchiron,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pchiron@objects[[1]])$null.deviance-
 summary(g.pchiron@objects[[1]])$deviance)/
summary(g.pchiron@objects[[1]])$null.deviance
extractAIC(g.pchiron@objects[[1]])[1]+1
extractAIC(g.pchiron@objects[[1]])[2]
summary(g.pchiron@objects[[1]])
confint(g.pchiron@objects[[1]])

# Running the base model using percent clingers
with(data.invert.taxal,hist(PCLING,seq(0,100,5)))
x<-with(data.invert.taxal,round((PCLING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCLING/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=11114/314)
g.pcling <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pcling)
sum(summary(g.pcling)$modelweights[1:9])
summary(g.pcling)$modelweights[1]
round(coef(g.pcling,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pcling@objects[[1]])$null.deviance-
 summary(g.pcling@objects[[1]])$deviance)/
summary(g.pcling@objects[[1]])$null.deviance
extractAIC(g.pcling@objects[[1]])[1]+1
extractAIC(g.pcling@objects[[1]])[2]
summary(g.pcling@objects[[1]])
confint(g.pcling@objects[[1]])

# Running the base model using percent shredders
with(data.invert.taxal,hist(PSHRED,seq(0,100,5)))
x<-with(data.invert.taxal,round((PSHRED/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PSHRED/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=5944.6/314)
g.pshred <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pshred)
sum(summary(g.pshred)$modelweights[1:9])
summary(g.pshred)$modelweights[1]
round(coef(g.pshred,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pshred@objects[[1]])$null.deviance-
 summary(g.pshred@objects[[1]])$deviance)/
summary(g.pshred@objects[[1]])$null.deviance
extractAIC(g.pshred@objects[[1]])[1]+1
extractAIC(g.pshred@objects[[1]])[2]
summary(g.pshred@objects[[1]])
confint(g.pshred@objects[[1]])

#Looking at interaction between epibenthic substrata and stream gradient
# create data set for plot with high gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                 ST_GRAD=rep(2,1)))
# plot of effects of epibenthic substrate on percent shredders when
# gradient is high

```

```

with(data.invert.taxal,plot(EPI_SUB,PSHRED,
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                                   with(data.invert.taxal,max(EPI_SUB))),ylim=c(0,100),
                           col="lightgray",
                           xlab="Standardized Epibenthic Substrata Score",
                           ylab="Percent Shredders",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of epifaunal substrate on percent shredders when
# gradient is average
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                        col="brown",lty=2))
# create data set for plot with low gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                  ST_GRAD=rep(-2,1)))
# plot of effects of epifaunal substrate on percent shredders when
# gradient is low
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                        col="red",lty=3))
legend(-2.5,100,legend=c("high gradient","average gradient","low gradient"),
       col=c("blue","brown","red"),
       lty=c(1,2,3),bty="n",y.intersp=0.5,cex=.6)

# Running the base model using percent flying
with(data.invert.taxal,hist(PFLYING,seq(0,100,5)))
x<-with(data.invert.taxal,round((PFLYING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PFLYING/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=6516.6/314)
g.pflying <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pflying)
sum(summary(g.pflying)$modelweights[1:5])
summary(g.pflying)$modelweights[1]
round(coef(g.pflying,select=2,icmethod="Burnham",varweighting="Johnson"),4)
(summary(g.pflying@objects[[1]])$null.deviance-
 summary(g.pflying@objects[[1]])$deviance)/
 summary(g.pflying@objects[[1]])$null.deviance
extractAIC(g.pflying@objects[[1]][1]+1)
extractAIC(g.pflying@objects[[1]][2])
summary(g.pflying@objects[[1]])
confint(g.pflying@objects[[1]])

# Looking at interaction between epibenthic substrata and watershed area
# create data set and plot with small watershed size, dlink average
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(-2,1),
                                  DLINK=rep(1,1)))
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
with(data.invert.taxal,plot(EPI_SUB,PFLYING,
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                                   with(data.invert.taxal,max(EPI_SUB))),
                           ylim=c(0,100),
                           col="lightgray",
                           xlab="Standardized Epibenthic Substrata Score",
                           ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB,(predict(g.pflying@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                        pch=1,col="blue",cex=.8))
# create data set and plot with medium watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                                  DLINK=rep(1,1)))
with(data.predict,lines(EPI_SUB,(predict(g.pflying@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                        col="brown",lty=2))
# create data set for plot with large watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(2,1),

```

```

                DLINK=rep(1,1))
# plot of effects of epibenthic substrata scores on percent flying inverts when
# watersheds size is high
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(-0.7,30,legend=c("small watershed","medium watershed","large watershed"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=0.2,cex=.6)
# Looking at interaction between epibenthic substrata and dlink
# create data set and plot with average watershed size, low dlink,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(-2,1)))
par(fig=c(.25,.75,.35,.70),new=T)
with(data.invert.taxal,plot(EPI_SUB,PFLYING,
                cex.axis=.7,cex.lab=.7,
                xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                with(data.invert.taxal,max(EPI_SUB))),
                ylim=c(0,100),
                col="lightgray",
                xlab="Standardized Epibenthic Substrata Score",
                ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                pch=1,col="blue",cex=.8))
# create data set and plot with average watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(0,1)))
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="brown",lty=2))
# create data set and plot with average watersheds size, dlink high,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(2,1)))
# plot of effects of epibenthic substrata scores on percent flying inverts when
# dlink is high
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(-.5,32,legend=c("low d-link","average d-link","high d-link"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)
# Looking at interaction between watershed and dlink
# create data set and plot with average epibenthic substrate scores, low dlink,
# and water size varied from small to large
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(-2,1)))
par(fig=c(.25,.75,0.05,.40),new=T)
with(data.invert.taxal,plot(ACREAGE,PFLYING,
                cex.axis=.7,cex.lab=.7,
                xlim=c(with(data.invert.taxal,min(ACREAGE)),
                with(data.invert.taxal,max(ACREAGE))),
                ylim=c(0,100),
                col="lightgray",
                xlab="Standardized Watershed Size",
                ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                pch=1,col="blue",cex=.8))
# create data set and plot with average epifaunal substrate, dlink average,
# and watershed size varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(0,1)))
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="brown",lty=2))
# create data set and plot with average epifaunal substrate, dlink high,
# and watershed size varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(2,1)))
# plot of effects of watershed size on percent flying inverts when
# dlink is high
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(2.5,32,legend=c("low d-link","average d-link","high d-link"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)
mtext("Percent Flying Invertebrates",2,-5,out=T,cex=.8)

```

CHAPTER 3
INFLUENCE OF ROADS AND IMPOUNDMENTS ON AQUATIC COMMUNITY
STRUCTURE IN HEADWATER STREAMS

3.1 INTRODUCTION

Scientists have long recognized that riverine systems have a hierarchical spatial structure, where stream habitats such as pools, runs, and riffles are combined to form reaches, which come together to form stream networks similar to the branching of a tree (Strahler 1964). The stream network consists of all interconnected streams and floodplains in a watershed, driven by fluvial and biological processes. In stream networks, the flow of material and energy is primarily restricted to the physical network, and the geometry of the branches can affect physical and biological processes and patterns (Campbell Grant et al. 2007). Elements of spatial structure such as basin shape, network pattern, and size differences between confluent channels can regulate the spatial distribution of physical diversity within river systems (Benda et al. 2004). These natural elements, as well as anthropogenic impacts from habitat fragmentation can also affect the availability of refugia, habitat diversity, and dispersal for aquatic fauna (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Smiley and Dibble 2008). We are also beginning to understand how network structure may influence both physical and biological patterns and processes in fish. However, our understanding of how elements of network structure such as position along a reach, position within the network, and distribution of habitat influence benthic macroinvertebrate dispersal and population connectivity is limited. We also know little about how these patterns and processes may

be disrupted as a result of human-driven landscape change such as stream barriers to movement and creation of artificial habitats such as stormwater and farm ponds.

Two major types of movement in streams include dispersal and migration. Dispersal is the one-way movement of organisms (or propagules) from their point of origin or release (Lincoln et al. 1998). It is a mechanism by which organisms acquire resources necessary to complete their life-cycle and ultimately increase their fitness, and it plays an important role in determining the distribution of aquatic fauna across stream networks (Ricklefs 1990; Dingle 1996). Dispersal is also important in population dynamics, especially when populations are patchily distributed and demographic rates vary among patches, such as when populations exhibit metapopulation or source-sink dynamics (Dunning et al. 1992). Migration is generally considered to be regular, long-distance movement of organisms among habitat patches in order to exploit new resources or different habitats (Dingle 1996). It is an important behavior used by biota with complex life cycles that require multiple habitat types to complete their life cycle. Dispersal and migration in streams can occur within the network (i.e., within the stream corridor) and out of the network (i.e., overland between adjacent streams; Campbell Grant et al. 2007).

Benthic macroinvertebrates primarily disperse through emergence as adults and through a mechanism called drift, but upstream movement of aquatic forms is possible. Drift involves the downstream transport of benthic macroinvertebrates by the force of moving water (Waters 1972; Benson and Pearson 1987). Drifting organisms are typically transported short distances (McLay 1970; Townsend and Hildrew 1976; Danehy et al. 2011), although Neves et al. (1979) documented drift for hundred of meters during

baseflow and over one kilometer during stormflow. In addition to downstream drift, many aquatic invertebrates will actively move upstream, primarily over short distances, but some will move more than two kilometers as larvae (Vaughan 2002). The more common type of dispersal is found among adult insects with complex life cycles involving metamorphosis and emergence of a terrestrial phase. Although little is known about dispersal distances for most taxa, as adult insects emerge, they typically disperse upstream before reproducing (Hershey et al. 1993; Bilton et al. 2001). Upstream flight may compensate for the downstream drift of larval forms (Waters 1972). Using mark-recapture techniques, Hershey et al. (1993) found that one-third to one-half of the adult mayfly *Baetis* (Ephemeroptera: Baetidae) population traveled 1.6 to 1.9 km upstream. Petersen et al. (2004) found that the majority of adult Ephemeroptera, Plecoptera, and Trichoptera (EPT) dispersed within or very close to the stream channel, although 10% of Plecoptera traveled more than 60 m from the stream channel. Winterbourne et al. (2007) showed similar results, but found that some female Trichoptera dispersed hundreds of meters from their natal stream. These studies suggest that most adult insect dispersal is within the stream corridor rather than laterally, although insects seem to have an inherent dispersal mechanism to colonize new habitats (Winterbourne et al. 2007).

Dispersal of fishes is confined entirely to the wetted stream channel and consists of movements to find suitable habitat for feeding, reproduction, and refugia. Movement can be migratory or more localized in nature, although it is thought that most freshwater fish have some sort of migratory behavior over time and space (Brönmark et al. 2014). Diadromous species (i.e., species that migrate between fresh and saltwater) are known to migrate long distances to complete their life cycle, with migrations ranging from

hundreds of meters to thousands of kilometers (Binder et al. 2011). Other species, such as resident fish in streams and lakes, do not usually travel beyond their home range, but will occupy different habitats during different seasons and portions of their life cycle. Although resident species are relatively sedentary, some have been found to travel long distances. For example, Gatz and Adams (1994) studied the movement of redbreast sunfish (*Lepomis auritus*), bluegill (*Lepomis macrochirus*), rock bass (*Ambloplites rupestris*), largemouth bass (*Micropterus salmoides*), and warmouth (*Lepomis gulosus*) over a three-year period in a Tennessee stream. They found that most individuals traveled less than 100 m along the channel, although several individuals of redbreast sunfish, largemouth bass, and bluegill traveled over 10 kilometers.

Dispersal of fish and benthic macroinvertebrates in streams is dependent on connectivity, the extent to which populations within a species' range are linked (Palumbi 2003). Connectivity of habitats is an important factor in maintaining biological diversity (Crist et al. 2005), as it can facilitate the movement of genes, individuals, species, and populations among habitat patches (Minor and Urban 2008). In streams with unaltered connectivity, factors such as stream size, position within the stream network, gradient, and distribution of habitat should dictate aquatic diversity and community structure. It is well documented that species richness in fish communities generally increases as stream size increases (Sheldon 1968, Platts 1979, Fairchild et al. 1998). The increase in diversity is due to a general increase in the size and heterogeneity of habitat, as well as differences in depth from the headwaters to the lower reaches. As described in the Riverine Continuum Concept (RCC; Vannote et al. 1980), aquatic community structure and function also changes with increasing stream size due to changes in geomorphology

and physical habitat. The RCC divides rivers into headwaters (1st to 3rd order streams), mid-reaches (4th to 6th order streams), and lower reaches (> 6th order streams).

Headwaters are usually characterized by narrow, highly shaded streams that receive organic input mostly from allochthonous materials in the form of leaves and sticks. The benthic macroinvertebrate community is dominated by shredders, which break down the coarse particulate organic matter. The fish community is low in diversity and largely invertivorous. Mid-reaches are characterized by a higher amount of autochthonous material in the form of periphyton due to their larger size, reduced currents, and more open canopies. However, allochthonous material also plays an important role in mid-reaches due to the surrounding forest. Collectors that collect and consume fine particulate organic matter, and grazers that consume periphyton, dominate the benthic macroinvertebrate community in mid-reaches. However, continued input of allochthonous material supports some shredders in mid-reaches. Mid-reaches are characterized by piscivorous and invertivorous fish species. In the lower reaches, particulate organic matter is common, but there is less primary production due to higher turbidity (Vannote et al. 1980). As a result, benthic macroinvertebrate communities in lower reaches are dominated by collectors, and fish communities are dominated by piscivorous and planktivorous species.

The RCC predicts that species richness will be the lowest in low-order streams, increasing with stream size until an expected maximum in medium-sized streams, where environmental variability is highest. Species richness would then decrease again in large-order streams due to the largely homogeneous habitat. Thus, plotting the number of species as a function of drainage area should produce a unimodal curve. A study of riffle

habitats at 10 locations on the Salmon River in Idaho by Minshall et al. (1995) supports this prediction, where species diversity peaked at sites in mid-reaches of streams. However, Melo and Froehlich (2001) found no evidence of a unimodal pattern of species richness with increasing stream size. In fact, their study showed that species richness generally decreased along a gradient of stream size. Thus, headwater streams can still support a diverse array of benthic macroinvertebrates, even in their upper reaches. For example, in a review of taxa dependent on headwaters, Meyer et al. (2007) found that three unmapped headwater streams supported over 290 aquatic fauna. Dieterich and Anderson (2000) found 202 aquatic or semiaquatic insect species in intermittent streams in western Oregon, some of which were unique to these types of streams. Although benthic macroinvertebrate taxa richness tends to be higher in perennial streams than intermittent streams (Williams 1996), some studies have shown similar diversity in both stream types (Miller and Gallaway 1996; Price et al. 2003).

The high diversity of benthic macroinvertebrates in headwater streams may be partly due to the low abundance of fish. Low order streams are typically dominated by small-bodied insectivorous and invertivorous fish (Vannote et al. 1980) such as minnows (Family Cyprinidae), madtom catfishes (*Noturus* spp), darters (Family Percidae), and sculpins (Family Cottidae) (Schlosser 1987). Insectivores feed exclusively on aquatic insects, although invertivorous fish feed on all benthic macroinvertebrates, including aquatic insects, crustaceans, and worms. Although non-insect taxa may make up a portion of their diet, invertivores prefer to prey on aquatic insects (Lotrich 1973; Trial et al. 1983; Todd and Stewart 1985; Tófoli et al. 2013). Due to their small size, shallow depths, and high gradient, headwater streams often cannot support self-sustaining fish

populations and are typically low in diversity (Schlosser 1987; Gomi et al. 2002; Richardson and Denehy 2007). Schlosser (1987) described such streams as “colonizing” due to their uniform conditions and shallow depths. These conditions support populations dominated by juvenile minnows and typically lack larger predatory fishes. Even intermittent portions of these streams can support some fish during portions of the year. When such streams dry, small pools often remain and will be used by young fish as shelter due to the lack of larger predatory fish (McDonough et al. 2011). As habitat heterogeneity and pool volume increase with stream size, species richness and fish density also increase due to the addition of larger minnows and younger sunfish (Family Centrarchidae) and suckers (Family Catostomidae) (Schlosser 1987). Based on Schlosser’s framework, streams with the largest pool depth and volume are considered “stable”. In these large streams, there are major shifts in fish size, composition, and trophic structure. Due to increased predation and competition, fish communities in larger systems support less small insectivores, invertivores and omnivores and fewer large piscivores.

Location within the stream network can also influence aquatic diversity and community structure. For example, fish found in headwater streams are more limited by local conditions than fish lower in the watershed, which have access to more of the stream network (Magalhães et al. 2002; Grenouillet et al. 2004; Hitt and Angermeier 2008a). Also, streams connected to larger rivers lower in the network tend to have more species than similarly sized streams connected to smaller streams (Gorman 1986; Osborne and Wiley 1992; Schaefer and Kerfoot 2004; Smith and Kraft 2005; Hitt and Angermeier 2006; Hitt and Angermeier 2011). For example, Osborne and Wiley (1992)

found a significant and positive relationship between fish species richness and downstream link (d-link), an index of the spatial location of a stream within a stream network. In their study, d-link explained the greatest portion of variance in diversity, which suggests that downstream processes affect fish community structure in tributary streams more than in similar sized streams further up the drainage. First to third order streams connected to rivers that are at least three orders of magnitude larger are described as adventitious. These tributaries produce unique conditions for aquatic fauna due to their proximity to the relatively species rich main channel, which facilitates greater dispersal compared to the headwaters of the mainstem (Gorman 1986). Thus, the downstream portions of adventitious streams near the confluence with the main channel tend to be higher in diversity and more variable over time. For example, Thomas and Hayes (2006) found that fish species richness was higher in adventitious streams than in the headwaters of the mainstem, and that fish species composition of adventitious streams was more similar to the mainstem than the headwaters.

The relationship between stream position and benthic macroinvertebrate diversity and community structure is far less studied, although some studies have produced results similar to those for fish communities. Brown and Swan (2010) found that benthic macroinvertebrate communities are dictated by environmental factors in the headwaters of streams and by dispersal in the mainstem. Similarly, Harrel and Dorris (1968) showed that benthic macroinvertebrate community structure on a 3rd order adventitious stream was more similar to the mainstem than on a similar size stream further upstream in the watershed, which also suggests dispersal-driven processes in streams more connected to the mainstem. However, no studies have explored the relationship between benthic

macroinvertebrate community structure and d-link, a metric that has been utilized for studies of fish. Although, based on the unimodal species distribution predicted by the RCC, you would expect a similar distribution for a plot of benthic macroinvertebrate species richness as a function of d-link.

It has been well documented that stream habitat has an influence on species diversity and composition (Reid 1961; Vannote et al. 1980; Benda et al. 2004). Habitat in streams is mediated by fluvial processes, which drive the distribution of benthic substrate, woody debris, and other habitat-forming materials that can affect benthic macroinvertebrate and fish community structure (Reice 1980; Duan et al. 2009; Martin et al. 2013). Stream confluences can provide distinct physical conditions that may create high quality habitat (Benda et al. 2004). Stream confluences can enhance diversity by increasing habitat heterogeneity, providing refugia, and allowing access to the mainstem for migration (Campbell Grant et al. 2007). The increase in heterogeneity is due to the size difference between confluent channels, which has an effect on reaches immediately upstream and downstream of the confluence (Benda et al. 2004). Upstream of confluences, there are lower gradients, wider channels and floodplains, increased wood recruitment, finer substrates, and greater lateral connectivity. Downstream of confluences, there are higher gradients, larger substrate sizes, deeper pools, and more bars. Hitt and Angermier (2008b, 2011) found that stream confluences could influence fish communities up to several kilometers within both main channels and tributaries. Similarly, Schaefer and Kerfoot (2004) found that mean fish diversity decreased as distance from the mouth of the stream increased. Confluences can also effect the composition of benthic macroinvertebrates. Downstream of confluences there is a unique

composition of taxa that are distinct from the mainstem and tributaries that feed them (Knispel and Castella 2003; Hellmann et al. 2015). Knispel and Castella (2003) found that benthic macroinvertebrate heterogeneity increased downstream of the confluence of a small tributary and a large glacier-fed stream. They concluded that the influence of the tributary on the main channel resulted in greater habitat heterogeneity through increased organic matter inputs and sediment supply, which may have resulted in a more diverse fauna. In contrast, some studies have shown no change in benthic macroinvertebrate density, taxa richness or functional feeding group composition downstream of confluences relative to upstream, despite distinct assemblages in both (MacNally et al. 2011). The above studies have focused on differences in benthic macroinvertebrate communities in the mainstem upstream and downstream of confluences, but very few have studied the effect of the confluence on the tributary stream. There is strong evidence that species composition in small streams is distinct from medium to large-sized streams (Vannote et al. 1980; Minshall et al. 1995; Melo and Froehlich 2001), thus you would expect that taxa richness and other measures of community structure would change the closer you are to a confluence. In a recent study, Wilson and McTammany (2014) found less similarity in community structure between a tributary stream and the mainstem, as the distance from the confluence increased on the tributary.

Alteration of stream hydrology and physical structure by humans can affect connectivity by creating physical barriers to the movement of organisms, which can have negative effects on biological communities (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Neville et al. 2006; Smiley and Dibble 2008). As barriers limit or eliminate upstream movement, remnant populations above the barriers become

fragmented and isolated, and can go locally extinct (Kruse et al. 2001), decreasing species diversity (Siligato and Böhmer 2002). Due to their linear nature and extent in the landscape, streams are particularly vulnerable to fragmentation, especially from road crossings and impoundments.

The United States (U.S.) road network covers approximately 2% of the continental U.S. (Cerulean 2002). As a result, the construction of roads can cause fragmentation of watersheds due to the placement of culverts at stream crossings. The severity of the impact depends on the type of road crossing and size and installation of culverts (Jackson 2003). Physical impacts of road crossings include increasing the detention time of water upstream of the crossing; altering the sediment transport and scouring of the channel during storm events; restricting the ability of woody debris to pass downstream; and impeding the movement of aquatic fauna by acting as a physical barrier (Jackson 2003). Physical barriers to movement are caused by elevation drops at the inlet or outlet of culverts; blocked or collapsed culverts; excessive water velocities within and around culverts; lack of bank edge areas above and below culverts; insufficient water depth within culverts; and discontinuity of channel substrate (Jackson 2003). These impacts can have a negative effect on benthic macroinvertebrate (Resh 2004; Khan and Colbo 2007; Peterson 2010) and fish (Benton et al. 2008; Burford et al. 2009) communities. For example, Peterson (2010) found that culverts cause a greater proportion of stressor-tolerant benthic macroinvertebrate taxa and an alteration of dominant feeding groups in streams below culverts. Resh (2004) found that culverts decrease the ability of non-insect macroinvertebrates to disperse upstream. For fish, culverts also limit the ability for movement upstream. Burford et al. (2009) found that

upstream movement of cutthroat trout averaged 2.45 times lower through culverts than through natural channels. In Burford's study, outlet drop was the most important factor reducing fish passage.

Impoundments (e.g., lakes and ponds), which also cause habitat fragmentation, are present along streams throughout much of the U.S. In Maryland, there are over 400 dams, ranging from 6 to 296 feet in height (Maryland Department of the Environment 2014). Busch and Larry (1996) estimated that 15,167 dams that prevent fish movement are present along the Atlantic coast. Dahl (2011) estimated that there are 2,980,000 agricultural ponds, 410,000 industrial ponds, and 963,000 urban ponds in the U.S., many of which are likely connected to stream systems. In addition, Liermann et al. (2010) found that nearly 50% of global ecoregions are obstructed by large and medium size dams. Impoundments can affect the physical, chemical, and biological characteristics of streams by altering substrate, sediment load, dissolved oxygen, and water temperature, and impeding the movement of aquatic fauna (Kittrell et al. 1958; Baxter 1977; Lessard and Hayes 2003; Falke and Gido 2006). Dams are a sink for sediment that would normally be transported downstream. Immediately upstream of the impoundment, coarse substrate can be embedded with sand and silt. In contrast, immediately downstream of impoundments, streams are often dominated by larger substrate due to the retention of fine sediment by the impoundment. These alterations to the stream can have a negative effect on both the upstream and downstream benthic macroinvertebrate (Ward and Stanford 1979; Lessard and Hayes 2003; Stranko et al. 2014) and fish communities (Lessard and Hayes 2003; Falke and Gido 2006; Katano et al. 2006; Lasne et al. 2007; Franssen and Tobler 2013; Stranko et al. 2014a). For example, Ward and Stanford

(1979) found that impoundments cause a shift in the trophic status of the downstream benthic macroinvertebrate community. This downstream shift was due to less leaf litter for shredders, more periphyton for scrapers, and more organic particles for collectors. Similarly, Lessard and Hayes (2003) showed that impoundments that increase summer temperature could cause a change in the composition of the macroinvertebrate community downstream. Upstream of large impoundments that block American eel (*Anguilla rostrata*) passage, benthic macroinvertebrate densities can decrease due to a greater abundance of benthic fish that eels would normally prey on (Stranko et al. 2014a).

For fish, ponds are usually a barrier to movement, causing isolation of upstream populations (Falke and Gido 2006). As a result, isolated populations are at risk of extinction if the system is degraded and subject to frequent stressors. For migratory species, connectivity is imperative for successful reproduction (Brönmark et al. 2014), and impoundments can block migratory fish from moving upstream. Katano et al. (2006), for example, found that the density and biomass of diadromous species was higher below impoundments than above impoundments. Impoundments can also affect the species richness and composition of the streams that feed them. Kashiwagi and Miranda (2009) found that streams that feed small impoundments supported a higher percentage of sunfish in upstream and downstream reaches than non-impounded streams. Franssen and Tobler (2013) found higher species richness, diversity and evenness above an impoundment than below the impoundment. This may have been due to the introduction of fish species from the pond to the stream, which increased the diversity at the stream-pond interface; although, it may have also been due to more degraded habitat downstream of the pond. Furthermore, in coldwater systems, densities of coldwater fish

may decrease downstream of ponds due to higher water temperatures in ponds feeding streams (Lessard and Hayes 2003).

Impoundments can also act as sources of non-native species. This could include species that are not native to Maryland, as well as other species introduced outside of their local range. In the Mid-Atlantic region, the majority of exotic species were introduced intentionally via stocking and aquarium release, or accidentally through bait release (Lapointe et al. 2016). Because most released species can tolerate local conditions, bait release represents the highest risk for invasive species introduction in the Mid-Atlantic region and has resulted in the establishment of at least 26 fish species in this region. Not all introductions have caused negative impacts, although some species have become established resulting in detrimental effects to native fauna (Jelks et al. 2008) and biodiversity (Gozlan et al. 2005), including some cascading effects (Crooks 2002). Some impacts to native species include predation, competition for resources, displacement from native habitat, hybridization and exposure to diseases (Gozlan et al. 2010). Due to the abundance of recreational fishing, bait bucket releases often occur on impoundments, which could not only cause detrimental effects to the species in the impoundment, but also to downstream fisheries.

Although we are beginning to understand how network structure may influence both physical and biological patterns and processes in fish, we know little about how these patterns and processes may be disrupted as a result of human-driven landscape change such as stream barriers to movement and creation of artificial habitats such as stormwater and farm ponds. Numerous studies have shown that fish species diversity and community structure increase with greater measures of stream network structure

(Magalhães et al. 2002; Grenouillet et al. 2004), including studies that have examined the effect of stream size, distance to confluence, network position, and habitat on fish communities. It is also well known that human stream alteration can affect connectivity by creating physical barriers to movement, which can negatively affect biological communities (Warren and Pardew 1998; Vaughan 2002; Gibson et al. 2005; Neville et al. 2006; Smiley and Dibble 2008). Although there has been a wealth of research on the effect of stream blockages and sources (via impoundments) on aquatic biota, most have been at a small scale and none have combined both fish and benthic macroinvertebrate community data. Some of these studies have been large in scale and located in the Mid-Atlantic Region (Hitt and Angermeier 2006, 2008a, 2008b, 2011), but no large-scale study has looked at the effect of stream blockages (via road culverts and impoundments) and sources (via impoundments) on benthic macroinvertebrate and fish communities through the disruption of stream network structure.

In this chapter, I investigate whether road crossings and man-made impoundments (i.e., ponds and lakes) may be degrading benthic macroinvertebrate and fish communities in headwater streams through disruption of network structure. The study is based on the idea that fish and benthic macroinvertebrate diversity and community structure is dependent on the structure of the stream network, and that road culverts and impoundments will alter the natural network effects and ultimately the benthic macroinvertebrate and fish communities. Because road crossings and impoundments on first order streams could block fish movement from lower in the network, it was expected that the presence of these features would influence invertebrate community structure by limiting the occurrence of top predators in first-order streams (Figure 3.1).

Impoundments could also supplement the aquatic community by introducing fish and benthic macroinvertebrates into first order streams, which could impact community structure and predator-prey relationships (Figure 3.2).

These mechanisms were explored using existing Maryland Department of Natural Resources (MDNR) Maryland Biological Stream Survey (MBSS) benthic macroinvertebrate, fish, and environmental data collected from first-order streams in the Piedmont Plateau Physiographic Province of Maryland. To my knowledge, no study has used a large, state-wide data set to investigate the influence of natural network structure and habitat fragmentation on both benthic macroinvertebrate and fish communities. My general approach was to build models of benthic macroinvertebrate and fish assemblage structure that included the effects of local habitat conditions and natural network structure and ask if anthropogenic network structure could explain additional variation in assemblage structure beyond that accounted for by local habitat conditions and natural network structure. I investigated two sets of variables, one that represented roads and impoundments as potential isolating structure and one that represented impoundments as potential sources for both benthic macroinvertebrates and fish.

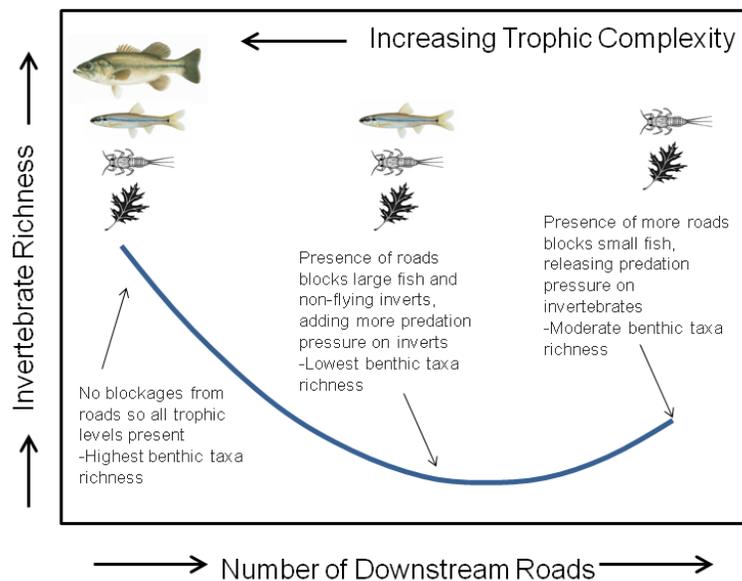


Figure 3.1. Conceptual model showing trophic level interactions among benthic macroinvertebrates, small predatory fish, and top predators in relation to the presence of downstream roads.

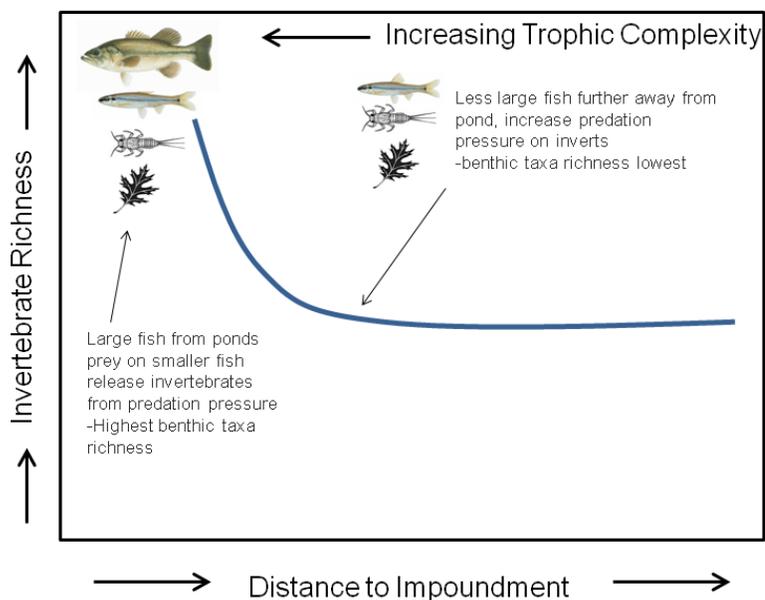


Figure 3.2. Conceptual model showing trophic level interactions among benthic macroinvertebrates, small predatory fish, and top predators in relation to the distance to impoundments.

3.2 METHODS AND MATERIALS

3.2.1 Study Streams

The MBSS was established in 1993 to assess the ecological condition of Maryland's 1st through 4th order non-tidal streams by measuring chemical, physical, and biological parameters. It is a probability-based stream sampling program designed to assess stream conditions with known precision at various spatial scales. The program mostly includes random (probabilistic) sites, although numerous targeted sites are sampled each year (e.g. Sentinal sites; Becker et al. 2010). Probabilistic sampling sites were established by the MBSS using a random sampling approach, stratified by year, basin, and stream order, depending on sampling round.

This study used the MBSS probabilistic and targeted monitoring data collected on 1st order streams in the lowlands and highlands of the Piedmont Plateau Physiographic Province of Maryland, from 1995-2014. Data were not used for streams west of the Piedmont to limit the influence of higher-gradient, geomorphologically different streams in the western part of the State. Similarly, sites were not chosen in Maryland's Coastal Plain region due to differences in geomorphology and fauna. First-order streams were chosen for this study for several reasons. First, they make up the majority of stream miles (and MBSS sites) in stream networks and provide important ecological functions to the downstream network (Meyer et al. 2003). Also, since first order streams are abundant and somewhat isolated from the rest of the network, they are vulnerable to anthropogenic impacts from roads and impoundments. I was also interested in the effect of downstream habitats on tributary streams, rather than the effect of headwater streams on downstream

resources. Lastly, I felt that it was important to limit the influence of differences in stream size on macroinvertebrate and fish communities.

All first-order MBSS sampling sites from 1995 through 2014 were overlaid onto the National Hydrography Dataset Plus (NHD; McKay et al. 2012) in ArcMap 10.2.1 (ESRI 2013). This dataset was chosen over other existing stream layers due to its wide use and extensive coverage across Maryland and surrounding states. Other hydrography data were explored for the counties covered by the Piedmont, but were not used due to differences in methods of derivation and inconsistencies among coordinate systems. Similarly, because watersheds do not stop at state boundaries, it was important to have a dataset that extended outside of Maryland.

For MBSS sites that occurred above the terminus of NHD streams, streams were extended to the sites based on USGS 7.5 minute topographic quadrangle maps. The MBSS dataset includes multiple sites in each watershed, as well as multiple years of data for some sites. If more than one site was present in a given first-order watershed, one site was randomly chosen to be used for the analysis. Similarly, for sites with multiple years of data, one year of data was randomly chosen to be used for the analysis. As discussed further below, sites with ≤ 60 organisms were also removed from the dataset. The resultant dataset used for this study includes 346 total benthic macroinvertebrate sampling sites and 351 fish sampling sites (Figure 3.3).

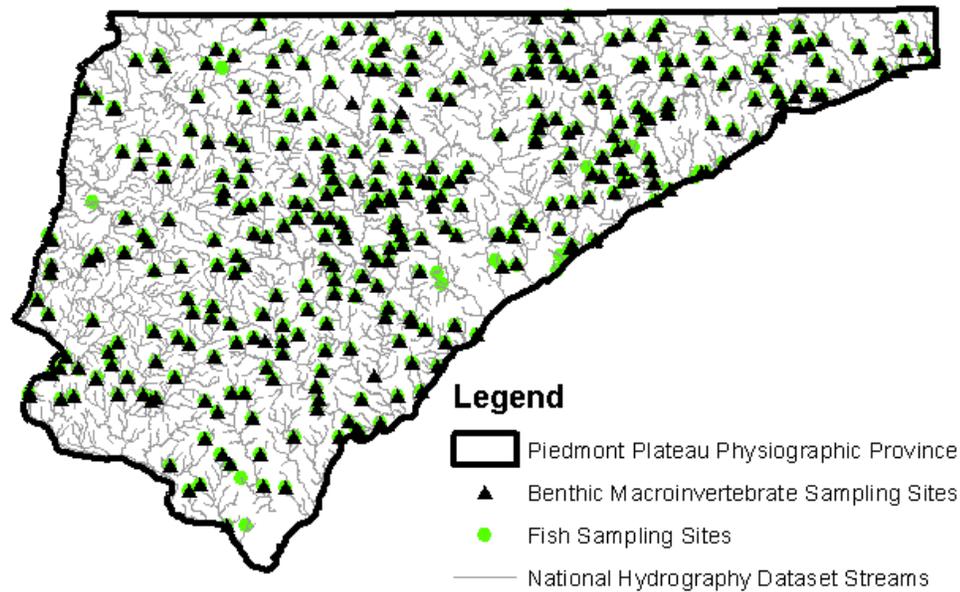


Figure 3.3. Map of Maryland’s Piedmont Plateau physiographic province showing 346 benthic macroinvertebrate sampling sites (black) and 351 fish sampling sites (green) on 1st order streams, sampled from 1995-2014.

3.2.2 Data Collection

Five dependent variables were used to characterize benthic macroinvertebrate community structure, including rarefied taxa richness, percent Chironomidae, percent clingers, percent shredders, and percent flying invertebrates (Table 3.1). These variables were chosen to provide a variety of community structure attributes based on taxonomy (rarefied taxa richness), tolerance of anthropogenic stressors (percent Chironomidae), habitat preference (percent clingers), trophic classification (percent shredders), and mode of movement (percent flying invertebrates). Rarefied taxa richness, percent clingers, percent shredders, and percent flying invertebrates are predicted to decrease in response to human disturbance. Percent Chironomidae is predicted to increase in response to human disturbance.

Six dependent variables were used to characterize fish community structure, including species richness, native species richness, non-native species richness, biomass per square meter, number of benthic species, and percent generalists, omnivores, and invertivores (Table 3.1). These variables were chosen to provide a variety of community structure attributes based on composition (Species Richness, Number of Benthic Species), abundance (Biomass per Square Meter), origin (Native Species Richness, Non-native Species Richness), and trophic composition (Percent Generalists, Omnivores, and Invertivores). Species richness, native species richness, number of benthic species, and biomass per square meter are predicted to decrease in response to human disturbance. Non-native species richness and percent generalists, omnivores, and invertivores are predicted to increase in response to human disturbance. Several of the 351 fish sampling sites did not result in the collection of any individuals of fish. However, because I was able to use linear regression models for species richness and native species richness I retained the entire dataset, including sites with no individuals (and thus no species), for these models. On the other hand, sites with no individuals are automatically given values of zero for the other dependent variables (i.e., native species richness; non-native species richness; biomass per square meter; number of benthic species; and percent generalists, omnivores, and invertivores), which may skew the results of their models. Thus, a subset of the 351 sites was retained that only contained sites with at least one species of fish. This second fish data set included 323 sites and was used for the models for non-native species richness; biomass per square meter; number of benthic species; and percent generalists, omnivores, and invertivores.

Table 3.1. Benthic macroinvertebrate and fish community variables explored in Chapter 3. The code for each variable is listed parenthetically.

Benthic Macroinvertebrate Community Variables	Fish Community Variables
Rarified Taxa Richness (NTAXA_RAR)	Species Richness (NTAXA)
Percent Flying Invertebrates (PFLYING)	Native Species Richness (NTAXA_NAT)
Percent Chironomidae (PCHIRON)	Non-native Species Richness (NTAXA_NONNAT)
Percent Shredders (PSHRED)	Biomass Per Square Meter (BIOM_MSQ)
Percent Clingers (PCLING)	Number of Benthic Species (NUMBENTSP)
	Percent Generalists, Omnivores and Invertivores (PGEOMIV)

Five independent variables were used to measure the effect of isolation (via road culverts and impoundments) and sources (via impoundments) on benthic macroinvertebrates and fish communities (Table 3.2). Isolation variables included the number of roads and the presence of downstream impoundments between the sample site and the nearest confluence. Source variables included the number of upstream impoundments, the distance to the nearest upstream impoundment, and the distance to the nearest downstream impoundment.

Two covariates were used to account for the effects of network structure, including d-link and distance to nearest confluence (Table 3.2). D-link is a measure of adjacent habitat characteristics and distance to downstream confluence is a measure of the isolation of the sample reach from the downstream confluence and adjacent habitat. Three covariates were included to account for the effects of local habitat conditions on macroinvertebrate community structure. These covariates included stream gradient,

drainage area, epifaunal substrate score, and instream habitat score. Other covariates such as imperviousness and conductivity, which could account for other variation from human disturbance, were not incorporated into this analysis. It was felt that these measures might be highly correlated with epifaunal substrate, instream habitat, and the number of downstream roads, making it difficult to include them in models together. Percent Chironomidae, percent shredders, percent clingers, drainage area, gradient, and epifaunal substrate were obtained from the MBSS master database. Rarified taxa richness, percent flying invertebrates, distance to nearest confluence, and d-link were measured as part of this study.

Table 3.2. Independent variables and covariates used in Chapter 3 to measure the effect of isolation and sources on benthic macroinvertebrates and fish communities. The code for each variable is listed parenthetically.

Independent Variables	Type	Covariates
Number of Roads Downstream (ROADS_DS)	Isolation	Gradient (ST_GRAD)
Presence of Impoundments Downstream (IMP_DS)	Isolation	Epifaunal Substrate (EPI_SUB)
Number of Impoundments Upstream (NUM_IMP_US)	Source	Instream Habitat (INSTRHAB)
Distance to Impoundment Upstream (DIST_IMP_US)	Source	Drainage Area (AREA)
Distance to Impoundment Downstream (DIST_IMP_DS)	Source	Distance to Nearest Confluence (DIST_CON) D-link (DLINK)

Benthic Macroinvertebrate Community Variables

Benthic macroinvertebrates samples were previously collected at each site by the MBSS using protocols for spring sampling (Kazyak 1995; Kazyak 1997; Kazyak 2000; Stranko et al. 2007; Stranko et al. 2014b). Samples were collected during the Spring Index Period, from March 1 through April 30. Field collection included sampling 1.85 m² of best available benthic macroinvertebrate habitat at each site using a 540 µm mesh d-framed dipnet. Habitat types sampled include cobble/gravel, snags/leafpacks, undercut banks, root-wads, and submerged vegetation. Beginning at the downstream end of the 75-m site, the D-net was placed firmly in the substrate of the riffle area or other habitat feature while organisms were dislodged through rubbing or kicking of the substrate in a 0.09 m² area in front of the net. Large woody debris and rootwads were jabbed with the d-net, where the surface of the debris or rootwad was agitated by the lower frame of the net in an attempt to dislodge benthic macroinvertebrates clinging to the surface. This process was repeated until 1.85 m² of substrate was sampled throughout the reach. The sample was washed into a 540 µm sieve bucket and placed in a labelled sample container with 90% ethanol solution and transported to the MDNR benthic processing laboratory.

Benthic macroinvertebrate samples were processed, subsampled, and identified by taxonomists using protocols detailed in Boward and Friedman (2000). In the laboratory, samples were transferred to a gridded tray and subsampled using a fixed-count method. Trays contained 100, 5 cm X 5 cm square grids. Grids were randomly selected and organisms were picked until a total of 120 organisms were counted; after 120 organisms were picked, the grid containing the 120th organism was picked in its entirety and any

additional extra organisms in the cell were included from the sample. Organisms were identified to genus, or the lowest taxonomic level possible. Chironomidae larvae and Oligochaeta were slide-mounted and identified using MBSS methods (Boward and Friedman 2000). Data were entered into a Microsoft Access database and checked by the MBSS staff, where several benthic macroinvertebrate variables were calculated for use in the Maryland Benthic Index of Biotic Integrity (BIBI; Stribling et al. 1998). Where available, benthic macroinvertebrate variables were obtained by the MBSS for use in this study.

Benthic samples were subsampled using a fixed count approach, with a target count of 120 organisms. However, due to differences in sample size, the actual number of organisms identified can range from zero to greater than 120. Thus, to reduce any bias due to differences in subsample size, benthic macroinvertebrate data from each site were rarified to the minimum subsample size used by the MBSS to calculate the BIBI (60; Michael Kashiwagi, personal communication), prior to calculation of taxa richness. Rarification was performed using the Vegan Package in R (Oksanen et al. 2013).

Percent Chironomidae is the percent of the sample comprised of non-biting midge (Family Chironomidae) larvae and pupae (Stribling et al. 1998). Percent clingers is the percent of the sample comprised of individuals primarily adapted to riffle habitats. Percent shredders is the percent of the sample comprised of individuals adapted to utilize (i.e., shred) coarse particulate organic matter as a food source. Percent flying invertebrates was defined as the percent of the sample comprised of individuals that have an adult stage that emerges from the stream as a flying insect to disperse. Using the U.S. Environmental Protection Agency's Functional Traits Database (USEPA 2012), Merritt

and Cumins (2008), and the MBSS master taxa list, each benthic macroinvertebrate taxon was classified as a flying invertebrate or a non-flying invertebrate.

Fish Community Variables

The total number of species is a measure of the overall variety of the fish assemblage (Southerland et al. 2005) and excluded individuals reported as hybrids or unidentifiable species. The number of native species included those species classified as native to the Chesapeake Bay Drainage (Southerland et al. 2005) exclusive of hybrids and unidentifiable species. The number of non-native species included those species non-native to the Chesapeake Bay Drainage (Southerland et al. 2005) excluding hybrids and unidentifiable species. The number of benthic species included those species that reside primarily on the stream bottom (Southerland et al. 2005). The biomass per square meter is the total mass (g) of fish captured at a site, divided by the surface area fished (Southerland et al. 2005). The surface area fished was determined by multiplying the reach length (75 m) by the wetted width, which was averaged from four standard locations measured in the reach. The percent generalists, omnivores, and invertivores is the percent of the sampled fish community comprised of individuals in the generalist, omnivore, and invertivore functional feeding groups (Southerland et al. 2005).

Isolation and Source Variables

The number of ponds upstream of an MBSS site was determined using a combination of ArcMap (ESRI 2013) and Google Earth. Ponds within the site drainage area were initially identified in ArcMap using 2014 six inch resolution color infrared (CIR) aerial imagery for the State of Maryland, obtained from the Maryland iMAP server. This type of imagery is preferred for determining the presence of deepwater

habitats (Dahl and Bergeson 2009), which are identified by their dark signature. In this study, it was assumed that a dark-signature feature represented a pond that was likely to support a source population of fish or benthic macroinvertebrates, or both. Ponds that appeared to be under construction during the sampling year using aerial imagery were not counted, as they were not likely to contain a fish community. Similarly, wastewater treatment ponds were not included. A combination of USGS 7.5 minute topo quads, aerial imagery, and NHD streams were used to determine whether the pond was hydrologically connected to the MBSS site. Because areal imagery represents a snapshot in time, and the pond may not have been present during the time of the field sampling, each pond was further verified using multiple years of aerial imagery in Google Earth. This imagery dated back to before the MBSS sampling program began and was a good indicator of pond construction. Ponds determined to be present prior to the field sampling were digitized in ArcGIS using the 2014 CIR imagery. The smallest pond identified was 0.023 ac in size. The number of ponds upstream of a site was determined using the Count function in the pond attributes table for each site drainage area.

The distance to nearest upstream pond was measured in ArcMap (ESRI 2013). Using the Trace tool, a polyline was created and traced from the MBSS point to the approximate location of the nearest upstream pond's outfall using the NHD layer. The distance was determined by creating a field in the attributes table, and using the Calculate Geometry function to determine segment length (m) for each site. When no ponds were found upstream of a site, twice the maximum distance to any upstream impoundment was used to maintain observations in the data set. Approximately 25% of the sample sites had no impoundment upstream.

The distance to nearest downstream pond was measured in ArcGIS (ESRI 2013). Using the Trace tool, a polyline was created and traced from the MBSS point to the approximate location of the nearest downstream pond's inlet using the NHD layer. The distance was determined by creating a field in the attributes table, and using the Calculate Geometry function to determine the segment length (m) for each site. Several MBSS sites were located adjacent to the Chesapeake and Ohio (C and O) Canal downstream of the site. In instances where there were no ponds between the MBSS site and the C and O Canal, the canal was used as the downstream pond due to its function as a lentic waterbody.

The presence of impoundments downstream of an MBSS site and above the nearest confluence was determined by comparing the distance to a downstream confluence to the distance to a downstream pond. If the distance to the downstream pond was less than the distance to a confluence then I assigned IMP_DS as "yes". If the distance to the downstream pond was greater than the distance to a confluence, then I assigned IMP_DS as "no". The presence of a downstream pond was represented as an ordinal categorical variable.

The number of roads downstream of an MBSS site and above the nearest confluence was determined using a combination of ArcGIS (ESRI 2013) and Google Earth. The presence of road crossings downstream of each site and above the next confluence were initially identified in ArcGIS using 2014 six inch resolution CIR aerial imagery and the roads layer from the Maryland iMAP server. Other private roads and railroad crossings that appeared on aerial imagery, but did not show up on the roads layer were also counted, with the exception of golf cart path crossings, which were not

considered stream blockages as they are generally clear span bridges. Because the roads may not have been present during the time of the field sampling, each road crossing was further verified using multiple years of aerial imagery in Google Earth. This imagery dated back to before the MBSS sampling program began and was a good indicator of road construction. The number of roads was represented as an ordinal categorical variable, with three ordinal categories including no road crossings, one road crossing, two or more roads crossings.

Covariates

Catchments for the calculation of drainage area were created for each MBSS stream sampling location. Catchments were generated in ArcMap 10.1.3 (ESRI 2012) using sampling point locations collected by MBSS, digital images of USGS topographic maps with 20-foot contour lines, Maryland Department of the Environment's (MDE) 12-digit watershed boundary polygons, and the 1:100,000 scale stream reach file from the NHDPlus. All input and output geospatial data were projected in North American Datum of 1983 (NAD83), Maryland State Plane, meters.

One polygon for each catchment was created by drawing a polygon starting just downstream of the sampling point to ensure that the point fell inside of the resulting polygon. Catchment polygons were snapped to MDE's 12-digit watershed polygons when the catchment polygon shared a ridgeline with the 12-digit watershed. Snapping to the 12-digit watershed ensured consistent watershed boundaries to reduce the chance of overlapping adjacent watersheds and other topological errors. The drainage area was determined using the Calculate Geometry function.

Several quality control (QC) checks were completed on the catchment polygon dataset. Catchments were visually checked to ensure that each catchment only intersected the NHDPlus stream reach file at one location, and that catchments were drawn for the stream reaches upstream of the sampling location. For the sites located close to a confluence, stream order from the NHDPlus was compared to stream order from the MBSS dataset to ensure that catchments included the correct stream reaches. The Repair Geometry tool in ArcMap was used to identify and repair catchment polygons that had null geometry, self-intersections, or other geometry errors. A log of repaired geometries was kept with the original files. Topology rules were created for the polygon dataset and identified topology errors were corrected in the final catchment polygon dataset.

Distance to nearest confluence was also measured in ArcMap (ESRI 2013). Using the Trace tool, a polyline was created and traced from the MBSS point to the nearest downstream confluence using the NHD layer. The distance was determined by creating a field in the attributes table, and using the Calculate Geometry function to determine the segment length (m) for each site.

D-link was first described by Osborne and Wiley (1992) as the magnitude of the link of a channel below the next downstream confluence (Figure 3.4) and is a measure of the spatial position of a tributary within the drainage network. D-link was measured using the Stream Order tool in the Spatial Analyst extension in ArcMap (ESRI 2013). One meter DEM data were obtained from the U.S. Geologic Survey and the Fill tool was used to fill any holes or “sinks” in the DEM. The filled DEM was input into the Flow Direction tool to determine the direction water moved across the surface. The flow

direction raster was then used to create the flow accumulation raster and a conditional statement was then used to generate a raster stream network from the flow accumulation raster. The resulting stream network was compared to the NHD stream network in the study area to confirm accuracy. The raster stream network was assigned stream order values using the Stream Order tool and choosing the Shreve method of ordering. The Shreve stream order is the link magnitude of a given stream (Shreve 1966). The link magnitude of the downstream link (d-link) was determined by intersecting the polylines created for the distance to the nearest downstream confluence with the Shreve raster stream network.

Stream gradient was measured by MBSS at each site during the Spring Index Period, from March 1 through April 30. From 1995 through 1997, stream gradient was measured over the length of each site using an inclinometer (Kazyak 1995; Kazyak 1997). After 1997, stream gradient was measured over the length of each site using a levelometer (Kazyak 2000; Stranko et al. 2007; Stranko et al. 2014b). Gradient was determined by recording the difference in water surface height from the 0 m to the 75 m locations of the MBSS site as compared to a level plane.

Epifaunal substrate data were collected by the MBSS during the Summer Index Period, from June 1 through September 30, as part of their summer habitat assessment (Kazyak 1995; Kazyak 1997; Stranko et al. 2007; Stranko et al. 2014b). The epifaunal substrate metric is a qualitative score meant to rate the suitability of habitat for benthic macroinvertebrates at each site. This habitat parameter was visually estimated at each site in the field using a scale of 0 to 20 based on standard criteria on the MBSS Habitat Assessment Guidance Sheet (Table 3.3).

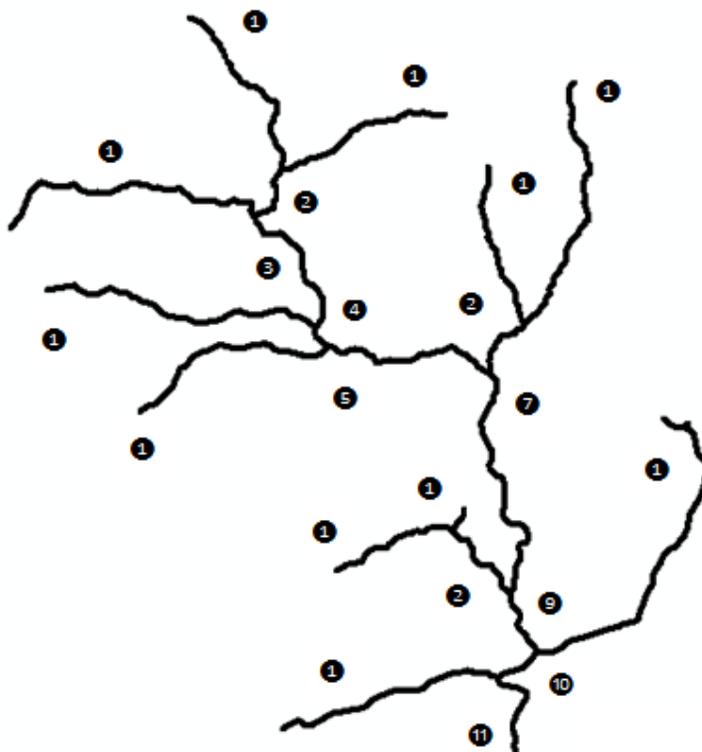


Figure 3.4. Determination of the d-link of a monitoring site. The d-link is the magnitude of the link of a channel below the next downstream confluence. After Osborne and Wiley (1992).

Table 3.3. The MBSS criteria for determining epifaunal substrate score.

Optimal (16-20)	Suboptimal (11-15)	Marginal (6-10)	Poor (0-5)
Preferred substrate abundant, stable, and at full colonization potential (riffles well developed and dominated by cobble; and/or woody debris prevalent, not new, and not transient)	Abund. of cobble with gravel &/or boulders common; or woody de-bris, aquatic veg., undercut banks, or other productive surfaces common but not prevalent /suited for full colonization	Large boulders and/or bedrock prevalent; cobble, woody debris, or other preferred surfaces uncommon	Stable substrate lacking; or particles are over 75% surrounded by fine sediment or flocculent material

Instream fish habitat for each site was determined by MBSS during their summer habitat assessment (Kazyak 1995; Kazyak 1997; Stranko et al. 2007; Stranko et al. 2014b). This habitat parameter was visually estimated at each site in the field using a

scale of 0-20 based on standard criteria on the MBSS Habitat Assessment Guidance Sheet (Table 3.4).

Table 3.4. MBSS criteria for determining instream habitat score.

Optimal (16-20)	Suboptimal (11-15)	Marginal (6-10)	Poor (0-5)
Greater than 50% of a variety of cobble, boulder, submerged logs, undercut banks, snags, root wads, aquatic plants, or other stable habitat	30-50% of stable habitat. Adequate habitat	10-30% mix of stable habitat. Habitat availability less than desirable	Less than 10% stable habitat. Lack of habitat is obvious

3.3 STATISTICAL ANALYSIS

The relationship between the benthic macroinvertebrate and fish community structure variables (Table 3.1) and the independent variables and covariates (Table 3.2) was analyzed using an Information Theoretic Approach (ITA). The ITA uses the principal of parsimony, multiple working hypotheses, and strength of evidence to select the best fitting model for the data at hand (Burnham and Anderson 2002). Using this approach, models were developed based on the hypothesized relationships between benthic macroinvertebrate and fish community structure and the independent variables. All possible models derived from the full model were considered, including all independent variables and covariables and their second-order interactions.

Two categories of impact models were developed for this analysis. Isolation models were developed to determine the effects of isolation from roads and downstream impoundments on benthic macroinvertebrate and fish community structure. Source models were developed to determine the potential effects of supplementation from

impoundments on benthic macroinvertebrate and fish community structure. Models were run separately for benthic macroinvertebrates and fish.

Each model was fit using R statistical software (R Core Team 2014) and the `glmulti` package (Calcagno 2013). Prior to fitting each model, correlations between covariates were examined to determine whether certain covariates were highly correlated and needed to be removed from the dataset to avoid co-linearity among independent variables (Table 3.11). Based on this analysis, epifaunal substrate was highly correlated with instream habitat ($R^2=-0.79$). Because the epifaunal substrate score is a measure of benthic macroinvertebrate habitat quality and the instream habitat score is a measure of fish habitat quality, epifaunal substrate was only used as a covariate in the benthic macroinvertebrate models and instream habitat was only used as a covariate in the fish models. Because no other strong correlations were observed, all other covariates were included in some models together. However, because I was interested in the relative influence of the network structure and local habitat variables, independent variables were standardized before fitting models. Variables were standardized using the scale function in R, which subtracts the mean and divides it by the standard deviation so the parameter estimates are all on the same scale and can be compared to assess importance. In addition, because d-link data were strongly right-skewed, these data were log-transformed prior to fitting models. For the benthic macroinvertebrate models, rarified taxa richness were normally distributed, thus to keep the interpretation of model parameters as simple as possible a linear model was fit. However, I used logistic regression for dependent variables reported as percentages, such as percent Chironomidae, percent clingers, percent shredders, and percent flying invertebrates.

Because residual deviances and degrees of freedom suggested the data were over-dispersed, logistic regression models included a scale parameter to correct for the over-dispersed nature of the data. For the fish models, a linear model was fit for species richness, native species richness, and biomass per square meter since these variables were normally distributed. A poisson regression was used for non-native species richness and benthic species richness. A logistic regression model was used for percent generalists, omnivores, and invertivores. Because residual deviances and degrees of freedom suggested the data were overdispersed for the non-native species model and the percent generalists, omnivores, and invertivores, a scale parameter was included in these models.

Model comparisons were made using Akaike's information criterion corrected for small sample size (AICc) and its associated measures (Burnham and Anderson 2002). The best-fit model was identified as the model with the smallest AICc value. The weight of evidence for best fitting model was determined by calculating Akaike weights (w_i), which indicate the probability that the model is the best among the set of candidate models, and the evidence ratio, which determines how well the best model fits compared to the rest. For logistic regressions I calculated Pseudo R^2 value as the null deviance minus residual deviance divided by the null deviance. Model parameter estimates and 95% confidence intervals were calculated using parameter profiles and the confint function in R (Venables and Ripley 2002). The R code for the statistical analysis is included in Appendix B.

3.4 RESULTS

3.4.1 Effect of Isolation from Roads and Impoundments on Benthic

Macroinvertebrate Community Structure

Relationship between Independent Variables

There was a significant relationship between the occurrence of roads and the occurrence of impoundments between sample sites and the downstream confluence ($\chi^2 = 75.29$; $df = 2$; $P < 0.001$). However, this dependency was not complete. When there were no impoundments between the sample site and the downstream confluence, 53% of the time there was one or more road crossings. In contrast, when there was one or more impoundments between the sample site and the downstream confluence, there were no roads only 13% of the time. Because the dependence between road occurrence and pond occurrence was not complete I included both in models.

Isolation Model Results

The base models for macroinvertebrate community characteristics are reported on in Chapter 2. Modelling of benthic macroinvertebrate community characteristics after incorporating potential isolation effects resulted in from 1 to 2 models falling within 2 AICc units of the top model, depending on the characteristic modelled. Isolation models accounted for between 0% and 5% more variation when compared to base models including only local habitat and natural network effects (Tables 2.4 and 3.5). When models including the effects of road crossings and ponds between the sample site and downstream confluence were compared to models with only local habitat and natural network structure, models with only local habitat and natural network structure provided

the best fit for percent Chironomidae and percent shredders (Table 3.5). For percent shredders no model was within 2 AICc units of the top model that included only local habitat and natural network structure effects.

Table 3.5. Summary of best fit models and model statistics for benthic macroinvertebrate community variables analyzed at 347 sampling sites in the Piedmont of Maryland.

Dependent variable	Best-fit Model	K	R^2 or Pseudo- R^2	w_i	ΔAIC
NTAXA_RAR	ROADS_DS + IMP_DS	12	0.16	0.50	10.02
PCHIRON	xy ~ 1	6	0.05	0.38	
PCLING	ROADS_DS + IMP_DS + IMP_DS:ROADS_DS	9	0.12	0.62	600.65
PSHRED	xy ~ 1	5	0.04	0.50	
PFLYGIN	ROADS_DS + IMP_DS	11	0.22	0.75	382.18

Table 3.6. Importance of independent isolation variables included in models of macroinvertebrate community structure as estimated by percentage of models within two AICc units of the top model that contained the isolation variable of interest. The base model included different combinations of local-scale and natural network structure variables (see Table 2.5).

Independent Variable	DEPENDENT VARIABLE	
	NTAXA_RAR	PCHIRON
ROADS_DSone	1	0.33
ROADS_DSsome	1	0.33
IMP_DSyes	1	0.18
IMP_DSyes:ROADS_DSone	0.49	
IMP_DSyes:ROADS_DSsome	0.49	

For rarified taxa richness, percent clingers, and percent flying insects, increasing number of roads had a negative effect, but for the percent clinger the effects of roads depended on the presence or absence of ponds (Table 3.7). The presence of one downstream road was negatively associated with rarified taxa richness and percent flying insects. However, the effects of roads decreased with increasing number of roads for rarified taxa richness (Figure 3.3), but increased for percent flying insects (Figure 3.4). For rarified taxa richness the model including the interaction term between presence and absence of roads and ponds was within 2 AICc units of the best model, but the 95% confidence intervals for the parameter estimates involved in the interaction broadly overlapped zero, so I do not discuss that model here. The effect of downstream roads on percent clingers was dependent on the presence of downstream impoundments. In first order streams with no downstream impoundments, percent clingers decreased as the number of roads increased. This decrease was stronger when more than one road was present. However, when impoundments were present, percent clingers only slightly decreased with an increasing number of roads (Figure 3.5). Based on the absolute magnitude of parameter estimates, the presence of one or more downstream road was the most important variable explaining rarified taxa richness and percent clingers.

The presence of downstream impoundments was positively associated with rarified taxa richness and percent flying insects. This variable was the second most important variable explaining rarified taxa richness and the third most important variable explaining percent flying insects.

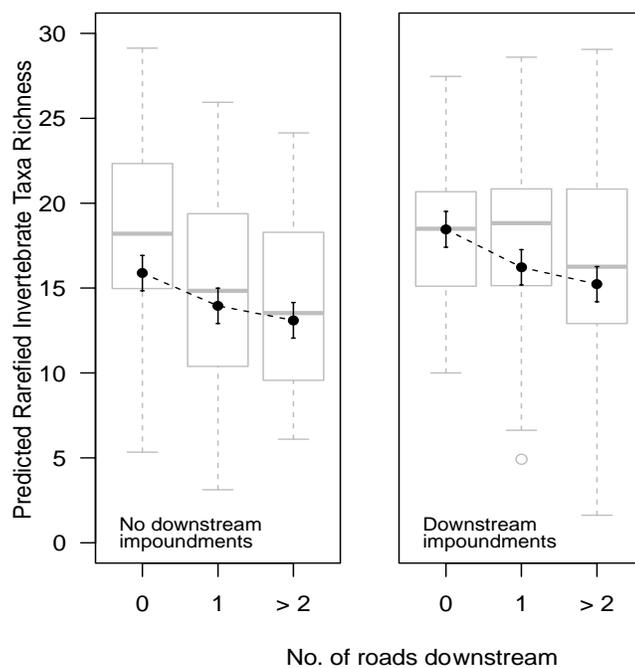


Figure 3.3. Relationship between the presence or absence of roads and ponds between sampling sites and downstream confluences with other streams and rarefied macroinvertebrate taxa richness in first-order, Piedmont streams of Maryland. Predicted means and standard error bars from the isolation model are in black and box-and-whisker plots of raw data distributions are in grey in the background for sites with no downstream ponds (left) and sites with downstream ponds (right).

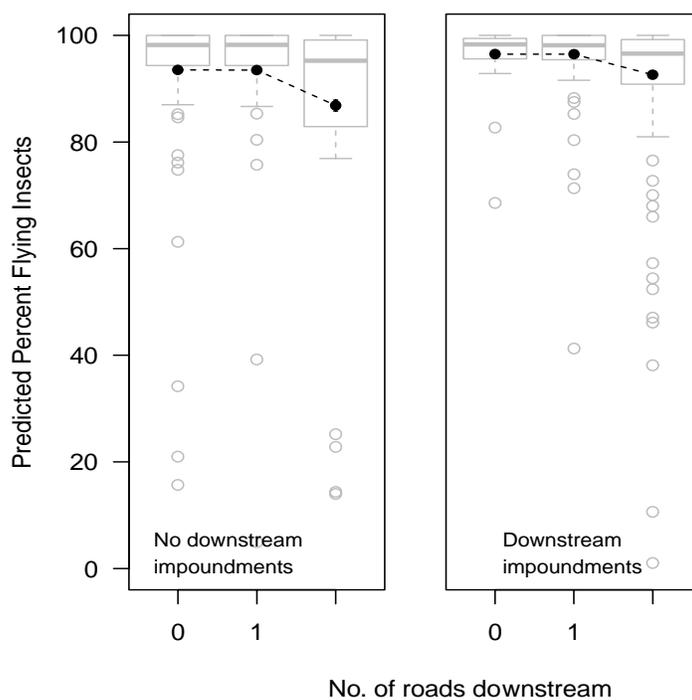


Figure 3.4. Relationship between the presence or absence of roads and ponds between sampling sites and downstream confluences with other streams and percent flying insects in first-order, Piedmont streams of Maryland. Predicted means and standard error bars from the isolation model are in black and box-and-whisker plots of raw data distributions are in grey in the background for sites with no downstream ponds (left) and sites with downstream ponds (right).

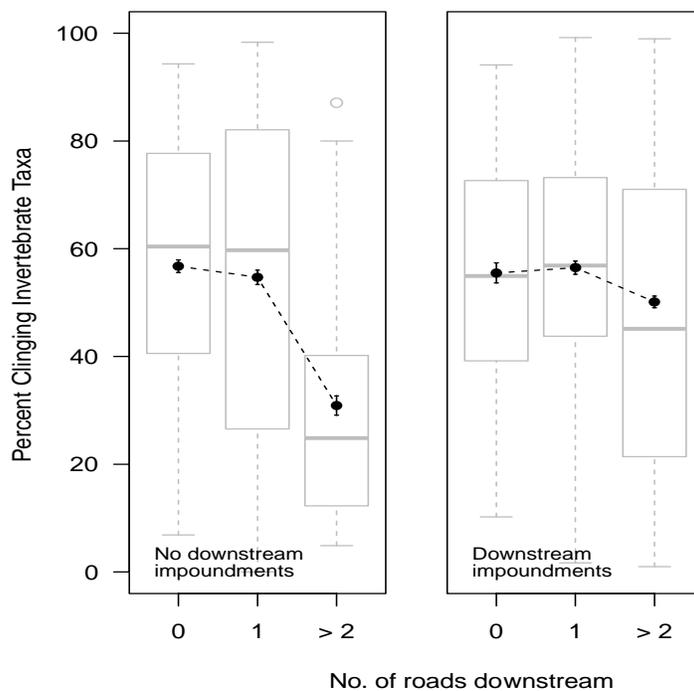


Figure 3.5. Illustration of interactions between isolation (measured as number of roads downstream and the presence of downstream impoundments) in a model of percent clingers for benthic macroinvertebrates in first-order, Piedmont streams of Maryland. Predicted means and standard error bars from the isolation model are in black and box-and-whisker plots of raw data distributions are in grey in the background for sites with no downstream ponds (left) and sites with downstream ponds (right).

Table 3.7. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing invertebrate assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of isolation (number of roads and presence of impoundments), in-stream habitat quality (epibenthic substrata, stream gradient, and stream size) and network structure (distance to confluence and D-link).

INDEPENDENT VARIABLE	DEPENDENT VARIABLE				
	NTAXA_RAR	PCHIRON	PCLING	PSHRED	PFLYING
Intercept	2.77 (2.69 to 2.84)	-0.32 (-0.34 to -0.30)	0.27 (0.22 to 0.32)	-1.58 (-1.61 to -1.56)	2.67 (2.59 to 2.76)
ST_GRAD	0.10 (0.06 to 0.14)			0.05 (0.03 to 0.08)	
EPI_SUB	0.10 (0.06 to 0.14)		0.26 (0.24 to 0.28)	0.07 (0.04 to 0.10)	0.59 (0.55 to 0.63)
AREA	-0.06 (-0.11 to 0)	0.11 (0.09 to 0.13)			0.41 (0.35 to 0.47)
DIST_CON		-0.20 (-0.22 to -0.18)	-0.07 (-0.10 to -0.05)		
DLINK	-0.05 (-0.09 to -0.01)	0.14 (0.12 to 0.16)			-0.18 (-0.22 to -0.14)
EPI_SUB:ST_GRAD				0.17 (0.14 to 0.20)	
ST_GRAD:AREA	-0.07 (-0.13 to -0.01)				
EPI_SUB:DLINK					-1.58 (-1.61 to -1.56)
EPI_SUB:AREA	0.04 (0 to 0.08)				0.28 (0.23 to 0.34)
AREA:DLINK	0.06 (0.01 to 0.11)				0.22 (0.16 to 0.28)
ROADS_DSone	-0.13 (-0.23 to -0.03)		-0.08 (-0.15 to -0.02)		-0.01 (-0.12 to 0.10)
ROADS_DSsome	-0.19 (-0.30 to -0.09)		-1.08 (-1.17 to -0.98)		-0.79 (-0.89 to -0.68)
IMP_DSyes	0.15 (0.06 to 0.24)		-0.05 (-0.14 to 0.04)		0.64 (0.55 to 0.73)
ROADS_DSone:IMP_DSyes			0.12 (0.01 to 0.23)		
ROADS_DSsome:IMP_DSyes			0.86 (0.73 to 0.99)		

3.4.2 Effect of Sources from Impoundments on Benthic Macroinvertebrate

Community Structure

Source Model Results

Modelling of benthic macroinvertebrate community characteristics incorporating potential source effects resulted in from 3 to 13 models falling within 2 AICc units of the top model, depending on the characteristic modelled (Table 3.8). Although the sum of weights ($\sum w_i | \Delta AICc < 2$) for models within 2 AICc units of the top model and the weight of the top model ranged 0.50 to 0.66 and 0.14 to 0.24, respectively, I focus on the top models here as they capture the more important relationships. When the importance of independent variable is measured by the number of models in which the variable appeared out of those within 2 AICc units of the top model, variables not included in the top model appeared in 69% or less of the models, while variables that appeared in the top model appeared in 76% to 100% of the models (Table 3.9). Moreover, the majority of the 95% confidence intervals for parameter estimates for the isolation variable in the top models did not contain zero (Table 3.10). Source models added 0% to 3% variation when compared to base models (Tables 2.4 and 3.8). The change in AICc values between the isolation models and the base models ranged from 0 to 214.12 units (Table 3.8).

Table 3.8. Summary of best fit models and model statistics for benthic macroinvertebrate community variables analyzed at 347 sampling sites in the Piedmont of Maryland.

Dependent variable	Best-fit Model	K	R ² or Pseudo-R ²	w _i	# Models Within 2 AICc	Sum of w _i	ΔAIC
NTAXA_RAR	DIST_IMP_US + DIST_IMP_DS	11	0.15	0.14	13	0.52	6.44
PCHIRON	xy ~ 1	5	0.05	0.20	4	0.54	0.00
PCLING	DIST_IMP_US	5	0.09	0.24	3	0.50	170.80
PSHRED	NUM_IMP_US + DIST_IMP_US + DIST_IMP_DS	8	0.07	0.16	7	0.66	214.12
PFLYING	NUM_IMP_US	9	0.19	0.19	5	0.61	152.11

Table 3.9. Importance of independent isolation variables included in models of benthic invertebrate community structure as estimated by percentage of models within two AICc units of the top model that contained the isolation variable of interest. The base model included different combinations of local-scale and natural network structure variables (see Table 2.5).

Independent Variable	Dependent Variables				
	NTAXA_RAR	PCHIRON	PCLING	PSHRED	PFLYING
DIST_IMP_US	0.76	0.60	0.91	0.76	0.29
DIST_IMP_DS	1	0.39	0.14	0.96	0.51
NUM_IMP_US	0.69	0.46	0.39	0.84	1
DIST_IMP_DS: NUM_IMP_US	0.10	0.05		0.25	0.14
DIST_IMP_US: NUM_IMP_US		0.21	0.18	0.23	
DIST_IMP_DS: DIST_IMP_US	0.10	0.02		0.13	

Parameter Results for Isolation Variables

Among the three source variables, (i.e., number of upstream impoundments, distance to nearest upstream impoundment, and distance to nearest downstream

impoundment), the distance to the nearest upstream impoundment was the most common variable observed in the top models (Table 3.10). However, unlike isolation variables, source variables were not as important as local habitat and natural network structure variables. In no cases were interactions between source variables included in the top models. The distance to nearest upstream impoundment was negatively associated with three benthic macroinvertebrate community variables, including rarified taxa richness, percent clingers, and percent shredders. Distance to nearest upstream impoundment was the most important variable explaining percent clingers. The other source variables, distance to nearest downstream impoundment and number of upstream impoundments, were associated with two benthic macroinvertebrate community variables. The distance to nearest downstream impoundment was negatively associated with rarified taxa richness. The number of upstream impoundments was negatively associated with percent shredders and positively associated with percent flying insects. Distance to nearest downstream impoundment was the second most important variable explaining percent shredders and percent flying insects.

Table 3.10. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing invertebrate assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of sources (number of upstream impoundments, distance to upstream impoundment, distance to downstream impoundment), in-stream habitat quality (epibenthic substrata, stream gradient, and stream size) and network structure (distance to confluence and D-link).

INDEPENDENT VARIABLE	DEPENDENT VARIABLE				
	NTAXA_RAR	PCHIRON	PCLING	PSHRED	PFLYING
Intercept	2.73 (2.69 to 2.77)	-0.32 (-0.34 to -0.3)	0.1 (0.08 to 0.12)	-1.6 (-1.63 to -1.57)	2.72 (2.67 to 2.77)
ST_GRAD	-0.09 (-0.14 to -0.05)			0.03 (0 to 0.06)	
EPI_SUB	0.11 (0.07 to 0.15)		0.08 (0.05 to 0.11)	0.08 (0.05 to 0.11)	0.64 (0.6 to 0.68)
AREA	-0.08 (-0.14 to -0.03)	0.11 (0.09 to 0.13)			0.11 (0.04 to 0.19)
DIST_CON		0.14 (0.12 to 0.16)	-0.11 (-0.13 to -0.08)		
DLINK	-0.04 (-0.07 to 0)	-0.2 (-0.22 to -0.18)			-0.20 (-0.24 to -0.16)
DIST_IMP_DS	-0.05 (-0.09 to -0.01)			0.15 (0.12 to 0.17)	
DIST_IMP_US	-0.04 (-0.08 to <0.01)		-0.14 (-0.16 to -0.12)	-0.12 (-0.15 to -0.09)	
NUM_IMP_US				-0.16 (-0.2 to -0.12)	0.49 (0.41 to 0.57)
EPI_SUB:ST_GRAD				0.17 (0.14 to 0.2)	
ST_GRAD:AREA	-0.08 (-0.14 to -0.02)				
EPI_SUB:DLINK					-0.16 (-0.2 to -0.13)
EPI_SUB:AREA	0.05 (0 to 0.09)				-0.16 (-0.2 to -0.13)
AREA:DLINK	0.06 (0.01 to 0.11)				0.21 (0.14 to 0.27)

3.4.3 Effect of Network Variables and Habitat Covariates on Fish Community

Structure

Relationship between Independent Variables

D-link, the network structure variable used as a measure of adjacent habitat characteristics, ranged from 2 to 20317 and was highly skewed to the right ($\mu = 347.4$; $SD = 2316.6$). The distance to the nearest confluence, which was used as a measure of isolation of the site from the downstream confluence, ranged from 0 m to 9096 m ($\mu = 1555.0$ m; $SD = 1350.6$ m). Drainage area, one of the covariates used to represent local habitat conditions, ranged from 8.5 ha to 1704.5 ha ($\mu = 238.3$ ha; $SD = 228.7$ ha). The other two local habitat covariates, stream gradient and instream habitat score, ranged from <0.1 m to 10 m ($\mu = 1.5$ m; $SD = 1.1$ m) and 1 to 19 ($\mu = 12.0$; $SD = 3.5$), respectively.

Table 3.11. Correlation matrix for network and habitat variables included in models of fish community characteristics. Pearson correlation coefficients are in the top half of the matrix and their respective p -values are in the lower half of the matrix.

Dependent Variable	Independent Variable					
	AREA	ST_GRAD	EPI_SUB	INSTRHAB	DIST_CON	DLINK
AREA		-0.33	0.19	0.27	-0.15	-0.02
ST_GRAD	<0.001		0.1	0.01	-0.03	0.05
EPI_SUB	<0.001	0.0629		0.79	-0.06	0.06
INSTRHAB	<0.001	0.8047	<0.001		-0.11	0.07
DIST_CON	0.006	0.6348	0.2327	0.0466		0.03
DLINK	0.777	0.3907	0.2567	0.1701	0.5562	

The only strong correlation among independent variables was between epifaunal substrate score and instream habitat score (Table 3.11). Because these variables were highly correlated and because the instream habitat score is a measure of fish habitat

quality, epifaunal substrate score was removed from the analysis. There were no other strong correlations among any of the independent variables ($|r| < 0.34$ in all cases) and no relationship between the network measures of d-link and distance to the confluence (Table 3.11). There were weak correlations among the local-scale variables that appeared to be driven by stream size. As watershed area (and stream size) increased gradient decreased and instream habitat scores increased. Although these relationships were significant (Table 3.11), because they were weak I included all local-scale variables in the full models of fish response to local and network structure variables.

Model Results

Modelling of fish community characteristics using local habitat and network structure variables resulted in from 9 to 32 models falling within 2 AICc units of the top model, depending on the characteristic modelled (Table 3.12). Although the sum of weights ($\sum w_i | \Delta AICc < 2$) for models within 2 AICc units of the top model and the weight of the top model ranged 0.26 to 0.49 and 0.03 to 0.06, respectively, I focus on the top models here as they capture the more important relationships. When the importance of independent variable is measured by the number of models in which the variable appeared out of those within 2 AICc units of the top model, variables not included in the top model appeared in 69% or less of the models, while variables that appeared in the top model appeared in 45% to 100% of the models (Table 3.13). Moreover, the majority of the 95% confidence intervals for parameter estimates for top models did not contain zero (Table 3.14), while all estimates for parameters not included in the top models but appearing in model-averaged models did include zero (Appendix A).

Table 3.12. Summary of top models and model statistics for fish community variables analyzed at stream sampling sites in the Piedmont of Maryland.

Dependent variable	Best-fit Model	K	R ² or Pseudo -R ²	w _i	# Models Within 2 AICc	Sum of w _i	Model Type
NTAXA	INSTRHAB + ST_GRAD + AREA + DIST_CON + DLINK + AREA:INSTRHAB + DLINK:INSTRHAB + DLINK:DIST_CON	10	0.51	0.06	9	0.27	linear
NTAXA_NAT	INSTRHAB + ST_GRAD + AREA + DIST_CON + DLINK + AREA:INSTRHAB + AREA:ST_GRAD + DLINK:INSTRHAB	10	0.49	0.04	17	0.35	linear
NTAXA_NONAT	INSTRHAB + ST_GRAD + AREA + DIST_CON + DLINK + AREA:INSTRHAB + DIST_CON:INSTRHAB + DLINK:DIST_CON	10	0.21	0.05	11	0.26	quasipoisson
BIOM_MSQ	INSTRHAB + ST_GRAD + AREA + DIST_CON + DLINK + AREA:INSTRHAB + DIST_CON:AREA + ST_GRAD:DLINK + AREA:DLINK	11	0.21	0.05	13	0.30	linear
NUMBENTSP	ST_GRAD + INSTRHAB + AREA + DIST_CON	6	0.20	0.03	32	0.49	poisson
PGEOMIV	INSTRHAB + ST_GRAD + AREA + DIST_CON + DLINK + DIST_CON:INSTRHAB + AREA:DLINK + DLINK:DIST_CON	10	0.16	0.03	25	0.42	quasibinomia 1

Table 3.13. Importance of independent variables included in models of fish community structure as estimated by percentage of models within two AICc units of the top model that contained the variable of interest.

Independent Variable	DEPENDENT VARIABLE					
	NTAXA	NTAXA_NAT	NTAXA_NONAT	BIOM_MSQ	NUMBENTSP	PGEOMIV
ST_GRAD	1	1	1	1	1	0.91
INSTRHAB	1	1	1	1	1	1
AREA	1	1	1	1	1	0.83
DIST_CON	1	1	1	0.93	1	1
DLINK	1	1	1	1	0.69	1
AREA:INSTRHAB	1	0.74	0.76	1	0.07	0.09
DLINK:INSTRHAB	1	1		0.35	0.45	
DIST_CON:ST_GRAD	0.08	0.04	0.09	0.06	0.02	0.19
AREA:DLINK	0.08	0.04	0.08	1	0.05	0.83
DIST_CON:INSTRHAB	0.08	0.04	1	0.07	0.34	0.45
INSTRHAB:ST_GRAD	0.09	0.24	0.31	0.06	0.09	0.41
DLINK:ST_GRAD	0.11	0.05	0.07	0.87	0.25	0.06
AREA:ST_GRAD	0.12	0.83	0.25	0.06	0.43	
AREA:DIST_CON	0.13	0.16	0.08	0.71	0.05	0.29
DIST_CON:DLINK	0.91	0.40	1	0.45		1

Local-scale Variables

All three local habitat variables (instream habitat score, stream gradient, and drainage area) were observed in the top models explaining fish community structure (Table 3.14). Drainage area was the most important variable explaining fish taxa richness and native fish taxa richness. Drainage area was positively associated with the number of benthic fish species. However, for the other dependent variables, the effects of drainage area depended on other local and network variables. For example, for taxa richness and native taxa richness, the effects of drainage area depended on instream habitat score. As instream habitat score increased, the effects of drainage area became stronger (Figures 3.4 and 3.5; top panel). For native taxa richness, the effects of drainage area also depended on stream gradient such that among small streams lower gradient streams had higher richness, but among larger streams higher gradient streams had higher richness (Figure 3.5; bottom panel). In the case of non-native species richness (Figure 3.6; top panel) and biomass per square meter (Figure 3.7 top panel), as instream habitat score decreased the effects of drainage area shifted from positive to negative. For biomass per square meter, there was also an interaction between drainage area and distance to nearest confluence. In this interaction, as distance to nearest confluence increased, the effects of drainage area shifted from positive to negative (Figure 3.7; middle panel). A similar shift occurred for the d-link and drainage area interaction for biomass per square meter (Figure 3.8) and percent generalists, omnivores, and invertivores (Figure 3.9; top panel).

Instream habitat score was the most important variable explaining fish biomass per square meter and percent generalists, omnivores, and invertivores, and was the

second-most important variable explaining fish taxa richness and native fish taxa richness. Instream habitat score was positively associated with the number of benthic fish species and involved in three interactions. For taxa richness and native taxa richness, the effect of instream habitat score was positive in all drainage area sizes, but stronger as instream habitat scores increased (Figures 3.4 and 3.5; top panel). There was also an interaction between instream habitat score and d-link for taxa richness (Figure 3.4; middle panel) and native taxa richness (Figure 3.5; middle panel). In this case, the importance of d-link increased with habitat degradation (as indicated by decreasing instream habitat scores). In the case of non-native species richness (Figure 3.6; top panel) and biomass per square meter (Figure 3.7; top panel), the effects of drainage area depended on stream degradation, such that non-native species richness and biomass increased with drainage area in streams with moderate to good habitat conditions, but decreased in degraded streams with low instream habitat scores. There was also an interaction between instream habitat score and distance to nearest confluence for non-native taxa richness and percent generalists, omnivores, and invertivores. In the case of non-native taxa richness, as distance to nearest confluence increased the effects of instream habitat score shifted from slightly positive to negative (Figure 3.6; middle panel). For percent generalists, omnivores, and invertivores, the effects of instream habitat score were strongest when distance to confluence was medium to large (Figure 3.9; top panel).

Stream gradient was the most important variable explaining non-native fish taxa richness, the second-most important variable explaining biomass per square meter and number of benthic species, and the third-most important variable explaining fish taxa

richness. It was negatively associated with taxa richness, non-native taxa richness, number of benthic species, and percent generalists, omnivores, and invertivores. However, for the number of native taxa and biomass per square meter, the effects of stream gradient depended on drainage area and d-link, respectively (Table 3.14). For native taxa richness, the effects of gradient were positive in all drainage area sizes, but stronger as gradient increased (Figure 3.5; bottom panel). For biomass per square meter, when gradient was high, biomass decreased as d-link increased (Figure 3.7; bottom panel). A similar, but weaker relationship was observed when gradient was average. However, when gradient was low, biomass increased as d-link increased.

Table 3.14. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing fish assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of in-stream habitat quality (instream habitat, stream gradient, and stream size) and network structure (distance to confluence and D-link).

Independent Variable	DEPENDENT VARIABLE					
	NTAXA	NTAXA_NAT	NTAXA_NONAT	BIOM_MSQ	NUMBENTSP	PGEOMIV
Intercept	5.57 (5.25 to 5.90)	5.61 (5.28 to 5.94)	-0.67 (-0.85 to -0.50)	7.06 (6.41 to 7.72)	-0.22 (-0.36 to -0.10)	1.92 (1.89 to 1.95)
ST_GRAD	-0.88 (-1.21 to -0.55)	-0.42 (-0.79 to -0.05)	-0.44 (-0.68 to -0.23)	-1.16 (-1.89 to -0.43)	-0.25 (-0.42 to -0.10)	-0.24 (-0.27 to -0.21)
INSTRHAB	1.14 (0.81 to 1.47)	0.62 (0.32 to 0.93)	0.16 (<0.01 to 0.33)	1.64 (0.97 to 2.32)	0.24 (0.11 to 0.37)	-0.66 (-0.68 to -0.63)
AREA	1.70 (1.33 to 2.07)	1.85 (1.39 to 2.30)	0.08 (-0.07 to 0.22)	0.65 (-0.10 to 1.40)	0.16 (0.06 to 0.25)	0.04 (0.02 to 0.05)
DIST_CON	-0.62 (-0.94 to -0.31)	-0.41 (-0.70 to -0.13)	-0.44 (-0.65 to -0.25)	-0.47 (-1.11 to 0.17)	-0.28 (-0.44 to -0.14)	0.45 (0.41 to 0.48)
DLINK	0.42 (0.11 to 0.74)	0.39 (0.10 to 0.67)	-0.01 (-0.18 to 0.15)	-0.13 (-0.77 to 0.51)		0.18 (0.16 to 0.20)
INSTRHAB:AREA	0.41 (0.04 to 0.78)	0.29 (-0.06 to 0.63)	0.13 (<0.01 to 0.27)	1.08 (0.30 to 1.85)		
INSTRHAB:DLINK	-0.41 (-0.73 to -0.09)	-0.54 (-0.83 to -0.25)				
INSTRHAB:DIST_CON			0.26 (0.07 to 0.47)			-0.25 (-0.29 to -0.22)
DIST_CON:AREA				0.57 (0.01 to 1.13)		
DIST_CON:DLINK	-0.31 (-0.62 to <0.01)		-0.30 (-0.51 to -0.11)			0.24 (0.21 to 0.27)
ST_GRAD:AREA		0.41 (-0.04 to 0.86)				
ST_GRAD:DLINK				-0.68 (-1.31 to -0.06)		
AREA:DLINK				-1.08 (-1.90 to -0.26)		-0.24 (-0.26 to -0.21)

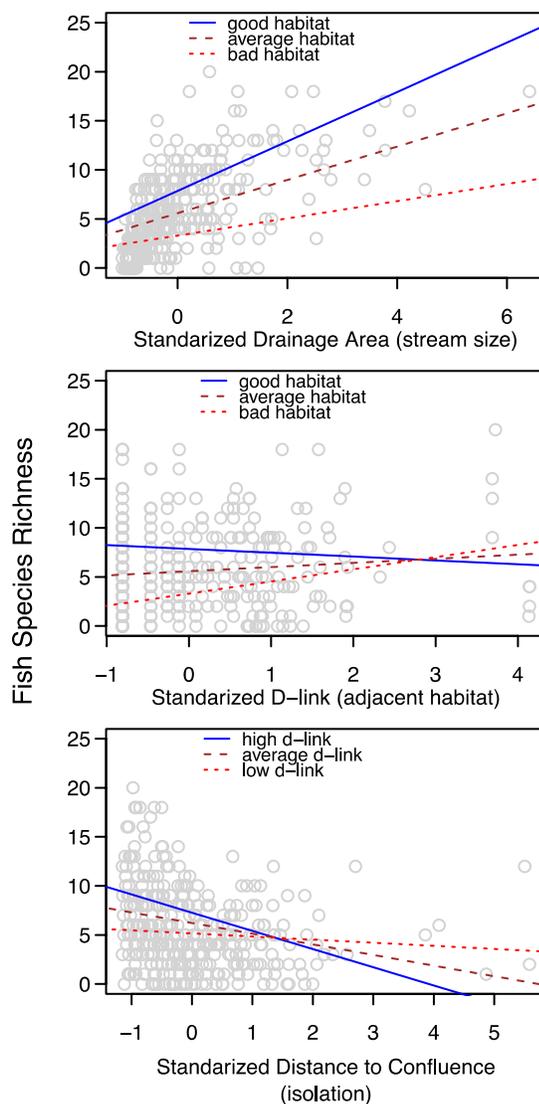


Figure 3.4. Illustration of interactions among local habitat quality (measured as instream habitat score), stream size (measured as drainage area), downstream habitat (measured as d-link), and isolation (measured as distance to nearest confluence) in a model of fish taxa richness in first-order, Piedmont streams of Maryland.

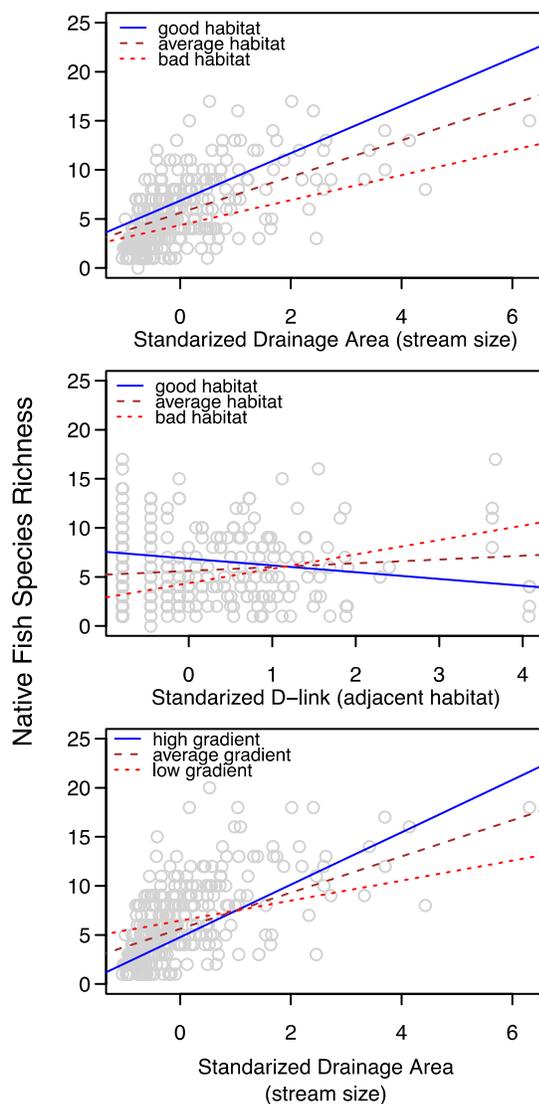


Figure 3.5. Illustration of interactions among local habitat quality (measured as instream habitat score), stream size (measured as drainage area), downstream habitat (measured as d-link), and isolation (measured as distance to nearest confluence) in a model of native fish taxa richness in first-order, Piedmont streams of Maryland.

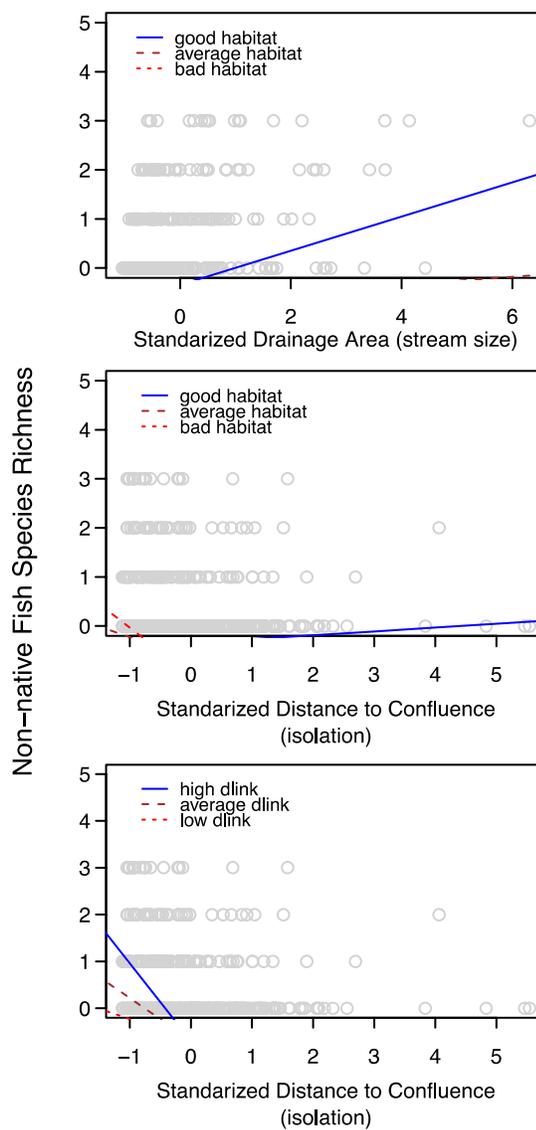


Figure 3.6. Illustration of interactions among local habitat quality (measured as instream habitat score), stream size (measured as drainage area), downstream habitat (measured as d-link), and isolation (measured as distance to nearest confluence) in a model of non-native fish taxa richness in first-order, Piedmont streams of Maryland.

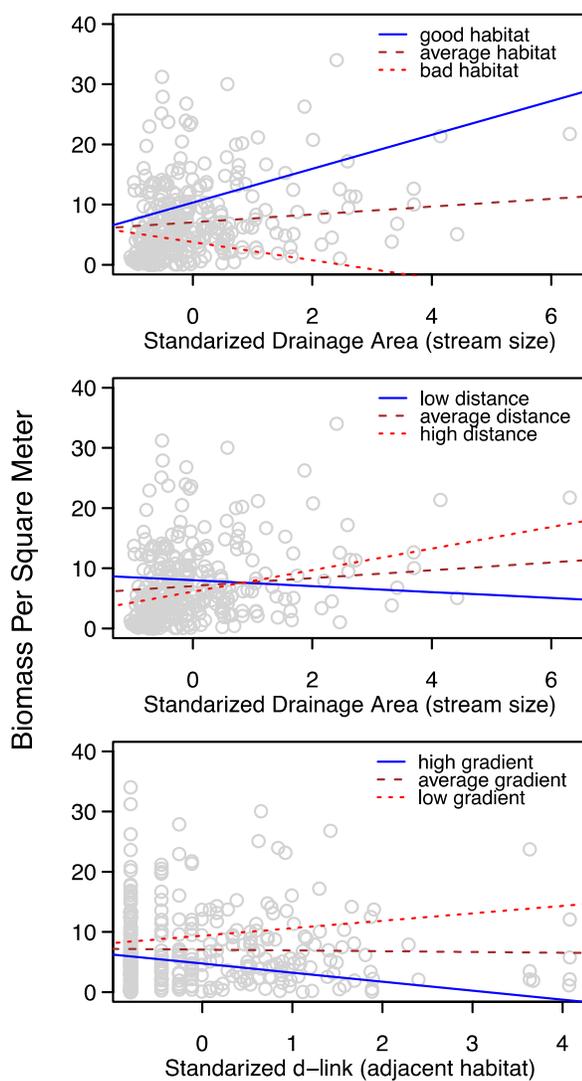


Figure 3.7. Illustration of interactions among local habitat quality (measured as gradient and instream habitat score), stream size (measured as drainage area), downstream habitat (measured as d-link), and isolation (measured as distance to nearest confluence) in a model of fish biomass per square meter in first-order, Piedmont streams of Maryland.

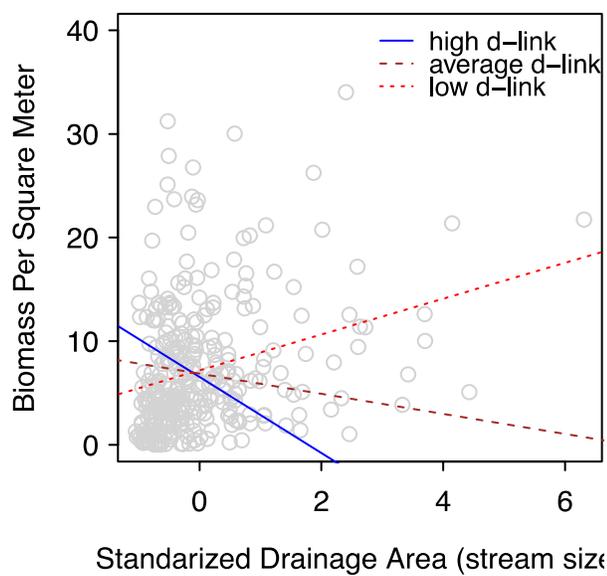


Figure 3.8. Illustration of interactions between stream size (measured drainage area) and downstream habitat (measured as d-link) in a model of biomass per square meter in first-order, Piedmont streams of Maryland.

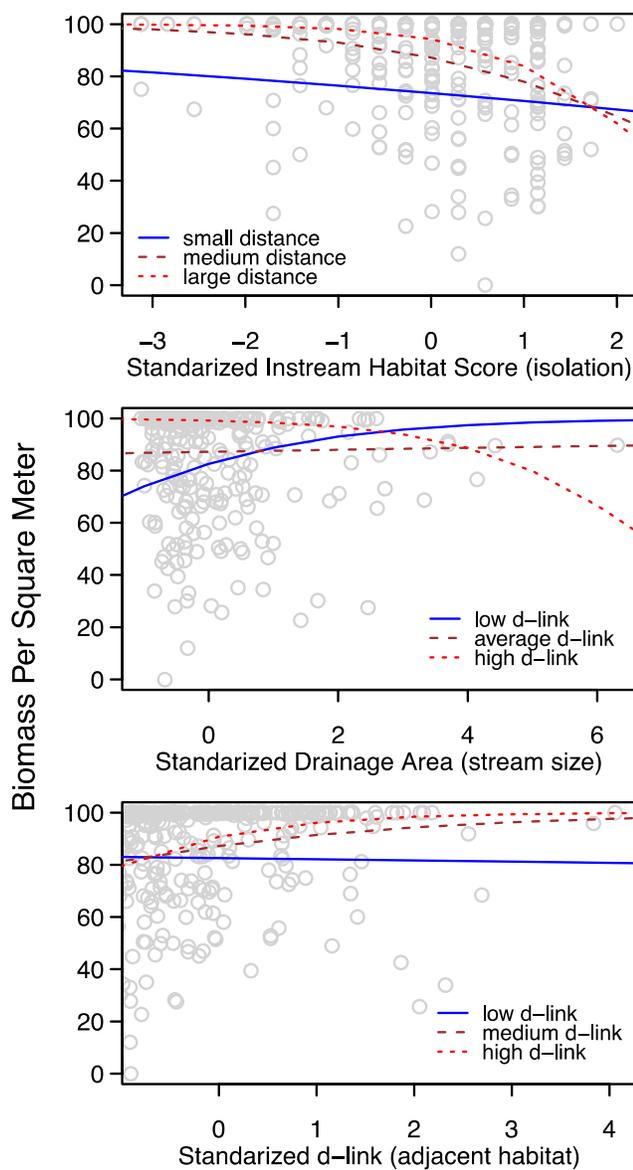


Figure 3.9. Illustration of interactions among local habitat quality (measured as instream habitat score), stream size (measured as drainage area), downstream habitat (measured as d-link), and isolation (measured as distance to nearest confluence) in a model of fish generalists, omnivores, and invertivores in first-order, Piedmont streams of Maryland.

Network Structure Variables

One or both of the network structure variables of d-link and distance to the confluence were included in models of fish community structure. The effects of network structure variables did depend on local habitat conditions in some cases and there were interaction terms between d-link and distance to confluence included in the top models of fish community structure (Table 3.14). Between the two network structure variables, the most common variable observed in the top models was distance to nearest confluence, which was observed in all 6 models. Distance to nearest confluence was the most important variable explaining non-native taxa richness and the number of benthic species and the second-most important variable explaining percent generalists, omnivores and invertivores. Distance to nearest confluence was negatively associated with native taxa richness and the number of benthic species. However, for non-native taxa richness and percent generalists, omnivores, and invertivores, the effects of distance to nearest confluence depended on instream habitat quality (Table 3.14). In the case of non-native taxa richness, as instream habitat quality increased, the effect of distance to nearest confluence went from negative to positive (Figure 3.6; middle panel). For percent generalists, omnivores, and invertivores, the effects of instream habitat score were strongest when distance to confluence was medium to large (Figure 3.9; top panel). For biomass per square meter, the effect of distance to nearest confluence depended on drainage area, where the effects of drainage area shifted from positive to negative as distance to nearest confluence increased, (Figure 3.7; middle panel). Another interaction occurred between distance to nearest confluence and d-link for taxa richness and non-

native taxa richness. As d-link values increased, the effect of distance to nearest confluence became stronger.

D-link was observed in every model, except the model for the number of benthic species. There was an interaction between instream habitat score and d-link for taxa richness (Figure 3.4; middle panel) and native taxa richness (Figure 3.5; middle panel). In this interaction, as d-link increased the effects of instream habitat score shifted from negative to positive. There was also an interaction between distance to nearest confluence and d-link for taxa richness and non-native taxa richness, where as d-link values increased, the effects of distance to nearest confluence became stronger. The relationship between biomass per square meter and d-link was dependent on stream gradient. As gradient increased, the effects of d-link on biomass shifted from positive to negative. A similar shift occurred for the d-link/drainage area interaction for biomass per square meter (Figure 3.8) and percent generalists, omnivores, and invertivores (Figure 3.9; top panel).

3.4.4 Effect of Isolation from Roads and Impoundments on Fish Community Structure

Isolation Model Results

Modeling of fish community characteristics after incorporating potential isolation effects resulted in from 1 to 4 models falling within 2 AICc units of the top model, depending on the characteristic modelled (Table 3.15). Among models falling within 2 AICc units of the top model, all included one or both isolation variables with the exception of the model for percent omnivores, insectivores and grazers, where no model

was within 2 AICc units of the null model including only local habitat and natural network structure variables. For biomass and number of benthic species, one (biomass) or both (benthic species) isolation variables were included in the top model, but not in all models within 2 AICc units of the top model included these isolation variables (Table 3.16). No models within 2 AICc units of the top isolation model included interactions among isolation variables.

Table 3.15. Summary of top models and model statistics for fish community variables analyzed at stream sampling sites in the Piedmont of Maryland.

Dependent variable	Best-fit Model	K	R ² or Pseudo R ²	w _i	# Models Within 2 AICc	Sum of w _i	ΔAIC
NTAXA	ROADS_DS + IMP_DS	13	0.54	0.83	1	0.83	15.75
NTAXA_NAT	ROADS_DS + IMP_DS	13	0.51	0.73	1	0.73	7.53
NTAXA_NONAT	IMP_DS	11	0.23	0.74	1	0.74	4.27
BIOM_MSQ	IMP_DS	11	0.21	0.53	2	0.82	2.99
NUMBENTSP	ROADS_DS + IMP_DS	9	0.22	0.36	4	0.95	1.12
PGEOMIV	xy ~ 1	10	0.16	0.61	1	0.61	0.00

Table 3.16. Importance of independent variables included in models of fish community structure as estimated by percentage of models within two AICc units of the top model that contained the variable of interest.

Independent Variable	Dependent Variable	
	BIOM_MSQ	NUMBENTSP
IMP_DSyes	0.64	0.56
ROADS_DSone		0.64
ROADS_DSsome		0.64
ST_GRAD	1	1
INSTRHAB	1	1
AREA	1	1
DIST_CON	1	1
AREA:INSTRHAB	1	
AREA:DIST_CON	1	
DLINK:ST_GRAD	1	
AREA:DLINK	1	

Parameter Results for Isolation Variables

Of the two isolation variables (number of downstream roads and the presence of downstream impoundments), the presence of downstream impoundments was the most common variable observed among the top models describing fish community structure. The presence of downstream impoundments was positively associated with five fish community structure variables, including taxa richness, native taxa richness, non-native taxa richness, biomass per square meter, and number of benthic species (Table 3.17). Presence of downstream impoundments was the second-most important variable explaining taxa richness, biomass per square meter, and the number of benthic species, and the third-most important variable explaining native taxa richness and non-native taxa richness. The presence of one downstream road was negatively associated with fish taxa richness, native fish taxa richness, and number of benthic species (Table 3.17). However,

this relationship was stronger when more than one road was present for fish taxa richness, native taxa richness, and number of benthic species (Figure 3.10). The presence of more than one road was the most important variable explaining the number of benthic species, second-most important variable explaining native taxa richness, and the third-most important variable explaining taxa richness.

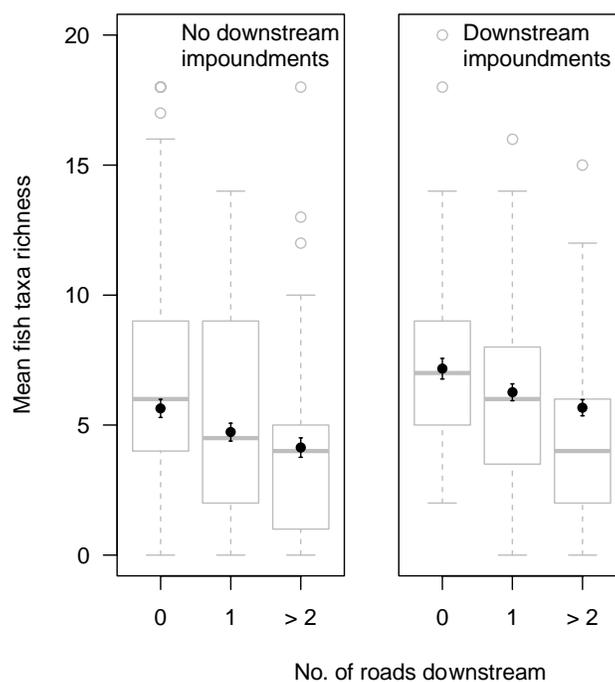


Figure 3.10. Relationship between the presence or absence of roads and ponds between sampling sites and downstream confluences with other streams and fish species richness in first-order, Piedmont streams of Maryland. Predicted means and standard error bars from the isolation model are in black and box-and-whisker plots of raw data distributions are in grey in the background for sites with no downstream ponds (left) and sites with downstream ponds (right).

Table 3.17. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing fish assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of isolation (number of roads and presence of impoundments), in-stream habitat quality (epibenthic substrata, stream gradient, and stream size) and network structure (distance to confluence and D-link).

Independent Variable	DEPENDENT VARIABLE					
	NTAXA	NTAXA_NAT	NTAXA_NONAT	BIOM_MSQ	NUMBENTSP	PGOMIV
Intercept	5.64 (4.95 to 6.32)	5.71 (5.08 to 6.35)	-0.94 (-1.22 to -0.67)	6.33 (5.28 to 7.40)	-0.15 (-0.42 to 0.12)	1.92 (1.89 to 1.95)
ST_GRAD	-0.83 (-1.16 to -0.51)	-0.37 (-0.73 to <0.01)	-0.45 (-0.69 to -0.23)	-1.21 (-1.93 to -0.48)	-0.24 (-0.41 to -0.08)	-0.24 (-0.27 to -0.21)
INSTRHAB	1.05 (0.72 to 1.37)	0.58 (0.27 to 0.89)	0.18 (0.02 to 0.35)	1.64 (0.97 to 2.31)	0.22 (0.09 to 0.36)	-0.66 (-0.68 to -0.63)
AREA	1.82 (1.45 to 2.18)	1.95 (1.49 to 2.40)	0.11 (-0.04 to 0.25)	0.73 (-0.03 to 1.49)	0.17 (0.08 to 0.27)	0.04 (0.02 to 0.05)
DIST_CON	-0.70 (-1.10 to -0.30)	-0.44 (-0.81 to -0.06)	-0.61 (-0.87 to -0.37)	-0.82 (-1.57 to -0.08)	-0.23 (-0.44 to -0.03)	0.45 (0.41 to 0.48)
DLINK	0.37 (0.06 to 0.68)	0.35 (0.06 to 0.63)	-0.04 (-0.22 to 0.12)			0.18 (0.16 to 0.20)
ROADS_Dsone	-0.91 (-1.70 to -0.12)	-0.72 (-1.43 to -0.01)			-0.16 (-0.44 to 0.11)	
ROADS_Dssome	-1.50 (-2.43 to -0.58)	-1.13 (-1.98 to -0.28)			-0.44 (-0.83 to -0.07)	
IMP_DSyes	1.53 (0.79 to 2.28)	1.05 (0.38 to 1.73)	0.44 (0.10 to 0.78)	1.34 (-0.16 to 2.84)	0.24 (-0.04 to 0.53)	
INSTRHAB:AREA	0.36 (<-0.01 to 0.73)	0.26 (-0.08 to 0.60)	0.13 (-0.01 to 0.27)	1.06 (0.29 to 1.84)		
INSTRHAB:DLINK	-0.37 (-0.68 to -0.06)	-0.52 (-0.81 to -0.23)				
INSTRHAB:DIST_CON			0.28 (0.07 to 0.49)			-0.25 (-0.29 to -0.22)
DIST_CON:AREA				0.57 (0.01 to 1.12)		
DIST_CON:DLINK	-0.25 (-0.55 to 0.06)		-0.29 (-0.51 to -0.09)			0.24 (0.21 to 0.27)
ST_GRAD:AREA		0.44 (<-0.01 to 0.89)				
ST_GRAD:DLINK				-0.66 (-1.28 to -0.05)		
AREA:DLINK				-1.02 (-1.83 to -0.20)		-0.24 (-0.26 to -0.21)

3.4.5 Effect of Sources from Impoundments on Fish Community Structure

Source Model Results

Modeling of fish community characteristics after incorporating potential source effects resulted in from 3 to 6 models falling within 2 AICc units of the top model, depending on the characteristic modelled (Table 3.18). Although the sum of weights ($\sum w_i | \Delta AICc < 2$) for models within 2 AICc units of the top model and the weight of the top model ranged 0.50 to 0.81 and 0.19 to 0.26, respectively, I focus on the top models here as they capture the more important relationships. When the importance of independent variable is measured by the number of models in which the variable appeared out of those within two AICc units of the top model, variables not included in the top model appeared in 52% or less of the models, while source variables that appeared in the top model appeared in 54% to 100% of the models (Table 3.19). Moreover, the majority of the 95% confidence intervals for parameter estimates for top models did not contain zero (Table 3.20), while all estimates for parameters not included in the top models but appearing in model-averaged models did include zero (Appendix A). Source models added from 0% to 6% variation when compared to base models (Table 3.18). The change in AIC values between the isolation models and the base models ranged from 0 to 28.20 units (Table 3.18).

Table 3.18. Summary of top models and model statistics for fish community variables analyzed at stream sampling sites in the Piedmont of Maryland.

Dependent variable	Best-fit Model	K	R^2 or Pseudo R^2	w_i	# Models Within 2 AICc	Sum of w_i	ΔAIC
NTAXA	DIST_IMP_US + DIST_IMP_DS	12	0.56	0.26	3	0.51	28.20
NTAXA_NAT	DIST_IMP_UP + DIST_IMP_DS	12	0.50	0.24	4	0.56	6.07
NTAXA_NO NAT	DIST_IMP_US + DIST_IMP_DS	12	0.27	0.20	5	0.62	19.75
BIOM_MSQ	DIST_IMP_US + DIST_IMP_DS+NUM_IMP_US+NUM_IMP_US:DIST_IMP_US	13	0.23	0.20	4	0.81	5.83
NUMBENTSP	DIST_IMP_US + DIST_IMP_DS	8	0.25	0.19	6	0.64	5.07
PGEOMIV	xy ~ 1	10	0.16	0.26	3	0.50	0.00

Table 3.19. Importance of independent variables included in models of fish community structure as estimated by percentage of models within two AICc units of the top model that contained the variable of interest.

Independent Variable	DEPENDENT VARIABLE					
	NTAXA	NTAXA_NAT	NTAXA_NONAT	BIOM_MSQ	NUMBENTSP	PGEOMIV
DIST_IMP_US	1	0.75	1	1	0.54	0.28
DIST_IMP_DS	1	1	0.85	1	1	0.20
NUM_IMP_US	0.25	0.16	0.52	1	0.39	
AREA	1	1	1	1	1	1
DIST_CON	1	1	1	1	1	1
DLINK	1	1	1			1
INSTRHAB	1	1	1	1	1	1
ST_GRAD	1	1	1	1	1	1
DIST_IMP_DS:NUM_IMP_US			0.32		0.13	
DIST_IMP_US:NUM_IMP_US				1		
DIST_IMP_DS:DIST_IMP_US	0.24	0.16			0.12	
AREA:DIST_CON				1		
AREA:DLINK						1
AREA:INSTRHAB	1	1	1	1		
AREA:ST_GRAD		1				
DIST_CON:DLINK	1		1			1
DIST_CON:INSTRHAB			1			1
DLINK:INSTRHAB	1	1				
DLINK:ST_GRAD				1		

Parameter Results for Source Variables

Among the three source variables, (i.e., number of upstream impoundments, distance to nearest upstream impoundment, and distance to nearest downstream impoundment), the distance to the nearest upstream and distance to nearest downstream impoundments were the most common variables observed in the top models (Table 3.20). The distance to nearest upstream impoundment was negatively associated with taxa richness, native taxa richness, non-native taxa richness, and the number of benthic species. It was the most important variable explaining non-native taxa richness and biomass per square meter. However, the effect of the distance to the nearest upstream impoundment on biomass depended on the number of upstream impoundments (Figure 3.11). The strongest negative effect of distance to nearest upstream impoundment on biomass was when there were a high number of upstream impoundments. This effect was less apparent when there were a moderate number of upstream impoundments and was non-existent when the number of upstream impoundments was low. The distance to nearest downstream impoundment was negatively associated with taxa richness, native taxa richness, non-native taxa richness, biomass per square meter, and the number of benthic species. The number of upstream impoundments was the third-most important variable explaining fish biomass per square meter. However, its effect on biomass depended on the distance to upstream impoundments (Figure 3.11), as discussed above.

Table 3.20. Parameter estimates and 95% confidence intervals (parenthetically) for the best models describing fish assemblage characteristics from first-order streams in the Piedmont of Maryland. Models include the effects of potential sources (distance to upstream impoundment, distance to downstream impoundment, and number of upstream impoundments), in-stream habitat quality (epibenthic substrata, stream gradient, and stream size) and network structure (distance to confluence and D-link).

Independent Variable	DEPENDENT VARIABLE					
	NTAXA	NTAXA_NAT	NTAXA_NONAT	BIOM_MSQ	NUMBENTSP	PGEMOIV
Intercept	5.57 (5.26 to 5.88)	5.58 (5.25 to 5.91)	-0.78 (-0.98 to -0.59)	5.01 (3.32 to 6.70)	-0.24 (-0.38 to -0.11)	1.92 (1.89 to 1.95)
ST_GRAD	-0.80 (-1.13 to -0.48)	-0.43 (-0.80 to -0.06)	-0.43 (-0.67 to -0.20)	-1.22 (-1.94 to -0.49)	-0.24 (-0.41 to -0.08)	-0.24 (-0.27 to -0.21)
INSTRHAB	1.06 (0.74 to 1.38)	0.66 (0.36 to 0.97)	0.15 (-0.01 to 0.31)	1.76 (1.09 to 2.42)	0.24 (0.11 to 0.38)	-0.66 (-0.68 to -0.63)
AREA	1.58 (1.22 to 1.95)	1.74 (1.28 to 2.21)	0.04 (-0.11 to 0.19)	0.12 (-1.06 to 1.30)	0.14 (0.05 to 0.24)	0.04 (0.02 to 0.05)
DIST_CON	-0.51 (-0.82 to -0.21)	-0.35 (-0.63 to -0.06)	-0.38 (-0.59 to -0.19)	-0.32 (-0.96 to 0.33)	-0.25 (-0.41 to -0.11)	0.45 (0.41 to 0.48)
DLINK	0.46 (0.15 to 0.76)	0.41 (0.13 to 0.70)	~ 0 (-0.17 to 0.16)			0.18 (0.16 to 0.20)
DIST_IMP_US	-0.60 (-0.91 to -0.28)	-0.26 (-0.55 to 0.03)	-0.47 (-0.72 to -0.25)	-3.57 (-6.4 to -0.75)	-0.12 (-0.27 to 0.02)	
DIST_IMP_DS	-0.58 (-0.88 to -0.28)	-0.35 (-0.63 to -0.07)	-0.15 (-0.32 to <0.01)	-0.85 (-1.47 to -0.22)	-0.16 (-0.30 to -0.03)	
NUM_IMP_US				-1.62 (-4.03 to 0.79)		
NUM_IMP_US:DIST_IMP_US				-4.8 (-8.56 to -1.03)		
INSTRHAB:AREA	0.39 (0.03 to 0.75)	0.29 (-0.05 to 0.63)	0.14 (0 to 0.28)	1.06 (0.28 to 1.84)		
INSTRHAB:DLINK	-0.30 (-0.61 to 0)	-0.46 (-0.76 to -0.17)				
INSTRHAB:DIST_CON			0.23 (0.04 to 0.43)			-0.25 (-0.29 to -0.22)
DIST_CON:AREA				0.67 (0.11 to 1.24)		
DIST_CON:DLINK	-0.23 (-0.53 to 0.07)		-0.27 (-0.48 to -0.07)			0.24 (0.21 to 0.27)
ST_GRAD:AREA		0.35 (-0.10 to 0.80)				
ST_GRAD:DLINK				-0.43 (-1.04 to 0.18)		
AREA:DLINK						-0.24 (-0.26 to -0.21)

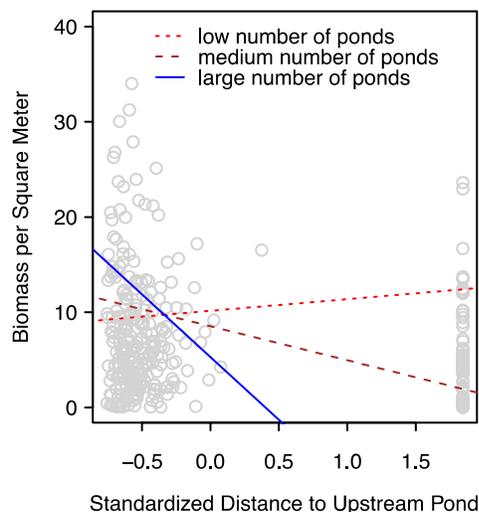


Figure 3.11. Illustration of interactions between the number of upstream impoundments and the distance to the nearest upstream impoundment in a model of fish biomass per square meter in first-order, Piedmont streams of Maryland.

3.5 DISCUSSION

The results of this study suggest that road crossings and impoundments may be degrading benthic macroinvertebrate and fish communities in first-order streams through the disruption of network structure. However, incorporating measures of local habitat, stream size, and stream network structure into models provided some additional information regarding the effect of these elements on fish community structure. Based on my results, several patterns were apparent and are discussed in detail below.

1. Fish community structure was dependent on local habitat conditions and stream network structure. Many of the variables explored were dependent on other variables, which may be due to the influence of higher trophic levels, suggesting top-down effects and habitat complementation.

2. Both benthic macroinvertebrates and fish responded to measures of anthropogenic isolation, including some potential top-down effects. Both assemblages responded negatively to roads, which may suggest an isolation effect of roads, but the effect of impoundments appears to be related to impoundments acting as faunal sources.
3. Measures of potential faunal sources suggest that impoundments are acting as sources for benthic macroinvertebrates and fish, including non-native species.

3.5.1 The Effect of Network Structure and other Covariates on Fish and Benthic macroinvertebrate Communities

The effect of local habitat, stream size, and stream network structure explored in Chapter 2 suggest that these variables are important in explaining benthic macroinvertebrate community structure, although the influence of higher trophic levels and habitat complementation was also apparent. For a detailed discussion of how local habitat (as measured by epifaunal substrate and stream gradient), stream size (as measured by drainage area), and stream network structure (as measured by habitat adjacency and isolation) shape benthic macroinvertebrate communities in first order streams in Maryland's Piedmont region, see the discussion section in Chapter 2.

The results of this study are consistent with previous research on the influence of stream size (Sheldon 1968; Platts 1979; Fairchild et al. 1998), local habitat (Roth et al. 1999), and stream network structure (Osborne and Wiley 1992; Schaefer and Kerfoot 2004; Hitt and Angermier 2008b, 2011) on fish communities, although these data provide new insights into how these variables shape community structure. The effect of stream

size on fish taxa richness, native fish taxa richness, non-native fish taxa richness, biomass per square meter, and the number of benthic species could be partially due to a general increase in the size and heterogeneity of habitat as stream size increases, although predator-prey interactions and habitat supplementation may also be occurring. For example, first order streams of all sizes with good habitat had higher taxa richness than similar sized streams with poor habitat. These results were expected, as both instream habitat score (Roth et al. 1999) and drainage area (Sheldon 1968; Platts 1979; Fairchild et al. 1998) have been previously linked to fish species richness. This relationship was somewhat similar for non-native taxa richness and biomass per square meter, but when habitat was poor, non-native taxa richness and biomass were much lower in larger streams that were degraded due to poor habitat. The lower biomass observed with increasing stream size in poor streams may be associated with the lack of areas for fish to hide, which would make them susceptible to predation from piscivores, which could occur in larger streams and have been shown to reduce fish taxa richness and abundance (Shurin and Allen 2001; Heinlein et al. 2010).

The interaction between stream size and distance to the nearest confluence for biomass per square meter may be related to species-area relationships as well as isolation from predatory fish. For sites closer to the confluence, biomass was relatively low and stream size had very little effect on biomass. On the other hand, the positive association between biomass and stream size for sites further from the confluence may be due to more habitat and depth with increasing stream size, as well as isolation from predatory fish further from the confluence.

Lastly, the effects of stream size on fish biomass and percent generalists, omnivores, and invertivores depended on d-link. For low d-link streams, biomass increased with stream size, which may be due to more habitat and depth with increasing stream size. Habitat supplementation could also be occurring, where organisms move between patches in the landscape to make use of substitutable resources (Dunning et al. 1992). In this case, two headwaters streams that come together each represents a similar patch of habitat. As a result, a disturbance in one stream may not have a big effect on the other, as colonist from the similar less disturbed stream may reduce the impacts to the more disturbed stream through rescue effects (Brown et al. 1977; Eriksson 2014), which could have contributed to the higher biomass observed for low d-link streams that were average and large in size. As d-link increased, however, more predatory fish may have been introduced from the larger main channel, which could explain why biomass decreased with stream size. The increase in percent generalists, omnivores, and invertivores with stream size for low d-link streams may be due to the abundance of insectivore taxa such as sculpins (Family Cottidae) and darters (Family Percidae) higher in the drainage. However, the rapid decrease in percent generalists, omnivores, and invertivores with increasing stream size for high d-link streams may be due to the presence of larger river species such as bass (*Micropterus* spp.) and lampreys (Family Petromyzontidae), which are classified as top predators and filter feeders, respectively by the MBSS (Southerland et al. 2005).

The effects of instream habitat score on the number of benthic species, fish taxa richness, native taxa richness, and non-native taxa richness could be partially due to habitat quality, as well as effects from higher trophic levels. A positive correlation

between instream habitat score and fish taxa richness has been previously documented using MBSS data (Roth et al. 1999), thus it was not surprising that the number of benthic species increased as instream habitat quality improved; fish taxa richness and non-native fish taxa richness increased with habitat quality for all stream sizes; fish taxa richness and native fish taxa richness increased with habitat quality for low and average d-link streams; and biomass increased with habitat quality for medium to large sized streams. The negative correlation between percent generalists, omnivores, and invertivores and instream habitat shown in the interaction with distance to nearest confluence is likely due to the presence of more specialist fish such as insectivores, predators, and grazers with greater habitat quality.

The negative effect of stream gradient on fish taxa richness, native fish taxa richness, non-native fish taxa richness, number of benthic species, and percent generalists, omnivores, and invertivores was likely due to the influence of channel gradients on movement, as fish have limited swimming abilities as gradient increases (Gomi et al. 2002; Richardson and Denehy 2007). Similarly, no matter how connected the stream was with the network, high gradient streams had lower fish biomass than low gradient streams. In this interaction, gradient had the most effect in high d-link streams and you would expect biomass to be low in high gradient streams with high d-links, since these streams typically support less species and biomass. High gradient streams with high d-link values are also very dissimilar to their confluent streams and less likely to receive migrants from the confluent stream due to a lack of similar habitat. Additionally, you would expect more piscivores in high d-link streams, which could potentially decrease biomass due to predation. On the other hand, low gradient streams are capable

of supporting more species/biomass, and are more similar to their confluent streams at high d-links.

In this study, distance to the nearest downstream confluence was the most important network scale variable explaining fish community structure, being associated with all six dependent variables. It was negatively associated with fish taxa richness, native fish taxa richness and the number of benthic species, and dependent on drainage area, instream habitat score and d-link for other community variables. Due to the change in substrate characteristics and flow, as well as the connection to the stream network at the confluence, it was expected that measures of fish community structure would be higher closer to the downstream confluence. These results are similar to other studies, which have found that confluences influence fish communities up to several kilometres in tributary streams (Hitt and Angermier 2008b, 2011) and fish diversity decreases as the distance from a confluence increases (Schaefer and Kerfoot 2004). As discussed previously, the effect of distance to nearest confluence on biomass per square meter was dependent on stream size. Distance to nearest confluence was also associated with non-native fish taxa richness and percent generalists, omnivores, and invertivores, although these relationships were dependent on instream habitat score (as discussed previously) and d-link. High d-link streams are much more different in size compared to their confluent streams than low d-link streams. As a result, non-native species richness would more rapidly decrease in high d-link streams the further you move upstream from a confluence. In contrast, since low d-link streams would be more similar in size as their confluent streams, non-native species richness would decline much slower as you move upstream from a confluence. Additionally, since there may be more piscivores the closer you are

to a confluence in high d-link streams, you would expect a decrease in richness due to predation.

In this analysis, d-link was associated with all dependent variables, except for the number of benthic species, although it was the least important of the two network scale variables. Although Osborne and Wiley (1992) found that d-link was positively correlated with fish species richness, my study shows that this relationship depends on other factors such as instream habitat quality and distance to nearest downstream confluence. My results also suggest that there are indirect effects from d-link on fish biomass due to more piscivores in larger high d-link streams. The presence of more piscivores in large d-link streams may also explain the decrease in percent generalists, omnivores, and invertivores with increasing stream size and d-link.

3.5.2 The Effect of Isolation from Roads on Fish and Benthic Macroinvertebrates

Due to their linear nature and extent in the landscape, first order streams are very vulnerable to anthropogenic alterations from the construction of roads, which may isolate downstream resources by altering network structure. The most substantial impact of anthropogenic isolation on local biota is its effect on colonization, which is important for supplementing populations or adding new species through rescue effects (Eriksson 2014). Based on the results of this study, several measures of benthic macroinvertebrate and fish community structure responded negatively to the number of downstream roads. In addition, in many instances, the effect of roads on community structure was stronger as the number of downstream roads increased. As a result of lowered rates of colonization, isolation from anthropogenic structures such as roads has been shown to lower species

richness (Nislow et al 2011; Perkin and Gido 2012). The negative effects shown in my study for these assemblages could be attributed to fragmentation from roads, as culverts have been shown to preclude the movement of stream fishes (Warren and Pardew 1998) and can limit fish passage to periods of storm runoff when flow is high enough to allow passage (Norman et al. 2009). In my study, the biggest effects of downstream roads on fish were when one road was present, with additional roads having less of an effect, suggesting that the presence of one road is enough of to decrease passage to a point that affects taxa richness. However, increasing the number of roads also increases the probability that at least one road was constructed in a way that represents a significant blockage. Culverts can also have a negative impact on benthic macroinvertebrates (Resh 2004), although most studies have shown impacts to downstream communities rather than to upstream movement (Khan and Colbo 2007; Peterson 2010). Most impacts to benthic macroinvertebrates from roads are likely due to changes in habitat from stream channelization, rather than from barriers to movement, as most benthic macroinvertebrates disperse as flying adults and are able to overcome obstructions (Vaughan 2002). Resh (2004), however, found that culverts decrease the ability of non-insect macroinvertebrates to disperse upstream, which may have contributed to the reduction in taxa richness shown in my study. Yet, this is not consistent with the decrease in percent flying invertebrates with the presence of more than one road. If culverts are a barrier to non-insect invertebrates, the presence of more than road would be expected to cause an increase in flying insects. However, roads with large traffic volumes could result in mortality of adult flying invertebrates as they cross roads in their upstream migration (Munoz et al. 2015), which may explain my results. Because flying

invertebrates are more mobile than other aquatic fauna, more than one road may be required to cause enough mortality from vehicle collision to have a big enough effect on flying invertebrates. The negative effect of downstream roads on percent clingers when no downstream impoundments were present may be related to changes in streambed particle composition caused by culverts. Culverts can change the detention time of water immediately upstream of culverts, which could decrease the particle size (Jackson 2003). Since clingers are adapted to living on riffle substrates, reductions in substrate size upstream of culverts may explain the lower proportion of clingers in my study.

Furthermore, the reduction in fish taxa richness observed in this study did not appear to indirectly affect benthic macroinvertebrate community structure. Since isolation has been shown to affect the ratio of predators to prey (Shulman and Chase 2007) and predator community composition (Chase et al. 2010), you would expect an increase in measures of benthic macroinvertebrate community structure with less fish, although the opposite effect was observed. This suggests that other factors such as water quality degradation due to impervious surfaces may be driving these results. The presence of downstream roads could be correlated with high imperviousness, which is shown to impact benthic macroinvertebrates and fish by reducing diversity and shifting to pollution tolerant taxa (Klein 1979; Pedersen and Perkins 1986; Stranko et al. 2005; Stanfield and Kilgour 2006). The abundance of pollution tolerant taxa such as aquatic worms (Class Oligochaeta), could better explain why percent flying invertebrates was lower when downstream roads were present.

3.5.3 Effect of Sources from Impoundments on Fish and Benthic

Macroinvertebrates

In contrast to roads, the significant positive correlation between the presence of downstream impoundments and fish taxa richness, native fish taxa richness, and non-native fish taxa richness did not appear to be related to isolation, rather to impoundments acting as faunal sources. Although the presence of dams in the lower reaches of rivers has led to declines in certain fish species (Falke and Gido 2006; Katano et al. 2006), my study only identified downstream impoundments on first order streams and did not include other impoundments lower in the network that may act as migration barriers. Furthermore, the majority of the impoundments in this study consisted of small stormwater and farm ponds, which may not be large enough to act as a significant barrier to fish migration. Both of these factors may explain why these results did not show isolation effects from the presence of downstream impoundments. Nevertheless, small impoundments can still affect fish species richness and composition of the streams that feed them (Kashiwagi and Miranda 2009; Franssen and Tobler 2013). The positive effects shown for the presence of downstream impoundments are generally consistent with the results from the analysis of the distance to nearest impoundments and the number of impoundment in the watershed. Previous studies have shown higher species richness, diversity and evenness above impoundments than below impoundments (Franssen and Tobler 2013), which is consistent with these results. In addition, the correlation between non-native fish taxa richness and impoundments could be due to the intentional introduction of exotic species into impoundments through stocking and aquarium release or accidental introduction through bait release (Lapointe et al. 2016).

Although not all introductions cause negative impacts, some species have resulted in detrimental effects to native fauna (Jelks et al. 2008) and biodiversity (Gozlan et al. 2005), including some cascading effects (Crooks 2002), which would be a concern to resource managers.

The significant positive correlation between the number of impoundments in the watershed and fish biomass for sites close to an upstream impoundment suggests that impoundments are also acting as a source for downstream fisheries. Similar results were observed for the distance to nearest upstream impoundment, which was negatively correlated with fish taxa richness, non-native fish taxa richness, and biomass per square meter. However, this relationship could also be due to impoundments causing a blockage at their outfall, which could result in greater density and species richness. Katano et al. (2006), for example, found that the density and biomass of diadromous species was higher below impoundments than above impoundments. Although it is not consistent with the results from the presence of downstream impoundments, this may also be a plausible explanation for the increase in fish richness and diversity close to upstream impoundments.

Because of the greater fish biomass and richness closer to upstream impoundments, it would be expected that measures of benthic macroinvertebrate community structure would have been affected by predation or top-down effects from higher trophic levels, although it is not clear whether either of these effects occurred. For benthic macroinvertebrates, there was a significant negative correlation between the distance to nearest upstream impoundment and both percent clingers and percent shredders. The relationship with percent clingers may have to do with the alteration of

sediment transport from the impoundments. Due to the retention of sediment, the streams that impoundments feed are starved of sediment and usually dominated by larger substrate. This attribute could explain why there were higher percent clingers closer to upstream impoundments. Another explanation could be that clingers are adapted to avoid predation due to their body morphology and adherence to substrates. Since fish richness and biomass increased near upstream impoundments, this may have increased predation on invertebrates that are less adapted to avoid predation, which would also explain the increase in percent clingers near upstream impoundments. The fact that percent shredders was also higher at sites closer to upstream impoundments could be due to the high retention of organic matter within the impoundments. Because impoundments retain organic matter that has been transported from their receiving streams, you would expect a greater number of shredders closer to the downstream outfall, which could be supplying detrital material downstream.

On the other hand, the distance to nearest downstream impoundment was negatively associated with rarified taxa richness and positively associated with percent shredders. The closer a site was to a downstream impoundment the more taxa were present. This may be due to the addition of more taxa from impoundments, which can support a very different benthic macroinvertebrate community (Williams 1996; Merritt and Cummins 2008). Due to differences in flow, water chemistry, and habitat, impoundments and other lentic habitats usually support a greater proportion of dragonflies and damselflies (Order Odonata), beetles (Order Coleoptera), true bugs (Order Hemiptera), flies (Order Diptera), and aquatic worms (Class Oligochaeta). Many lentic taxa are adapted to survive the standing water environment through interactions

with the surface film, strong swimming abilities, use of hemoglobin as an oxygen store, and transparency to avoid predation (Merritt and Cummins 2008). Some of these taxa can also occur in certain stream habitats, but are less frequent. For percent shredders, it was expected that this variable would be higher at the impoundment-stream interface due to the lower gradient and retention of organic matter in the impoundment, although this was not the case. The reduction in percent shredders closer to the impoundment may be due to the more lentic habitat closer to the impoundment. Due to the backwater effect from impoundments, areas closer to the inlet would be expected to support less shredders since these habitats are typically dominated by collector-gatherers and predators with lower abundances of other groups such as shredders, scrapers, and collector-filterers (Higgins and Merritt 1999; Bazzanti and Bella 2004). Another explanation could be that the reduction in percent shredders may be due to predation from fish, which were greater in biomass and species richness at the impoundment-stream interface.

The significant negative correlation between the number of upstream impoundments and percent shredders suggests that impoundments are holding organic matter and disconnecting the food source from shredder taxa. This is also consistent with the finding that percent shredders was higher closer to upstream impoundments. On the other hand, the positive correlation between percent flying invertebrates and the number of upstream impoundments suggests that impoundments are acting as sources of flying invertebrates due to their large surface area and abundance of flying taxa.

3.6 DATA LIMITATIONS

The results of this study suggest that roads are isolating benthic macroinvertebrate and fish communities, causing adverse effects through direct and indirect means. Man-made impoundments may also be affecting community structure through supplementation of benthic macroinvertebrates and fishes. In addition, to these anthropogenic effects, fish community structure was dependent on local habitat and stream network structure. Many of the variables explored were dependent on other variables, which may be due to the influence of higher trophic levels, suggesting top-down effects. The variation explained by these analyses depended on the assemblage studied, as the benthic macroinvertebrate analyses explained much less variation than the fish community analyses.

The best-fit models for benthic macroinvertebrates for the isolation analysis only explained between 4% and 22% of the variation in benthic macroinvertebrate community structure in first order streams from Maryland's Piedmont region (Table 3.5). Similarly, the source analysis only explained between 5% and 19% of variation (Table 3.8). The low variation explained was likely due to several factors, including the field sampling methodology, laboratory subsampling, and use of rarefaction prior to the analysis. The MBSS utilizes a rapid, semi-quantitative method for sampling benthic macroinvertebrates in streams. Using a D-framed dipnet, 20 jabs or kicks (totalling 1.85 m²) were collected from best available habitats chosen by the field crew and spread across a 75 meter reach in order to obtain a representative sample. Samples were also only collected once during the spring index period (March 1 – April 30), which doesn't account for seasonal variation in community composition. Variation is also introduced through the laboratory

methods. Organisms from field samples were randomly picked in the laboratory from a gridded tray until a targeted 120 organisms were obtained. Prior to identification, midges (Family Chironomidae) and aquatic worms (Class Oligochaeta) were further subsampled if they exceeded 10 individuals from any family/subfamily (Boward and Friedman 2000). Because the methodology requires the last grid to be picked in its entirety, and some samples may have very few organisms due to poor stream quality, the actual number of organisms identified ranged from 0 to greater than 120. As a result, benthic macroinvertebrate data from each site were rarified to 60 organisms, which is the minimum subsample size used by the MBSS to calculate the BIBI. Thus, due to the above factors, it is reasonable that the models only explained a low percentage of the variation in benthic macroinvertebrate community structure.

A much higher percent of variation was explained for the fish analyses. Between 16% and 51% of variation in fish community structure was explained in the local habitat and network structure analysis (Table 3.12). Similarly, 16% to 54% and 16% to 56% of variation was explained in the isolation and source analyses, respectively (Tables 3.15 and 3.18, respectively). The higher variation explained by the fish community analyses, as compared to benthic macroinvertebrates, is likely due to differences in sampling methods. The double-pass electrofishing technique used by the MBSS is designed to obtain a representative sample of the fish community, but the goal is to substantially deplete the fish after the second pass. Although the MBSS's methods for sampling benthic macroinvertebrates were also designed to collect a representative sample, they inherently introduce much of the variation due to their semi-quantitative methods.

3.7 IMPLICATIONS

Headwater streams comprise at least 80 percent of the stream network in the United States (Meyer et al. 2003). They provide important ecological functions to the downstream network, including flood control, maintenance of water quantity and quality, and provide habitat for a diverse flora and fauna, even in the upper reaches. Due to their linear nature and extent in the landscape, headwater streams are very vulnerable to anthropogenic alterations such as the construction of roads and impoundments, which may isolate downstream resources by altering network structure. Stream restoration is commonly used to try to ameliorate losses to headwater stream functions due to urbanization and other land use practices that contribute to stream degradation. Many resource agencies are now requiring restoration projects to prove that a restoration has achieved ecological improvement, although this is not well defined and can be quite difficult to quantify. Many practitioners have also believed that restoring habitat in a degraded stream will improve aquatic communities (i.e., the Field of Dreams Hypothesis; Palmer et al. 1997). This paradigm is due to the fact that stream habitat is linked to biological conditions in streams (Reice 1980; Duan et al. 2009; Martin et al. 2013), which my results have also corroborated. Yet, the fact is that most studies of stream restoration projects have shown little to no recovery in diversity of fish or benthic macroinvertebrates, even when habitat or biological improvement was a goal (Palmer et al. 2010; Stranko et al. 2012). For example, Stranko et al. (2012) found no significant difference between benthic macroinvertebrate and fish diversity in restored versus unrestored streams in Maryland's Piedmont region. Similarly, in a study of 78 independent stream restoration projects, Palmer et al. (2010) found no evidence that

habitat heterogeneity was the primary factor controlling benthic macroinvertebrate diversity. Given the current approaches for stream restoration in this region, the lack of increased biological diversity following stream restorations may be due to the irreversible effects of urbanizations and other land uses. Thus, some argue that it is more effective to invest in protecting watersheds rather than restoring urban streams to re-establish biological diversity (Stranko et al. 2012). Other restoration techniques that focus on the passage of fish and other fauna may be more likely to show positive results.

In my study, both fish and benthic macroinvertebrate structure were adversely impacted by the presence of roads (including indirect effects). Although it is not clear whether these effects were actually due to other water quality effects, these results suggest that highly disconnected streams should not be identified for stream restoration if the goal is to recover diversity, as these systems have a low potential for recovery, unless a goal of the project is to provide passage for aquatic fauna through culvert rehabilitation. In addition to habitat restoration, faunal passage is often a goal of stream restoration or culvert maintenance projects. If not properly designed, road culverts can block the natural movement patterns of fish and certain benthic macroinvertebrates. As long as poor habitat or degraded water quality does not impede dispersal, improving perched or failing culverts can restore longitudinal connectivity of habitats. While anadromous species have been a major focus of fish passage restoration efforts in the past, some studies have shown that culverts impede the movement of certain resident species (Warren and Pardew 1998; Benton et al. 2008; MacPherson et al. 2012). In my study, both fish and benthic macroinvertebrate community structure were adversely impacted by the presence of roads (including indirect effects). This could be due to road culverts

impeding the passage of these assemblages, although other confounding factors such as poor water quality could also explain this relationship. Even though my study examined the anthropogenic impacts of roads and impoundments on aquatic communities, it did not attempt to isolate variation explained by water quality degradation (e.g., imperviousness, conductivity). Instream habitat score, however, could be viewed as a surrogate for water quality degradation, as streams with poor water quality will likely lack habitat. Future research on the impacts of downstream culverts on individual taxa and their ability to traverse road crossings would be needed to further elucidate these results. Furthermore, additional studies may help support the argument for considering resident fish passage during the design and maintenance of culverts.

3.8 LITERATURE CITED

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**APPENDIX A: MEAN PARAMETER ESTIMATES FOR MODELS WITHIN TWO
AIC UNITS FOR BENTHIC MACROINVERTEBRATE AND FISH MODELS**

Table A.1. Mean parameter estimates for models within two AIC units for benthic macroinvertebrate isolation models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
Rarified Taxa Richness							
IMP_DSyes:ROADS_DSone	0.1034	0.0162	1	0.4925	-0.1466	0.3534	0.25
IMP_DSyes:ROADS_DSsome	0.0617	0.0096	1	0.4925	-0.1314	0.2548	0.1931
(Intercept)	2.7801	0.0018	2	1	2.6955	2.8647	0.0846
ROADS_DSone	-0.1649	0.0046	2	1	-0.2979	-0.0319	0.133
ROADS_DSsome	-0.2064	0.0052	2	1	-0.3477	-0.0651	0.1413
IMP_DSyes	0.0885	0.0083	2	1	-0.0909	0.2679	0.1794
EPI_SUB	0.1004	0.0004	2	1	0.0599	0.1409	0.0405
ST_GRAD	-0.0873	0.0006	2	1	-0.1355	-0.0391	0.0482
AREA	-0.0553	0.0008	2	1	-0.112	0.0014	0.0567
DLINK	-0.045	0.0004	2	1	-0.0842	-0.0058	0.0392
AREA:EPI_SUB	0.0409	0.0005	2	1	-0.0022	0.084	0.0431
AREA:ST_GRAD	-0.0689	0.0008	2	1	-0.1252	-0.0126	0.0563
AREA:DLINK	0.0603	0.0006	2	1	0.0112	0.1094	0.0491
Percent Chironomidae							
IMP_DSyes	0.0084	0.0002	1	0.1824	-0.0214	0.0382	0.0298
ROADS_DSone	0.0103	0.0003	1	0.3296	-0.0254	0.046	0.0357
ROADS_DSsome	0.0991	0.0178	1	0.3296	-0.1637	0.3619	0.2628
(Intercept)	-0.3674	0.0031	3	1	-0.4772	-0.2576	0.1098
AREA	0.1156	0.0001	3	1	0.0948	0.1364	0.0208
DLINK	-0.1964	0.0001	3	1	-0.2176	-0.1752	0.0212
DIST_CON	0.109	0.0013	3	1	0.0378	0.1802	0.0712

Table A.2. Mean parameter estimates for models within two AIC units for benthic macroinvertebrate source models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ (Alpha =0.05)
Rarified Taxa Richness							
DIST_IMP_DS:DIST_IMP_US	-0.0019	0	1	0.0971	-0.0099	0.0061	0.008
DIST_IMP_DS:NUM_IMP_US	0.0042	0.0001	1	0.1006	-0.0123	0.0207	0.0165
NUM_IMP_US	0.0212	0.0011	10	0.6887	-0.0452	0.0876	0.0664
DIST_IMP_US	-0.0247	0.0006	10	0.7593	-0.0715	0.0221	0.0468
(Intercept)	2.7318	0.0005	13	1	2.6879	2.7757	0.0439
DIST_IMP_DS	-0.0473	0.0004	13	1	-0.0866	-0.008	0.0393
EPI_SUB	0.1101	0.0004	13	1	0.0696	0.1506	0.0405
ST_GRAD	-0.093	0.0006	13	1	-0.1413	-0.0447	0.0483
AREA	-0.0931	0.0013	13	1	-0.1635	-0.0227	0.0704
DLINK	-0.0352	0.0004	13	1	-0.0742	0.0038	0.039
AREA:EPI_SUB	0.0448	0.0005	13	1	0.0007	0.0889	0.0441
AREA:ST_GRAD	-0.0749	0.0009	13	1	-0.1334	-0.0164	0.0585
AREA:DLINK	0.0551	0.0007	13	1	0.0049	0.1053	0.0502
Percent Chironomidae							
DIST_IMP_DS:DIST_IMP_US	-0.0003	0	1	0.024	-0.0017	0.0011	0.0014
DIST_IMP_DS:NUM_IMP_US	0.0049	0.0001	3	0.0537	-0.0133	0.0231	0.0182
DIST_IMP_US:NUM_IMP_US	-0.1294	0.0424	5	0.2081	-0.5344	0.2756	0.405
DIST_IMP_DS	-0.0055	0.0001	12	0.3937	-0.0248	0.0138	0.0193
NUM_IMP_US	-0.0839	0.0155	12	0.4581	-0.3286	0.1608	0.2447
DIST_IMP_US	-0.0409	0.018	12	0.601	-0.3049	0.2231	0.264
(Intercept)	-0.3773	0.0083	17	1	-0.5569	-0.1977	0.1796
AREA	0.1426	0.0007	17	1	0.0905	0.1947	0.0521
DLINK	-0.1955	0.0001	17	1	-0.217	-0.174	0.0215
DIST_CON	0.1335	0.0001	17	1	0.1116	0.1554	0.0219
Percent Clingers							
DIST_IMP_DS	0.0004	0	1	0.1355	-0.0031	0.0039	0.0035
DIST_IMP_US:NUM_IMP_US	0.0874	0.0209	1	0.1784	-0.1969	0.3717	0.2843
NUM_IMP_US	0.0219	0.0042	2	0.3943	-0.1063	0.1501	0.1282

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
DIST_IMP_US	-0.0721	0.0114	4	0.909	-0.2819	0.1377	0.2098
(Intercept)	0.1359	0.0042	5	1	0.0089	0.2629	0.127
EPI_SUB	0.2722	0.0001	5	1	0.2501	0.2943	0.0221
DIST_CON	-0.1101	0.0001	5	1	-0.1336	-0.0866	0.0235
Percent Shredders							
DIST_IMP_DS:DIST_IMP_US	-0.0065	0.0001	2	0.1257	-0.0294	0.0164	0.0229
DIST_IMP_US:NUM_IMP_US	0.0118	0.001	4	0.2264	-0.0496	0.0732	0.0614
DIST_IMP_DS:NUM_IMP_US	0.0205	0.001	3	0.2548	-0.0408	0.0818	0.0613
DIST_IMP_US	-0.0779	0.003	11	0.7607	-0.185	0.0292	0.1071
NUM_IMP_US	-0.1185	0.0031	12	0.8441	-0.2276	-0.0094	0.1091
DIST_IMP_DS	0.147	0.0005	13	0.964	0.1042	0.1898	0.0428
(Intercept)	-1.5895	0.0005	16	1	-1.6316	-1.5474	0.0421
EPI_SUB	0.0809	0.0002	16	1	0.0505	0.1113	0.0304
ST_GRAD	0.0315	0.0003	16	1	-0.002	0.065	0.0335
EPI_SUB:ST_GRAD	0.1745	0.0002	16	1	0.1435	0.2055	0.031
Percent Flying Insects							
DIST_IMP_DS:NUM_IMP_US	0.0208	0.0013	1	0.1371	-0.0511	0.0927	0.0719
DIST_IMP_US	-0.0247	0.0013	2	0.2872	-0.0961	0.0467	0.0714
DIST_IMP_DS	-0.0435	0.0022	3	0.5143	-0.1367	0.0497	0.0932
(Intercept)	2.7192	0.0006	5	1	2.6702	2.7682	0.049
NUM_IMP_US	0.4571	0.0038	5	1	0.3361	0.5781	0.121
EPI_SUB	0.6382	0.0004	5	1	0.5987	0.6777	0.0395
AREA	0.1149	0.0017	5	1	0.035	0.1948	0.0799
DLINK	-0.195	0.0004	5	1	-0.2331	-0.1569	0.0381
AREA:EPI_SUB	0.2908	0.001	5	1	0.2271	0.3545	0.0637
DLINK:EPI_SUB	-0.1539	0.0004	5	1	-0.1909	-0.1169	0.037
AREA:DLINK	0.192	0.0013	5	1	0.121	0.263	0.071

Table A.3. Mean parameter estimates for models within two AIC units for fish base models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+/- (Alpha =0.05)
Taxa Richness							
DIST_CON:ST_GRAD	-0.001	0.003	1	0.081	-0.033	0.031	0.032
AREA:DLINK	0.001	0.003	1	0.081	-0.035	0.037	0.036
DIST_CON:INSTRHAB	-0.003	0.002	1	0.082	-0.035	0.029	0.032
INSTRHAB:ST_GRAD	-0.008	0.003	1	0.094	-0.057	0.041	0.049
DLINK:ST_GRAD	-0.012	0.004	1	0.105	-0.074	0.05	0.062
AREA:ST_GRAD	0.028	0.014	1	0.122	-0.098	0.154	0.126
AREA:DIST_CON	0.018	0.005	1	0.127	-0.06	0.096	0.078
DIST_CON:DLINK	-0.286	0.032	8	0.913	-0.631	0.059	0.345
(Intercept)	5.588	0.029	9	1	5.255	5.921	0.333
ST_GRAD	-0.857	0.033	9	1	-1.211	-0.503	0.354
INSTRHAB	1.135	0.029	9	1	0.802	1.468	0.333
AREA	1.72	0.042	9	1	1.321	2.119	0.399
DIST_CON	-0.624	0.026	9	1	-0.941	-0.307	0.317
DLINK	0.423	0.026	9	1	0.104	0.742	0.319
AREA:INSTRHAB	0.413	0.037	9	1	0.035	0.791	0.378
DLINK:INSTRHAB	-0.409	0.028	9	1	-0.737	-0.081	0.328
Native Taxa Richness							
AREA:DLINK	0.000795	0.001426	1	0.040735	-0.017282	0.015692	0.016487
DIST_CON:INSTRHAB	0.001081	0.000816	1	0.041262	-0.01452	0.012358	0.013439
DIST_CON:ST_GRAD	0.001709	0.001626	1	0.04146	-0.02106	0.017642	0.019351
DLINK:ST_GRAD	-0.00537	0.001662	1	0.052066	-0.03348	0.02274	0.02811
AREA:DIST_CON	0.024381	0.006179	3	0.164397	-0.074814	0.123576	0.099195
INSTRHAB:ST_GRAD	0.043585	0.01201	4	0.236979	-0.206579	0.119409	0.162994
DIST_CON:DLINK	-	0.018896	7	0.40135	-0.324081	0.165265	0.244673

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
	0.079408						
AREA:INSTRHAB	0.215619	0.040207	13	0.741104	-0.177425	0.608663	0.393044
AREA:ST_GRAD	0.359751	0.073933	14	0.8329	-0.167215	0.886717	0.526966
(Intercept)	5.611091	0.033464	17	1	5.252674	5.969508	0.358417
INSTRHAB	0.623173	0.0264	17	1	0.303846	0.9425	0.319327
	-						
ST_GRAD	0.432461	0.046149	17	1	-0.851953	-0.012969	0.419492
AREA	1.843484	0.070228	17	1	1.327096	2.359872	0.516388
	-						
DIST_CON	0.422016	0.021913	17	1	-0.713133	-0.130899	0.291117
DLINK	0.384954	0.021292	17	1	0.097859	0.672049	0.287095
	-						
DLINK:INSTRHAB	0.498495	0.023943	17	1	-0.802763	-0.194227	0.304268
Non-native Taxa Richness							
DLINK:ST_GRAD	0.003	0.001	1	0.07	-0.018	0.024	0.021
AREA:DIST_CON	0.005	0.001	1	0.081	-0.02	0.03	0.025
AREA:DLINK	-0.005	0.001	1	0.083	-0.03	0.02	0.025
DIST_CON:ST_GRAD	-0.012	0.004	1	0.089	-0.071	0.047	0.059
AREA:ST_GRAD	0.031	0.005	3	0.249	-0.081	0.143	0.112
INSTRHAB:ST_GRAD	-0.044	0.009	4	0.306	-0.199	0.111	0.155
AREA:INSTRHAB	0.099	0.007	8	0.762	-0.064	0.262	0.163
(Intercept)	-0.657	0.008	11	1	-0.837	-0.477	0.18
INSTRHAB	0.144	0.008	11	1	-0.032	0.32	0.176
ST_GRAD	-0.432	0.015	11	1	-0.675	-0.189	0.243
AREA	0.129	0.01	11	1	-0.06	0.318	0.189
DIST_CON	-0.441	0.011	11	1	-0.65	-0.232	0.209
DLINK	-0.004	0.007	11	1	-0.17	0.162	0.166
DIST_CON:INSTRHAB	0.243	0.011	11	1	0.039	0.447	0.204
DIST_CON:DLINK	-0.301	0.011	11	1	-0.503	-0.099	0.202
Biomass Per Square Meter							
DIST_CON:ST_GRAD	-0.002	0.013	1	0.058	-0.059	0.055	0.057

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
AREA:ST_GRAD	-0.003	0.016	1	0.058	-0.069	0.063	0.066
INSTRHAB:ST_GRAD	0.005	0.009	1	0.059	-0.05	0.06	0.055
DIST_CON:INSTRHAB	0.011	0.009	1	0.066	-0.058	0.08	0.069
DLINK:INSTRHAB	-0.16	0.097	5	0.346	-0.688	0.368	0.528
DIST_CON:DLINK	0.239	0.128	6	0.453	-0.423	0.901	0.662
AREA:DIST_CON	0.365	0.12	9	0.706	-0.315	1.045	0.68
DLINK:ST_GRAD	-0.556	0.145	11	0.871	-1.291	0.179	0.735
DIST_CON	-0.399	0.114	12	0.932	-1.061	0.263	0.662
(Intercept)	7.047	0.113	13	1	6.385	7.709	0.662
INSTRHAB	1.619	0.12	13	1	0.937	2.301	0.682
ST_GRAD	-1.181	0.145	13	1	-1.93	-0.432	0.749
AREA	0.615	0.157	13	1	-0.162	1.392	0.777
DLINK	-0.103	0.107	13	1	-0.747	0.541	0.644
AREA:INSTRHAB	1.06	0.161	13	1	0.272	1.848	0.788
AREA:DLINK	-0.966	0.197	13	1	-1.837	-0.095	0.871
Number of Benthic Species							
DIST_CON:ST_GRAD	0	0	1	0.021	-0.006	0.006	0.006
AREA:DLINK	0.002	0	2	0.047	-0.009	0.013	0.011
AREA:DIST_CON	0.002	0	2	0.05	-0.009	0.013	0.011
AREA:INSTRHAB	-0.003	0	3	0.074	-0.018	0.012	0.015
INSTRHAB:ST_GRAD	-0.006	0.001	4	0.094	-0.036	0.024	0.03
DLINK:ST_GRAD	-0.026	0.004	8	0.253	-0.121	0.069	0.095
DIST_CON:INSTRHAB	0.036	0.005	11	0.342	-0.086	0.158	0.122
AREA:ST_GRAD	0.048	0.006	14	0.432	-0.094	0.19	0.142
DLINK:INSTRHAB	-0.05	0.005	14	0.447	-0.183	0.083	0.133
DLINK	-0.041	0.004	22	0.689	-0.159	0.077	0.118
(Intercept)	-0.205	0.005	32	1	-0.343	-0.067	0.138
ST_GRAD	-0.212	0.008	32	1	-0.392	-0.032	0.18
INSTRHAB	0.236	0.005	32	1	0.094	0.378	0.142
AREA	0.208	0.006	32	1	0.059	0.357	0.149
DIST_CON	-0.285	0.006	32	1	-0.442	-0.128	0.157

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
Percent Generalists, Omnivores, and Invertivores							
DLINK:ST_GRAD	0.0038	0.0002	2	0.058	-0.0102	0.0178	0.014
AREA:INSTRHAB	0.0089	0.0009	3	0.0852	-0.023	0.0408	0.0319
DIST_CON:ST_GRAD	0.0389	0.0068	5	0.1896	-0.085	0.1628	0.1239
AREA:DIST_CON	-0.0335	0.0028	7	0.2918	-0.1267	0.0597	0.0932
INSTRHAB:ST_GRAD	0.0799	0.0098	11	0.4084	-0.1063	0.2661	0.1862
DIST_CON:INSTRHAB	-0.1027	0.0134	11	0.4485	-0.326	0.1206	0.2233
AREA	0.0103	0.0015	20	0.828	-0.053	0.0736	0.0633
AREA:DLINK	-0.1901	0.0078	20	0.828	-0.3219	-0.0583	0.1318
ST_GRAD	-0.2557	0.0114	22	0.9059	-0.4169	-0.0945	0.1612
(Intercept)	1.8765	0.0015	25	1	1.8081	1.9449	0.0684
INSTRHAB	-0.5809	0.0026	25	1	-0.6698	-0.492	0.0889
DIST_CON	0.3976	0.0043	25	1	0.2836	0.5116	0.114
DLINK	0.1461	0.0009	25	1	0.0948	0.1974	0.0513
DIST_CON:DLINK	0.2433	0.0003	25	1	0.2092	0.2774	0.0341

Table A.4. Mean parameter estimates for models within two AIC units for fish isolation models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+-(Alpha =0.05)
Biomass Per Square Meter							
IMP_DSyes	0.856149	0.784865	1	0.640215	-0.88284	2.595138	1.738989
(Intercept)	6.591507	0.346865	2	1	5.434483	7.748531	1.157024
-	-	-	-	-	-	-	-
ST_GRAD	1.194083	0.137432	2	1	-1.923488	-0.464678	0.729405
INSTRHAB	1.636625	0.115196	2	1	0.968824	2.304426	0.667801
AREA	0.696995	0.148761	2	1	-0.061849	1.455839	0.758844
-	-	-	-	-	-	-	-
DIST_CON	0.696674	0.158039	2	1	-1.478302	0.084954	0.781628
AREA:INSTRHAB	1.070844	0.154545	2	1	0.297355	1.844333	0.773489
AREA:DIST_CON	0.56621	0.080055	2	1	0.009509	1.122911	0.556701
DLINK:ST_GRAD	-0.67553	0.098926	2	1	-1.294371	-0.056689	0.618841
-	-	-	-	-	-	-	-
AREA:DLINK	1.041014	0.172403	2	1	-1.857959	-0.224069	0.816945
Number of Benthic Species							
IMP_DSyes	0.12743	0.024828	2	0.556604	-0.177648	0.432508	0.305078
-	-	-	-	-	-	-	-
ROADS_DSone	0.096029	0.01796	2	0.635823	-0.353911	0.161853	0.257882
-	-	-	-	-	-	-	-
ROADS_DSsome	0.272718	0.066167	2	0.635823	-0.776725	0.231289	0.504007
(Intercept)	-0.16573	0.02459	4	1	-0.464142	0.132682	0.298412
-	-	-	-	-	-	-	-
ST_GRAD	0.244329	0.007116	4	1	-0.410293	-0.078365	0.165964
INSTRHAB	0.227802	0.00487	4	1	0.090516	0.365088	0.137286
AREA	0.167472	0.00234	4	1	0.072302	0.262642	0.09517
-	-	-	-	-	-	-	-
DIST_CON	0.243861	0.013457	4	1	-0.468544	-0.019178	0.224683

Table A.5. Mean parameter estimates for models within two AIC units for fish source models.

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ (Alpha =0.05)
Taxa Richness							
DIST_IMP_DS:DIST_IMP_US	0.021332	0.005834	1	0.236263	-0.081365	0.124029	0.102697
NUM_IMP_US	0.053379	0.02817	1	0.252654	-0.184218	0.290976	0.237597
(Intercept)	5.568313	0.024987	3	1	5.2574	5.879226	0.310913
-	-	-	-	-	-	-	-
DIST_IMP_US	0.588908	0.027352	3	1	-0.913894	-0.263922	0.324986
-	-	-	-	-	-	-	-
DIST_IMP_DS	0.584773	0.024498	3	1	-0.892478	-0.277068	0.307705
-	-	-	-	-	-	-	-
ST_GRAD	0.805112	0.026543	3	1	-1.125573	-0.484651	0.320461
INSTRHAB	1.060793	0.026239	3	1	0.742175	1.379411	0.318618
AREA	1.545979	0.047955	3	1	1.12396	1.967998	0.422019
-	-	-	-	-	-	-	-
DIST_CON	0.511615	0.023766	3	1	-0.814844	-0.208386	0.303229
DLINK	0.457606	0.024156	3	1	0.151895	0.763317	0.305711
AREA:INSTRHAB	0.382021	0.034293	3	1	0.017841	0.746201	0.36418
-	-	-	-	-	-	-	-
DLINK:INSTRHAB	0.303368	0.024317	3	1	-0.610093	0.003357	0.306725
-	-	-	-	-	-	-	-
DIST_CON:DLINK	0.231386	0.023215	3	1	-0.531087	0.068315	0.299701
Native Taxa Richness							
NUM_IMP_US	0.000567	0.011161	1	0.158071	-0.083012	0.084146	0.083579
DIST_IMP_DS:DIST_IMP_US	0.005745	0.00271	1	0.164659	-0.045005	0.056495	0.05075
-	-	-	-	-	-	-	-
DIST_IMP_US	0.194175	0.029581	3	0.752373	-0.531031	0.142681	0.336856
(Intercept)	5.586379	0.028337	4	1	5.255172	5.917586	0.331207
-	-	-	-	-	-	-	-
DIST_IMP_DS	0.360739	0.020375	4	1	-0.641575	-0.079903	0.280836
ST_GRAD	-	0.035143	4	1	-0.797042	-0.059336	0.368853

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
	0.428189						
INSTRHAB	0.659303	0.024039	4	1	0.354239	0.964367	0.305064
AREA	1.769198	0.061699	4	1	1.281693	2.256703	0.487505
	-						
DIST_CON	0.353597	0.021153	4	1	-0.639761	-0.067433	0.286164
DLINK	0.41185	0.020807	4	1	0.128028	0.695672	0.283822
AREA:INSTRHAB	0.286302	0.030299	4	1	-0.056172	0.628776	0.342474
AREA:ST_GRAD	0.36629	0.053029	4	1	-0.086772	0.819352	0.453062
	-						
DLINK:INSTRHAB	0.471099	0.022342	4	1	-0.765194	-0.177004	0.294095
Non-native Taxa Richness							
DIST_IMP_DS:NUM_IMP_US	0.033933	0.004551	2	0.319592	-0.079481	0.147347	0.113414
NUM_IMP_US	0.077269	0.01226	3	0.524646	-0.132278	0.286816	0.209547
	-						
DIST_IMP_DS	0.139923	0.009937	4	0.850862	-0.33222	0.052374	0.192297
	-						
(Intercept)	0.775546	0.009719	5	1	-0.969509	-0.581583	0.193963
	-						
DIST_IMP_US	0.443133	0.0154	5	1	-0.687251	-0.199015	0.244118
	-						
ST_GRAD	0.430193	0.014652	5	1	-0.668357	-0.192029	0.238164
INSTRHAB	0.152235	0.006814	5	1	-0.010177	0.314647	0.162412
	-						
AREA	0.014493	0.013157	5	1	-0.237146	0.20816	0.222653
	-						
DIST_CON	0.381454	0.010679	5	1	-0.584779	-0.178129	0.203325
	-						
DLINK	0.001067	0.007244	5	1	-0.168531	0.166397	0.167464
AREA:INSTRHAB	0.13318	0.005213	5	1	-0.008846	0.275206	0.142026
DIST_CON:INSTRHAB	0.23164	0.009871	5	1	0.036152	0.427128	0.195488
DIST_CON:DLINK	-	0.011112	5	1	-0.477001	-0.062209	0.207396

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ (Alpha =0.05)
	0.269605						
Biomass Per Square Meter							
(Intercept)	5.011565	0.736378	4	1	3.3231	6.70003	1.688465
NUM_IMP_US	1.618969	1.498468	4	1	-4.027572	0.789634	2.408603
DIST_IMP_US	3.574835	2.062761	4	1	-6.400795	-0.748875	2.82596
DIST_IMP_DS	0.847312	0.101153	4	1	-1.473106	-0.221518	0.625794
INSTRHAB	1.757065	0.114047	4	1	1.092582	2.421548	0.664483
ST_GRAD	1.215578	0.134581	4	1	-1.937406	-0.49375	0.721828
AREA	0.120353	0.357416	4	1	-1.055974	1.29668	1.176327
DIST_CON	0.316374	0.106645	4	1	-0.958932	0.326184	0.642558
DIST_IMP_US:NUM_IMP_US	-4.79819	3.663127	4	1	-8.564079	-1.032301	3.765889
AREA:INSTRHAB	1.058116	0.157513	4	1	0.277207	1.839025	0.780909
AREA:DIST_CON	0.674078	0.08356	4	1	0.105302	1.242854	0.568776
DLINK:ST_GRAD	-0.42821	0.096338	4	1	-1.038929	0.182509	0.610719
Number of Benthic Species							
DIST_IMP_DS:DIST_IMP_US	0.005337	0.000929	1	0.124816	-0.035381	0.024707	0.030044
DIST_IMP_DS:NUM_IMP_US	0.012332	0.001528	1	0.132473	-0.035333	0.059997	0.047665
NUM_IMP_US	0.035159	0.005261	3	0.387964	-0.088283	0.158601	0.123442
DIST_IMP_US	0.064411	0.006623	3	0.542809	-0.221616	0.092794	0.157205
(Intercept)	0.239405	0.004525	6	1	-0.371748	-0.107062	0.132343
DIST_IMP_DS	-0.16531	0.004794	6	1	-0.301526	-0.029094	0.136216
ST_GRAD	0.242714	0.007343	6	1	-0.411306	-0.074122	0.168592

Parameter	Estimate	Uncond. Variance	Nb Models	Importance	Lower CI (2.5%)	Upper CI (97.5%)	+ - (Alpha =0.05)
INSTRHAB	0.245387	0.004656	6	1	0.111131	0.379643	0.134256
AREA	0.120794	0.006326	6	1	-0.027753	0.269341	0.148547
-	-	-	-	-	-	-	-
DIST_CON	0.258157	0.005908	6	1	-0.409382	-0.106932	0.151225
Percent Generalists, Omnivores, and Invertivores							
DIST_IMP_DS	0.009761	0.000399	1	0.202927	-0.021365	0.040887	0.031126
DIST_IMP_US	0.027556	0.002003	1	0.279159	-0.050887	0.105999	0.078443
(Intercept)	1.922787	0.000224	3	1	1.893379	1.952195	0.029408
-	-	-	-	-	-	-	-
INSTRHAB	0.653348	0.000221	3	1	-0.682561	-0.624135	0.029213
-	-	-	-	-	-	-	-
ST_GRAD	0.239083	0.000213	3	1	-0.267722	-0.210444	0.028639
AREA	0.038723	0.000099	3	1	0.019399	0.058047	0.019324
DIST_CON	0.445123	0.000311	3	1	0.410399	0.479847	0.034724
DLINK	0.181011	0.00014	3	1	0.157773	0.204249	0.023238
-	-	-	-	-	-	-	-
DIST_CON:INSTRHAB	0.255802	0.000371	3	1	-0.293701	-0.217903	0.037899
-	-	-	-	-	-	-	-
AREA:DLINK	0.240118	0.000167	3	1	-0.26552	-0.214716	0.025402
DIST_CON:DLINK	0.234162	0.00026	3	1	0.202708	0.265616	0.031454

APPENDIX B: R CODE USED FOR DATA ANALYSIS

```

setwd("~/Grad School/Thesis/Data Analysis/Fish")
data.fish.taxa<-read.csv("Fish_Variables.csv",header=T)
data.fish.taxa.R<-read.csv("Fish_Variables_RichnessOnly.csv",header=T)
library(Hmisc)
library(rJava)
library(glmulti)
data.fish.rich<-
  as.data.frame(cbind(data.fish.taxa.R[17],
                      scale(data.fish.taxa.R[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa.R[7]),center=T,scale=T),
                      scale(data.fish.taxa.R[8:10],center=T,scale=T)))

data.fish.rich[1:3,]
data.fish.rich.2<-
  as.data.frame(cbind(data.fish.taxa[18:21],
                      data.fish.taxa[25],
                      data.fish.taxa[14:17],
                      scale(data.fish.taxa[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa[7]),center=T,scale=T),
                      scale(data.fish.taxa[8:10],center=T,scale=T)))

data.fish.rich.2[1:3,]

rcorr(as.matrix(data.fish.rich.2[,16:18]))

# Running the source model using fish taxa richness

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.rich.source <- glmulti(NTAXA~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
  fitfunction=glm.redefined,
  data=data.fish.rich,
  level=2,
  marginality=T,
  method="h",
  always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
  INSTRHAB*ACREAGE+INSTRHAB*DLINK+DIST_CON*DLINK")

print(g.rich.source)
summary(g.rich.source)$modelweights[1]
sum(summary(g.rich.source)$modelweights[1:3])
round(coef(g.rich.source,select=2,
  icmethod="Burnham",
  varweighting="Johnson"), 6)
summary(g.rich.source@objects[[1]])$r.squared
extractAIC(g.rich.source@objects[[1]])[1]+1
extractAIC(g.rich.source@objects[[1]])[2]
summary(g.rich.source@objects[[1]])$coef
confint(g.rich.source@objects[[1]])

# -----
# Running the source model using native species richness

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.natrich.source <- glmulti(NTAXA_NAT~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
  fitfunction=glm.redefined,
  data=data.fish.rich.2,
  level=2,
  marginality=T,
  method="h",
  always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
  ACREAGE*INSTRHAB+ACREAGE*ST_GRAD+DLINK*INSTRHAB")

print(g.natrich.source)
summary(g.natrich.source)$modelweights[1]
sum(summary(g.natrich.source)$modelweights[1:4])
round(coef(g.natrich.source,select=2,
  icmethod="Burnham",
  varweighting="Johnson"), 6)
summary(g.natrich.source@objects[[1]])$r.squared
extractAIC(g.natrich.source@objects[[1]])[1]+1
extractAIC(g.natrich.source@objects[[1]])[2]
summary(g.natrich.source@objects[[1]])$coef
confint(g.natrich.source@objects[[1]])

# Running the source model using nonnative species richness
summary(with(data.fish.rich.2,
  glm(NTAXA_NONNAT~INSTRHAB*ST_GRAD*ACREAGE*DIST_CON*DLINK*
  NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,family=poisson)))
options("glmulti-cvalue"=232.57/257)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.nonnatrich.source <- glmulti(NTAXA_NONNAT~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
  fitfunction=glm.redefined,
  data=data.fish.rich.2,
  family="poisson",
  crit="aicc",
  level=2,

```

```

        marginality=T,
        method="h",
        always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
ACREAGE*INSTRHAB+INSTRHAB*DIST_CON+DLINK*DIST_CON")
print(g.nonnatrigh.source)
summary(g.nonnatrigh.source)$modelweights[1]
sum(summary(g.nonnatrigh.source)$modelweights[1:5])
round(coef(g.nonnatrigh.source,select=2,
        icmethod="Burnham",
        varweighting="Johnson"), 6)
(summary(g.nonnatrigh.source@objects[[1]])$null.deviance-
summary(g.nonnatrigh.source@objects[[1]])$deviance)/
summary(g.nonnatrigh.source@objects[[1]])$null.deviance
extractAIC(g.nonnatrigh.source@objects[[1]])[1]+1
extractAIC(g.nonnatrigh.source@objects[[1]])[2]
summary(g.nonnatrigh.source@objects[[1]])$coef
confint(g.nonnatrigh.source@objects[[1]])

# Running the source model using biomass per square meter

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.biomass.source <- glmulti(BIOM_MSQ~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
        fitfunction=glm.redefined,
        data=data.fish.rich.2,
        level=2,
        marginality=T,
        method="h",
        always="+INSTRHAB + ST_GRAD + ACREAGE + DIST_CON +
ACREAGE:INSTRHAB + DIST_CON:ACREAGE + ST_GRAD:DLINK
+ ACREAGE:DLINK")

print(g.biomass.source)
summary(g.biomass.source)$modelweights[1]
sum(summary(g.biomass.source)$modelweights[1:4])
round(coef(g.biomass.source,select=2,
        icmethod="Burnham",
        varweighting="Johnson"), 6)
summary(g.biomass.source@objects[[1]])$r.squared
extractAIC(g.biomass.source@objects[[1]])[1]+1
extractAIC(g.biomass.source@objects[[1]])[2]
summary(g.biomass.source@objects[[1]])$coef
confint(g.biomass.source@objects[[1]])

#Looking at interaction between distance to nearest upstream impoundment and number of upstream impoundments
# create data set for plot with high number of impoundments
data.predict<-as.data.frame(cbind(DIST_IMP_US=seq(-5,7,1),DIST_IMP_DS=rep(0,13),INSTRHAB=rep(0,13),
        ST_GRAD=rep(0,13),DIST_CON=rep(0,13),ACREAGE=rep(0,13),
        DLINK=rep(0,13),NUM_IMP_US=rep(8,13)))
# plot of effects of distance to upstream impoundment on biomass when
# the number of impoundments is high
with(data.fish.rich.2,plot(DIST_IMP_US,BIOM_MSQ,
        xlim=c(with(data.fish.rich.2,min(DIST_IMP_US)),with(data.fish.rich.2,max(DIST_IMP_US))),
        ylim=c(0,40),col="lightgray",
        xlab="Standarized Distance to Nearest Upstream Pond",
        ylab="",cex.axis=.7,cex.lab=.7,pch=1,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DIST_IMP_US,predict(g.biomass.source@objects[[1]],
        newdata=data.predict),col="blue"))
# create data set for plot with average number of upstream impoundments
data.predict<-as.data.frame(cbind(DIST_IMP_US=seq(-5,7,1),DIST_IMP_DS=rep(0,13),INSTRHAB=rep(0,13),
        ST_GRAD=rep(0,13),DIST_CON=rep(0,13),ACREAGE=rep(0,13),
        DLINK=rep(0,13),NUM_IMP_US=rep(3.5,13)))
# plot of effects of distance to nearest upstream impoundment on biomass when
# the number of ponds is average
with(data.predict,lines(DIST_IMP_US,(predict(g.biomass.source@objects[[1]],
        newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low number of ponds
data.predict<-as.data.frame(cbind(DIST_IMP_US=seq(-5,7,1),DIST_IMP_DS=rep(0,13),INSTRHAB=rep(0,13),
        ST_GRAD=rep(0,13),DIST_CON=rep(0,13),ACREAGE=rep(0,13),
        DLINK=rep(0,13),NUM_IMP_US=rep(-1,13)))
# plot of effects of distance to nearest upstream impoundment on biomass when
# the number of upstream ponds is low
with(data.predict,lines(DIST_IMP_US,(predict(g.biomass.source@objects[[1]],
        newdata=data.predict)),col="red",lty=3))
legend(0.5,40,legend=c("high number of US ponds","average number of US ponds","low number of US ponds"),
        col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=1)
mtext("Biomass Per Square Meter",side=2,line=-2,outer=T,cex=.8)

# Running the source model using number of benthic species
summary(with(data.fish.rich.2,
        glm(NUMBENTSP~INSTRHAB*ST_GRAD*ACREAGE+DIST_CON+
        NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,family=poisson)))
options("glmulti-cvalue"=274.50/304)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
}

```

```

g.benrich.source <- glmulti(NUMBENTSP~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                             fitfunction=glm.redefined,
                             data=data.fish.rich.2,
                             family="poisson",
                             level=2,
                             marginality=T,
                             method="h",
                             always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON")

print(g.benrich.source)
summary(g.benrich.source)$modelweights[1]
sum(summary(g.benrich.source)$modelweights[1:6])
round(coef(g.benrich.source,select=2,
           icmethod="Burnham",
           varweighting="Johnson"), 6)
extractAIC(g.benrich.source@objects[[1]])[1]+1
extractAIC(g.benrich.source@objects[[1]])[2]
summary(g.benrich.source@objects[[1]])$coef
confint(g.benrich.source@objects[[1]])

# Running the source model using percent generalists, omnivores, and invertivores

x<-with(data.fish.rich.2,round((PGEOMIV/100)*TOTAL_IND,0))
y<-with(data.fish.rich.2,round(TOTAL_IND-((PGEOMIV/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.fish.rich.2,
             glm(xy~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK+
                DIST_CON*INSTRHAB+DLINK*DIST_CON+ACREAGE:DLINK+
                DIST_IMP_US*DIST_IMP_DS+DIST_IMP_US*NUM_IMP_US+DIST_IMP_DS*NUM_IMP_US
                ,family=binomial)))
options("glmulti-cvalue"=23005/308)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.pgeomiv.source <- glmulti(xy~DIST_IMP_US+DIST_IMP_DS+NUM_IMP_US,
                             data=data.fish.rich.2,
                             fitfunc=glm.redefined,
                             family="binomial",
                             crit="qaicc",
                             level=2,
                             marginality=T,
                             always="+INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK+
                             DIST_CON*INSTRHAB+ACREAGE:DLINK+DLINK*DIST_CON")

print(g.pgeomiv.source)
sum(summary(g.pgeomiv.source)$modelweights[1:3])
summary(g.pgeomiv.source)$modelweights[1]
round(coef(g.pgeomiv.source,select=2,
           icmethod="Burnham",
           varweighting="Johnson"), 6)
(summary(g.pgeomiv.source@objects[[1]])$null.deviance-
 summary(g.pgeomiv.source@objects[[1]])$deviance) /
 summary(g.pgeomiv.source@objects[[1]])$null.deviance
extractAIC(g.pgeomiv.source@objects[[1]])[1]+1
extractAIC(g.pgeomiv.source@objects[[1]])[2]
summary(g.pgeomiv.source@objects[[1]])$coef
confint(g.pgeomiv.source@objects[[1]])

```

```

setwd("~/Grad School/Thesis/Data Analysis/Fish")
data.fish.taxa.R<-read.csv("Fish_Variables_RichnessOnly.csv",header=T)
data.fish.taxa<-read.csv("Fish_Variables.csv",header=T)
library(Hmisc)
library(rJava)
library(glmulti)
data.fish.rich<-
  as.data.frame(cbind(data.fish.taxa.R[17],
                      scale(data.fish.taxa.R[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa.R[7]),center=T,scale=T),
                      data.fish.taxa.R[22:23]))

data.fish.rich[1:3,]
data.fish.rich.2<-
  as.data.frame(cbind(data.fish.taxa[18:21],
                      data.fish.taxa[25],
                      data.fish.taxa[14:17],
                      scale(data.fish.taxa[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa[7]),center=T,scale=T),
                      data.fish.taxa[22:23]))

data.fish.rich.2[1:3,]

# Running the isolation model using fish taxa richness
glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.rich.isolate <- glmulti(NTAXA~ROADS_DS+IMP_DS,
                          fitfunction=glm.redefined,
                          data=data.fish.rich,
                          level=2,
                          marginality=T,
                          method="h",
                          always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
INSTRHAB*ACREAGE+INSTRHAB*DLINK+DIST_CON*DLINK")

print(g.rich.isolate)
sum(summary(g.rich.isolate)$modelweights[1:1])
summary(g.rich.isolate)$modelweights[1]
round(coef(g.rich.isolate,select=2,
           icmethod="Burnham",
           varweighting="Johnson"), 6)
summary(g.rich.isolate@objects[[1]])$r.squared
extractAIC(g.rich.isolate@objects[[1]])[1]+1
extractAIC(g.rich.isolate@objects[[1]])[2]
summary(g.rich.isolate@objects[[1]])$coef
confint(g.rich.isolate@objects[[1]])

# -----
# plot of the effects of road and ponds downstream on fish species richness
means<-with(data.fish.taxa.R,as.data.frame(
  tapply(NTAXA,list(ROADS_DS,IMP_DS),mean)))
means
SE<-with(data.fish.taxa,as.data.frame(tapply(NTAXA,list(ROADS_DS,IMP_DS),sd)))/sqrt(
  with(data.fish.taxa.R,table(ROADS_DS,IMP_DS)))
SE
par(fig=c(0,.45,0,1))
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,2],
       plot.data[,2]+plot.data[,4],
       plot.data[,2]-plot.data[,4],
       xlab="",ylab="",
       ylim=c(0,10), xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("Mean fish taxa richness",2,line=3)
text(-0.1,10,"No downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)
par(fig=c(0.45,.9,0,1),new=T)
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,3],
       plot.data[,3]+plot.data[,5],
       plot.data[,3]-plot.data[,5],
       xlab="", ylab="",
       ylim=c(0,10), yaxt="n", xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("No. of roads downstream",1,line=3,at=-.3)
text(-0.1,10,"Downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)

#-----
#Running the isolation model using native species richness

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.natrich.isolate <- glmulti(NTAXA_NAT~ROADS_DS+IMP_DS,
                             fitfunction=glm.redefined,
                             data=data.fish.rich.2,

```

```

        level=2,
        marginality=T,
        method="h",
        always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
        ACREAGE*INSTRHAB+ACREAGE*ST_GRAD+DLINK*INSTRHAB")
print(g.natrigh.isolate)
sum(summary(g.natrigh.isolate)$modelweights[1:1])
summary(g.natrigh.isolate)$modelweights[1]
round(coef(g.natrigh.isolate,select=2,
           icmethod="Burnham",
           varweighting="Johnson"), 6)
summary(g.natrigh.isolate@objects[[1]])$r.squared
extractAIC(g.natrigh.isolate@objects[[1]])[1]+1
extractAIC(g.natrigh.isolate@objects[[1]])[2]
summary(g.natrigh.isolate@objects[[1]])$coef
confint(g.natrigh.isolate@objects[[1]])

# -----
# plot of the effects of road and ponds downstream on native fish species richness
means<-with(data.fish.taxa,as.data.frame(
  tapply(NTAXA_NAT,list(ROADS_DS,IMP_DS),mean))
SE<-with(data.fish.taxa,as.data.frame(tapply(NTAXA_NAT,list(ROADS_DS,IMP_DS),sd)))/sqrt(
  with(data.fish.taxa,table(ROADS_DS,IMP_DS)))
par(fig=c(0,.45,0,1))
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,2],
       plot.data[,2]+plot.data[,4],
       plot.data[,2]-plot.data[,4],
       xlab="",ylab="",
       ylim=c(0,10), xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("Mean native fish taxa richness",2,line=3)
text(-0.1,10,"No downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)
par(fig=c(0.45,.9,0,1),new=T)
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,3],
       plot.data[,3]+plot.data[,5],
       plot.data[,3]-plot.data[,5],
       xlab="", ylab="",
       ylim=c(0,10),yaxt="n", xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("No. of roads downstream",1,line=3,at=-.3)
text(-0.1,10,"Downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)

# -----
# Running the isolation model using non-native fish taxa richness
summary(with(data.fish.rich.2,
             glm(NTAXA_NONNAT~INSTRHAB*ST_GRAD*ACREAGE*DIST_CON*DLINK*ROADS_DS+IMP_DS,
                 family=poisson)))
options("glmulti-cvalue"=202.55/226)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
g.nonnatrich.isolate <- glmulti(NTAXA_NONNAT~ROADS_DS+IMP_DS,
                              fitfunction=glm.redefined,
                              data=data.fish.rich.2,
                              family="poisson",
                              crit="aicc",
                              level=2,
                              marginality=T,
                              method="h",
                              always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK+
                              ACREAGE*INSTRHAB+INSTRHAB*DIST_CON+DLINK*DIST_CON")

print(g.nonnatrich.isolate)
sum(summary(g.nonnatrich.isolate)$modelweights[1:1])
summary(g.nonnatrich.isolate)$modelweights[1]
round(coef(g.nonnatrich.isolate,select=2,
           icmethod="Burnham",
           varweighting="Johnson"), 6)
(summary(g.nonnatrich.isolate@objects[[1]])$null.deviance-
 summary(g.nonnatrich.isolate@objects[[1]])$deviance)/
 summary(g.nonnatrich.isolate@objects[[1]])$null.deviance
extractAIC(g.nonnatrich.isolate@objects[[1]])[1]+1
extractAIC(g.nonnatrich.isolate@objects[[1]])[2]
summary(g.nonnatrich.isolate@objects[[1]])$coef
confint(g.nonnatrich.isolate@objects[[1]])

# -----
# Running the isolation model using biomass per square meter
glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...)
g.biomass.isolate <- glmulti(BIOM_MSQ~ROADS_DS+IMP_DS,

```

```

fitfunction=glm.redefined,
data=data.fish.rich.2,
level=2,
marginality=T,
method="h",
always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+
ACREAGE:INSTRHAB+DIST_CON:ACREAGE+ST_GRAD:DLINK+
ACREAGE:DLINK")

print(g.biomass.isolate)
sum(summary(g.biomass.isolate)$modelweights[1:2])
summary(g.biomass.isolate)$modelweights[1]
round(coef(g.biomass.isolate,select=2,
icmethod="Burnham",
varweighting="Johnson"), 6)
summary(g.biomass.isolate@objects[[1]])$r.squared
extractAIC(g.biomass.isolate@objects[[1]])[1]+1
extractAIC(g.biomass.isolate@objects[[1]])[2]
summary(g.biomass.isolate@objects[[1]])$coef
confint(g.biomass.isolate@objects[[1]])

# -----
# Plot of the effects of ponds downstream on biomass per meter squared
means<-with(data.fish.taxa,as.data.frame(
tapply(BIOM_MSQ,list(ROADS_DS,IMP_DS),mean))
SE<-with(data.fish.taxa,as.data.frame(tapply(BIOM_MSQ,list(ROADS_DS,IMP_DS),sd)))/sqrt(
with(data.fish.taxa,table(ROADS_DS,IMP_DS)))
par(fig=c(0,.45,0,1))
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,2],
plot.data[,2]+plot.data[,4],
plot.data[,2]-plot.data[,4],
xlab="",ylab="",
ylim=c(0,10),xaxt="n",bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("Mean biomass per square meter",2,line=3)
text(-0.1,10,"No downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)
par(fig=c(0.45,.9,0,1),new=T)
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,3],
plot.data[,3]+plot.data[,5],
plot.data[,3]-plot.data[,5],
xlab="",ylab="",
ylim=c(0,10),yaxt="n",xaxt="n",bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("No. of roads downstream",1,line=3,at=-.3)
text(-0.1,10,"Downstream",pos=4)
text(-0.1,9.5,"impoundments",pos=4)

# -----
# Running the isolation model using number of benthic species
glm.redefined = function(formula, data, always="", ...) {
glm(as.formula(paste(deparse(formula), always)), data=data, ...)}
g.benrich.isolate <- glmulti(NUMBENTSP~ROADS_DS+IMP_DS,
fitfunction=glm.redefined,
data=data.fish.rich.2,
family="poisson",
level=2,
marginality=T,
method="h",
always="+ST_GRAD+INSTRHAB+ACREAGE+DIST_CON")

print(g.benrich.isolate)
sum(summary(g.benrich.isolate)$modelweights[1:4])
summary(g.benrich.isolate)$modelweights[1]
round(coef(g.benrich.isolate,select=2,
icmethod="Burnham",
varweighting="Johnson"), 6)
(summary(g.benrich.isolate@objects[[1]])$null.deviance-
summary(g.benrich.isolate@objects[[1]])$deviance)/
summary(g.benrich.isolate@objects[[1]])$null.deviance
extractAIC(g.benrich.isolate@objects[[1]])[1]+1
extractAIC(g.benrich.isolate@objects[[1]])[2]
summary(g.benrich.isolate@objects[[1]])$coef
confint(g.benrich.isolate@objects[[1]])

# -----
# Plot of the effects of ponds downstream on biomass per meter squared
means<-with(data.fish.taxa,as.data.frame(
tapply(NUMBENTSP,list(ROADS_DS,IMP_DS),mean))
SE<-with(data.fish.taxa,as.data.frame(tapply(NUMBENTSP,list(ROADS_DS,IMP_DS),sd)))/sqrt(
with(data.fish.taxa,table(ROADS_DS,IMP_DS)))
par(fig=c(0,.45,0,1))
par(mar=c(5,1.5,1,.5))

```

```

plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,2],
        plot.data[,2]+plot.data[,4],
        plot.data[,2]-plot.data[,4],
        xlab="",ylab="",
        ylim=c(0,2), xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("Mean number of benthic species",2,line=3)
text(-0.1,14,"No downstream",pos=4,cex=.8)
text(-0.1,12,"impoundments",pos=4,cex=.8)
par(fig=c(0.45,.9,0,1),new=T)
par(mar=c(5,1.5,1,.5))
plot.data<-cbind(labels=c(0,1,2),means,SE)
errbar(plot.data$labels,plot.data[,3],
        plot.data[,3]+plot.data[,5],
        plot.data[,3]-plot.data[,5],
        xlab="", ylab="",
        ylim=c(0,2), yaxt="n", xaxt="n", bty="n")
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("No. of roads downstream",1,line=3,at=-.3)
text(-0.1,14,"Downstream",pos=4,cex=.8)
text(-0.1,12,"impoundments",pos=4,cex=.8)

# -----
# Running the isolation model using percent generalists, omnivores, and invertivores
x<-with(data.fish.rich.2,round((PGEOMIV/100)*TOTAL_IND,0))
y<-with(data.fish.rich.2,round(TOTAL_IND-((PGEOMIV/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.fish.rich.2,
             glm(xy~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK+
                 DIST_CON:INSTRHAB+DLINK:ACREAGE+DLINK:DIST_CON+ROADS_DS*IMP_DS
                 ,family=binomial)))
options("glmulti-cvalue"=23067/309)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.pgeomiv.isolate <- glmulti(xy~ROADS_DS+IMP_DS,
                             data=data.fish.rich.2,
                             fitfunc=glm.redefined,
                             family="binomial",
                             crit="qaicc",
                             level=2,
                             marginality=T,
                             always="+INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK+
DIST_CON*INSTRHAB+ACREAGE:DLINK+DLINK*DIST_CON")

print(g.pgeomiv.isolate)
summary(g.pgeomiv.isolate)$modelweights[1]
sum(summary(g.pgeomiv.isolate)$modelweights[1:1])
extractAIC(g.pgeomiv.isolate@objects[[1]])[1]+1
extractAIC(g.pgeomiv.isolate@objects[[1]])[2]
summary(g.pgeomiv.isolate@objects[[1]])$coef
confint(g.pgeomiv.isolate@objects[[1]])
round(coef(g.pgeomiv.isolate,select=2,icmethod="Burnham",varweighting="Johnson"), 6)
(summary(g.pgeomiv.isolate@objects[[1]])$null.deviance-
summary(g.pgeomiv.isolate@objects[[1]])$deviance)/
summary(g.pgeomiv.isolate@objects[[1]])$null.deviance

```

```

setwd("~/Grad School/Thesis/Data Analysis/Fish/DLINK Test")
data.fish.taxa.R<-read.csv("Fish_Variables_RichnessOnly.csv",header=T)
data.fish.taxa<-read.csv("Fish_Variables.csv",header=T)
library(Hmisc)
library(rJava)
library(glmulti)
library(MASS)

# examination of correlations between independent variables
rcorr(as.matrix(data.fish.taxa.R[,2:7]))
# note that epibentic substrate and instream habitat are highly correlated (r = 0.76; P<< 0.001).
# Therefore, we have retained instrteam habitat and left benthis substate out of the models.
# instream habitat was the one related to fish if I remember correctly.

# creating data sets with standardized variables. Note that we include only those variable
# that we need. Scale function here takes columns 2 through 7 of the data.fish.taxa.R data
# set and centers the values (ie subtracts the mean) and scales them (ie divides by the
# standard deviation). The reason for this is so the parameter estimates are all on the same
# scale and can be compared to assess importance.
data.fish.rich<-
  as.data.frame(cbind(data.fish.taxa.R[17],
                      scale(data.fish.taxa.R[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa.R[7]),center=T,scale=T)
                    )
)
data.fish.rich[1:3,]
data.fish.rich.2<-
  as.data.frame(cbind(data.fish.taxa[18:21],
                      data.fish.taxa[25],
                      data.fish.taxa[14:17],
                      scale(data.fish.taxa[2:6],center=T,scale=T),
                      scale(log(data.fish.taxa[7]),center=T,scale=T)
                    )
)
data.fish.rich.2[1:3,]

install.packages('pastecs')
library(pastecs)
stat.desc(data.fish.taxa.R[2:7])

-----
# Running the base model using fish taxa richness
with(data.fish.rich,hist(NTAXA,seq(0,21,1)))
g.rich.base <- glmulti(NTAXA~ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK,
                      fitfunction="lm",
                      data=data.fish.rich,
                      level=2,
                      marginality=T)

print(g.rich.base)
sum(summary(g.rich.base)$modelweights[1:9]) # weight of model within 2 AICc of best model
summary(g.rich.base)$modelweights[1] # weight for best model
summary(g.rich.base@objects[[1]])$r.squared # produce r-squared for best model
round(coef(g.rich.base,select=2, # mean parameter estimate and unconditional
          icmethod="Burnham", # variances over models within 2 AICc units
          varweighting="Johnson"), 3) # of the best model
extractAIC(g.rich.base@objects[[1]])[1]+1 # k for the best model
# (note 1 has been added for error term)
extractAIC(g.rich.base@objects[[1]])[2] # AIC for best modle
summary(g.rich.base@objects[[1]])$coef # Parameter estimates for the best model
confint(g.rich.base@objects[[1]]) # 95% confidence intervals for the
# parameter estimates

-----
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
#Looking at interaction between instream habitat and acreage
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(2,13),
                                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                DLINK=rep(0,13)))
# plot of effects of drainage area on taxa richness when
# instream habitat is good
with(data.fish.rich,plot(ACREAGE,NTAXA,
                        cex.axis=.7,cex.lab=.7,
                        xlim=c(with(data.fish.rich,min(ACREAGE)),
                              with(data.fish.rich,max(ACREAGE))),ylim=c(0,25),
                        col="lightgray",
                        xlab="Standarized Drainage Area (stream size)",
                        ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE,(predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                DLINK=rep(0,13)))
# plot of effects of acreage on taxa richness when

```

```

# instream habitat is average
with(data.predict,lines(ACREAGE, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),
                        col="brown",lty=2))
# create data set for plot with bad instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(-2,13),
                                  ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                  DLINK=rep(0,13)))
# plot of effects of acreage on taxa richness when
# instream habitat is bad
with(data.predict,lines(ACREAGE, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),
                        col="red",lty=3))
legend(-1,30,legend=c("good habitat","average habitat","bad habitat"),
       col=c("blue","brown","red"),
       lty=c(1,2,3),bty="n",y.intersp=0.2,cex=.6)

#Looking at interaction between instream habitat and dlink
par(fig=c(.25,.75,.35,.7),new=T)
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(2,15),
                                  ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                                  ACREAGE=rep(0,15)))
# plot of effects of d-link on taxa richness when
# instream habitat is good
with(data.fish.rich,plot(DLINK,NTAXA,
                        xlim=c(with(data.fish.rich,min(DLINK)),
                               with(data.fish.rich,max(DLINK))),
                        ylim=c(0,25),col="lightgray",
                        xlab="Standarized D-link (adjacent habitat)",
                        ylab="",cex.axis=.7,cex.lab=.7,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DLINK, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),
                        col="blue"))
# create data set for plot with average instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(0,15),
                                  ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                                  ACREAGE=rep(0,15)))
# plot of effects of d-link on taxa richness when
# instream habitat is average
with(data.predict,lines(DLINK, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),col="brown",lty=2))
# create data set for plot with bad instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(-2,15),
                                  ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                                  ACREAGE=rep(0,15)))
# plot of effects of dlink on taxa richness when
# instream habitat is bad
with(data.predict,lines(DLINK, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),col="red",lty=3))
legend(2,26.5,legend=c("good habitat","average habitat","bad habitat"),
       col=c("blue","brown","red"),
       lty=c(1,2,3),bty="n",y.intersp=0.2,cex=.6)

par(fig=c(.25,.75,.05,.4),new=T,mgp=c(2,.4,0))
#Looking at interaction between distance to confluence and dlink
# create data set for plot with high dlink
data.predict<-as.data.frame(cbind(DIST_CON=seq(-5,6,1), INSTRHAB=rep(0,12),
                                  ST_GRAD=rep(0,12),DLINK=rep(4,12),
                                  ACREAGE=rep(0,12)))
# plot of effects of distance to confluence on taxa richness when
# dlink is high
with(data.fish.rich,plot(DIST_CON,NTAXA,
                        xlim=c(with(data.fish.rich,min(DIST_CON)),with(data.fish.rich,max(DIST_CON))),
                        ylim=c(0,25),col="lightgray",
                        xlab="Standarized Distance to Confluence\n(isolation)",
                        ylab="",cex.axis=.7,cex.lab=.7,pch=1,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DIST_CON,predict(g.rich.base@objects[[1]],
                                         newdata=data.predict),col="blue",lty=1))
# create data set for plot with average dlink is average
data.predict<-as.data.frame(cbind(DIST_CON=seq(-5,6,1), INSTRHAB=rep(0,12),
                                  ST_GRAD=rep(0,12),DLINK=rep(1.5,12),
                                  ACREAGE=rep(0,12)))
# plot of effects of distance to confluence on taxa richness when
# dlink is average
with(data.predict,lines(DIST_CON, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low dlink
data.predict<-as.data.frame(cbind(DIST_CON=seq(-5,6,1), INSTRHAB=rep(0,12),
                                  ST_GRAD=rep(0,12),DLINK=rep(-1,12),
                                  ACREAGE=rep(0,12)))
# plot of effects of distance to confluence on taxa richness when
# dlink is low
with(data.predict,lines(DIST_CON, (predict(g.rich.base@objects[[1]],
                                         newdata=data.predict)),col="red",lty=3))

```

```

legend(2,26.5,legend=c("high d-link","average d-link","low d-link"),
      col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=.2)
mtext("Fish Species Richness",side=2,line=-4,outer=T,cex=.8)

```

```

-----
# Running the base model using fish native taxa richness
with(data.fish.rich.2,hist(NTAXA_NAT,seq(0,20,1)))
g.natrigh.base <- glmulti(NTAXA_NAT~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK,
                        fitfunction="lm",
                        data=data.fish.rich.2,
                        level=2,
                        marginality=T)

print(g.natrigh.base)
sum(summary(g.natrigh.base)$modelweights[1:17])
summary(g.natrigh.base)$modelweights[1]
summary(g.natrigh.base@objects[[1]])$r.squared
round(coef(g.natrigh.base,select=2,
          icmethod="Burnham",
          varweighting="Johnson"), 6)
extractAIC(g.natrigh.base@objects[[1]])[1]+1
extractAIC(g.natrigh.base@objects[[1]])[2]
summary(g.natrigh.base@objects[[1]])$coef
confint(g.natrigh.base@objects[[1]])

# -----
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
#Looking at interaction between instream habitat and acreage
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(2,13),
                                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                DLINK=rep(0,13)))

# plot of effects of drainage area on native taxa richness when
# instream habitat is good
with(data.fish.rich.2,plot(ACREAGE,NTAXA_NAT,
                        cex.axis=.7,cex.lab=.7,
                        xlim=c(with(data.fish.rich.2,min(ACREAGE)),
                              with(data.fish.rich.2,max(ACREAGE))),ylim=c(0,25),
                        col="lightgray",
                        xlab="Standarized Drainage Area (stream size)",
                        ylab="",las=1,tck=-0.04,cex=.8))

with(data.predict,lines(ACREAGE,(predict(g.natrigh.base@objects[[1]],
                                       newdata=data.predict)),
                        pch=1,col="blue",cex=.8))

# create data set for plot with average instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                DLINK=rep(0,13)))

# plot of effects of acreage on native taxa richness when
# instream habitat is average
with(data.predict,lines(ACREAGE,(predict(g.natrigh.base@objects[[1]],
                                       newdata=data.predict)),
                        col="brown",lty=2))

# create data set for plot with bad instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(-2,13),
                                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                DLINK=rep(0,13)))

# plot of effects of acreage on native taxa richness when
# instream habitat is bad
with(data.predict,lines(ACREAGE,(predict(g.natrigh.base@objects[[1]],
                                       newdata=data.predict)),
                        col="red",lty=3))

legend(-1.3,30,legend=c("good habitat","average habitat","bad habitat"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)

#Looking at interaction between instream habitat and dlink
par(fig=c(.25,.75,.35,.7),new=T)
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1),INSTRHAB=rep(2,15),
                                ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                                ACREAGE=rep(0,15)))

# plot of effects of d-link on native taxa richness when
# instream habitat is good
with(data.fish.rich.2,plot(DLINK,NTAXA_NAT,
                        xlim=c(with(data.fish.rich.2,min(DLINK)),
                              with(data.fish.rich.2,max(DLINK))),
                        ylim=c(0,25),col="lightgray",
                        xlab="Standarized D-link (adjacent habitat)",
                        ylab="",cex.axis=.7,cex.lab=.7,las=1,tck=-0.04,cex=.8))

with(data.predict,lines(DLINK,(predict(g.natrigh.base@objects[[1]],
                                       newdata=data.predict)),
                        col="blue"))

# create data set for plot with average instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1),INSTRHAB=rep(0,15),
                                ST_GRAD=rep(0,15),DIST_CON=rep(0,15),

```

```

                ACREAGE=rep(0,15))
# plot of effects of d-link on native taxa richness when
# instream habitat is average
with(data.predict,lines(DLINK,(predict(g.natrich.base@objects[[1]],
                newdata=data.predict)),col="brown",lty=2))
# create data set for plot with bad instream habitat
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1),INSTRHAB=rep(-2,15),
                ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                ACREAGE=rep(0,15)))
# plot of effects of dlink on native taxa richness when
# instream habitat is bad
with(data.predict,lines(DLINK,(predict(g.natrich.base@objects[[1]],
                newdata=data.predict)),col="red",lty=3))
legend(2,26,legend=c("good habitat","average habitat","bad habitat"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)

par(fig=c(.25,.75,.05,.4),new=T,mgp=c(2,.4,0))
#Looking at interaction between drainage area and stream gradient
# create data set for plot with high gradient
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                ST_GRAD=rep(2,13),DLINK=rep(0,13),
                DIST_CON=rep(0,13)))
# plot of effects of drainage area on native taxa richness when
# gradient is high
with(data.fish.rich.2,plot(ACREAGE,NTAXA,
                xlim=c(with(data.fish.rich.2,min(ACREAGE)),with(data.fish.rich.2,max(ACREAGE))),
                ylim=c(0,25),col="lightgray",
                xlab="Standarized Drainage Area\n(stream size)",
                ylab="",cex.axis=.7,cex.lab=.7,pch=1,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE,predict(g.natrich.base@objects[[1]],
                newdata=data.predict),col="blue"))
# create data set for plot with average stream gradient
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                ST_GRAD=rep(0,13),DLINK=rep(0,13),
                DIST_CON=rep(0,13)))
# plot of effects of drainage area on native taxa richness when
# gradient is average
with(data.predict,lines(ACREAGE,(predict(g.natrich.base@objects[[1]],
                newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low gradient
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                ST_GRAD=rep(-2,13),DLINK=rep(0,13),
                DIST_CON=rep(0,13)))
# plot of effects of drainage area on native taxa richness when
# gradient is low
with(data.predict,lines(ACREAGE,(predict(g.natrich.base@objects[[1]],
                newdata=data.predict)),col="red",lty=3))
legend(-1.4,30,legend=c("high gradient","average gradient","low gradient"),
        col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=.2)
mtext("Native Fish Species Richness",side=2,line=-4,outer=T,cex=.8)

# -----
# Running the base model using fish non-native taxa richness

with(data.fish.taxa,hist(NTAXA_NONNAT,seq(0,20,1)))
summary(with(data.fish.rich.2,
        glm(NTAXA_NONNAT~INSTRHAB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=poisson)))
options("glmulti-cvalue"=303.80/291)
g.nonatrich.base <- glmulti(NTAXA_NONNAT~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK,
        fitfunction="glm",
        family="poisson",
        crit="qaicc",
        data=data.fish.rich.2,
        level=2,
        marginality=T)

print(g.nonatrich.base)
sum(summary(g.nonatrich.base)$modelweights[1:9])
summary(g.nonatrich.base)$modelweights[1]
(summary(g.nonatrich.base@objects[[1]])$null.deviance-
summary(g.nonatrich.base@objects[[1]])$deviance)/
summary(g.nonatrich.base@objects[[1]])$null.deviance
round(coef(g.nonatrich.base,select=2,icmethod="Burnham",varweighting="Johnson"),3)
extractAIC(g.nonatrich.base@objects[[1]])[1]+1
extractAIC(g.nonatrich.base@objects[[1]])[2]
summary(g.nonatrich.base@objects[[1]])$coef
confint(g.nonatrich.base@objects[[1]])

# -----
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
#Looking at interaction between instream habitat and acreage
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(2,13),
                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                DLINK=rep(0,13)))

```



```

newdata=data.predict),col="blue"))
# create data set for plot with average d-link
data.predict<-as.data.frame(cbind(DIST_CON=seq(-5,6,1),INSTRHAB=rep(0,12),
ST_GRAD=rep(0,12),DLINK=rep(1.5,12),
ACREAGE=rep(0,12)))
# plot of effects of distance to confluence on nonnative taxa richness when
# dlink is average
with(data.predict,lines(DIST_CON,(predict(g.nonatrigh.base@objects[[1]],
newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low d-link
data.predict<-as.data.frame(cbind(DIST_CON=seq(-5,6,1),INSTRHAB=rep(0,12),
ST_GRAD=rep(0,12),DLINK=rep(-1,12),
ACREAGE=rep(0,12)))
# plot of effects of distance to confluence on nonnative taxa richness when
# dlink is low
with(data.predict,lines(DIST_CON,(predict(g.nonatrigh.base@objects[[1]],
newdata=data.predict)),col="red",lty=3))
legend(-1.4,6,legend=c("high dlink","average dlink","low dlink"),
col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=.2)
mtext("Non-native Fish Species Richness",side=2,line=-4,outer=T,cex=.8)

# -----
# Running the base model using fish biomass per square meter
with(data.fish.taxa,hist(BIOM_MSQ))

g.biomass.base <- glmulti(BIOM_MSQ~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+DLINK,
fitfunction="lm",
data=data.fish.rich.2,
level=2,
marginality=T)

print(g.biomass.base)
sum(summary(g.biomass.base)$modelweights[1:13])
summary(g.biomass.base)$modelweights[1]
summary(g.biomass.base@objects[[1]])$r.squared
round(coef(g.biomass.base,select=2,icmethod="Burnham",varweighting="Johnson"), 3)
extractAIC(g.biomass.base@objects[[1]])[1]+1
extractAIC(g.biomass.base@objects[[1]])[2]
summary(g.biomass.base@objects[[1]])$coef
confint(g.biomass.base@objects[[1]])

# -----
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
#Looking at interaction between instream habitat and acreage
# create data set for plot with good instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(2,13),
ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
DLINK=rep(0,13)))
# plot of effects of drainage area on biomass when
# instream habitat is good
with(data.fish.rich.2,plot(ACREAGE,BIOM_MSQ,
cex.axis=.7,cex.lab=.7,
xlim=c(with(data.fish.rich.2,min(ACREAGE)),
with(data.fish.rich.2,max(ACREAGE))),ylim=c(0,40),
col="lightgray",
xlab="Standarized Drainage Area (stream size)",
ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
newdata=data.predict)),
pch=1,col="blue",cex=.8))
# create data set for plot with average instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
DLINK=rep(0,13)))
# plot of effects of acreage on biomass when
# instream habitat is average
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
newdata=data.predict)),
col="brown",lty=2))
# create data set for plot with bad instream habitat
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(-2,13),
ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
DLINK=rep(0,13)))
# plot of effects of acreage on biomass when
# instream habitat is bad
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
newdata=data.predict)),
col="red",lty=3))
legend(3,45,legend=c("good habitat","average habitat","bad habitat"),
col=c("blue","brown","red"),
lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)

#Looking at interaction between drainage area and distance to confluence
par(fig=c(.25,.75,.35,.7),new=T)
# create data set for plot with low distance to confluence

```

```

data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(0,13),
                                ST_GRAD=rep(0,13),DLINK=rep(0,13),
                                DIST_CON=rep(-2,13)))
# plot of effects of drainage area on biomass when
# distance to confluence is low
with(data.fish.rich.2,plot(ACREAGE,BIOM_MSQ,
                          xlim=c(with(data.fish.rich.2,min(ACREAGE)),
                                with(data.fish.rich.2,max(ACREAGE))),
                          ylim=c(0,40),col="lightgray",
                          xlab="Standarized Drainage Area (stream size)",
                          ylab="",cex.axis=.7,cex.lab=.7,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
                                         newdata=data.predict)),
                       col="blue"))
# create data set for plot with average distance to confluence
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(0,13),
                                ST_GRAD=rep(0,13),DLINK=rep(0,13),
                                DIST_CON=rep(0,13)))
# plot of effects of drainage area on biomass when
# distance to confluence is average
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
                                         newdata=data.predict)),col="brown",lty=2))
# create data set for plot with high distance to confluence
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(0,13),
                                ST_GRAD=rep(0,13),DLINK=rep(0,13),
                                DIST_CON=rep(2,13)))
# plot of effects of drainage area on biomass when
# distance to confluence is high
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
                                         newdata=data.predict)),col="red",lty=3))
legend(3,45,legend=c("low distance","average distance","high distance"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)

par(fig=c(.25,.75,.05,.4),new=T,mgp=c(2,.4,0))
#Looking at interaction between gradient and dlink
# create data set for plot with high gradient
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(0,15),
                                DIST_CON=rep(0,15),ST_GRAD=rep(2,15),
                                ACREAGE=rep(0,15)))
# plot of effects of dlink on biomass when
# gradient is high
with(data.fish.rich.2,plot(DLINK,BIOM_MSQ,
                          xlim=c(with(data.fish.rich.2,min(DLINK)),with(data.fish.rich.2,max(DLINK))),
                          ylim=c(0,40),col="lightgray",
                          xlab="Standarized dlink\n(adjacent habitat)",
                          ylab="",cex.axis=.7,cex.lab=.7,pch=1,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DLINK,predict(g.biomass.base@objects[[1]],
                                     newdata=data.predict),col="blue"))
# create data set for plot with average gradient
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(0,15),
                                ST_GRAD=rep(0,15),DIST_CON=rep(0,15),
                                ACREAGE=rep(0,15)))
# plot of effects of dlink on biomass when
# gradient is average
with(data.predict,lines(DLINK,(predict(g.biomass.base@objects[[1]],
                                     newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low gradient
data.predict<-as.data.frame(cbind(DLINK=seq(-5,9,1), INSTRHAB=rep(0,15),
                                ST_GRAD=rep(-2,15),DIST_CON=rep(0,15),
                                ACREAGE=rep(0,15)))
# plot of effects of dlink on biomass when
# gradient is low
with(data.predict,lines(DLINK,(predict(g.biomass.base@objects[[1]],
                                     newdata=data.predict)),col="red",lty=3))
legend(1.5,45,legend=c("high gradient","average gradient","low gradient"),
      col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=.2)
mtext("Biomass Per Square Meter",side=2,line=-4,outer=T,cex=.8)

#Looking at interaction between drainage area and dlink
# create data set for plot with high dlink
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(0,13),
                                DIST_CON=rep(0,13),ST_GRAD=rep(0,13),
                                DLINK=rep(4,13)))
# plot of effects of drainage area on biomass when
# dlink is high
with(data.fish.rich.2,plot(ACREAGE,BIOM_MSQ,
                          xlim=c(with(data.fish.rich.2,min(ACREAGE)),with(data.fish.rich.2,max(ACREAGE))),
                          ylim=c(0,40),col="lightgray",
                          xlab="Standarized Drainage Area\n(stream size)",
                          ylab="",cex.axis=.7,cex.lab=.7,pch=1,las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE,predict(g.biomass.base@objects[[1]],
                                     newdata=data.predict),col="blue"))
# create data set for plot with average dlink
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1), INSTRHAB=rep(0,13),

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```

                ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                DLINK=rep(1.5,13)))
# plot of effects of drainage area on biomass when
# dlink is average
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
                                         newdata=data.predict)),col="brown",lty=2))
# create data set for plot with low dlink
data.predict<-as.data.frame(cbind(ACREAGE=seq(-5,7,1),INSTRHAB=rep(0,13),
                                  ST_GRAD=rep(0,13),DIST_CON=rep(0,13),
                                  DLINK=rep(-1,13)))
# plot of effects of drainage area on biomass when
# dlink is low
with(data.predict,lines(ACREAGE,(predict(g.biomass.base@objects[[1]],
                                         newdata=data.predict)),col="red",lty=3))
legend(3.5,40,legend=c("high dlink","average dlink","low dlink"),
      col=c("blue","brown","red"),lty=c(1,2,3),bty="n",cex=.6,y.intersp=1)
mtext("Biomass Per Square Meter",side=2,line=-2,outer=T,cex=.8)

# -----
# Running the base model using number of benthic species

with(data.fish.taxa,hist(NUMBENTSP))
summary(with(data.fish.rich.2,
             glm(NUMBENTSP~INSTRHAB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=poisson)))
options("glmulti-cvalue"=262.83/291) # not needed because < 1
g.benrich.base <- glmulti(NUMBENTSP~ST_GRAD+INSTRHAB+ACREAGE+DIST_CON+DLINK,
                          fitfunction="glm",
                          family="poisson",
                          data=data.fish.rich.2,
                          level=2,
                          marginality=T)

print(g.benrich.base)
sum(summary(g.benrich.base)$modelweights[1:32])
summary(g.benrich.base)$modelweights[1]
(summary(g.benrich.base@objects[[1]])$null.deviance-
 summary(g.benrich.base@objects[[1]])$deviance)/
 summary(g.benrich.base@objects[[1]])$null.deviance
round(coef(g.benrich.base,select=2,icmethod="Burnham",varweighting="Johnson"), 3)
extractAIC(g.benrich.base@objects[[1]])[1]+1
extractAIC(g.benrich.base@objects[[1]])[2]
summary(g.benrich.base@objects[[1]])$coef
confint(g.benrich.base@objects[[1]])

# -----
# Running the base model using percent generalists, omnivores, and invertivores
with(data.fish.rich.2,hist(PGEOMIV,seq(0,100,5)))
# note that % generalist are hard to model as there are mostly near 100 or near 0 values
x<-with(data.fish.rich.2,round((PGEOMIV/100)*TOTAL_IND,0))
y<-with(data.fish.rich.2,round(TOTAL_IND-((PGEOMIV/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.fish.rich.2,
             glm(xy~INSTRHAB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=21664/291)
g.geomiv <- glmulti(xy~INSTRHAB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.fish.rich.2,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.geomiv)
sum(summary(g.geomiv)$modelweights[1:25])
summary(g.geomiv)$modelweights[1]
round(coef(g.geomiv,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.geomiv@objects[[1]])$null.deviance-
 summary(g.geomiv@objects[[1]])$deviance)/
 summary(g.geomiv@objects[[1]])$null.deviance
extractAIC(g.geomiv@objects[[1]])[1]+1
extractAIC(g.geomiv@objects[[1]])[2]
summary(g.geomiv@objects[[1]])$coef
confint(g.geomiv@objects[[1]])

# Looking at interaction between instream habitat and distance to confluence
# create data set and plot with short distance to confluence, drainage area average
# and instream habitat scores varied from low to high
data.predict<-as.data.frame(cbind(INSTRHAB=seq(-9,9,.1),ACREAGE=rep(0,1),
                                  DIST_CON=rep(-2,1),ST_GRAD=rep(0,1),DLINK=rep(1,1)))
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mfp=c(1,.4,0))
with(data.fish.rich.2,plot(INSTRHAB,PGEOMIV,
                          cex.axis=.7,cex.lab=.7,
                          xlim=c(with(data.fish.rich.2,min(INSTRHAB)),
                                with(data.fish.rich.2,max(INSTRHAB))),
                          ylim=c(0,100),
                          col="lightgray",
                          xlab="Standardized Instream Habitat Score",

```

```

        ylab="", las=1, tck=-0.04, cex=.8))
with(data.predict, lines(INSTRHAB, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        pch=1, col="blue", cex=.8))
# create data set and plot with medium distance to confluence, dlink average,
# and instream habitat scores varied from low to high
data.predict<-as.data.frame(cbind(INSTRHAB=seq(-9, 9, .1), ACREAGE=rep(0, 1),
        DLINK=rep(1, 1), DIST_CON=rep(0, 1), ST_GRAD=rep(0, 1)))
with(data.predict, lines(INSTRHAB, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        col="brown", lty=2))
# create data set for plot with large distance to confluence, dlink average,
# and instream habitat scores varied from low to high
data.predict<-as.data.frame(cbind(INSTRHAB=seq(-9, 9, .1), ACREAGE=rep(0, 1),
        DLINK=rep(1, 1), DIST_CON=rep(2, 1), ST_GRAD=rep(0, 1)))
# plot of effects of instream habitat scores on percent geomiv when
# distance to confluence is small
with(data.predict, lines(INSTRHAB, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        col="red", lty=3))
legend(-3.5, 35, legend=c("small distance", "medium distance", "large distance"),
        col=c("blue", "brown", "red"),
        lty=c(1, 2, 3), bty="n", y.intersp=.2, cex=.6)
# Looking at interaction between drainage area and dlink
# create data set and plot with average instream habitat, low dlink,
# and drainage area varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9, 9, .1), INSTRHAB=rep(0, 1),
        DLINK=rep(-2, 1), ST_GRAD=rep(0, 1), DIST_CON=rep(0, 1)))
par(fig=c(.25, .75, .35, .70), new=T)
with(data.fish.rich.2, plot(ACREAGE, PGEOMIV,
        cex.axis=.7, cex.lab=.7,
        xlim=c(with(data.fish.rich.2, min(ACREAGE)),
        with(data.fish.rich.2, max(ACREAGE))),
        ylim=c(0, 100),
        col="lightgray",
        xlab="Standardized Drainage Area (Stream Size)",
        ylab="", las=1, tck=-0.04, cex=.8))
with(data.predict, lines(ACREAGE, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        pch=1, col="blue", cex=.8))
# create data set and plot with medium instream habitat, dlink average,
# and drainage area varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9, 9, .1), INSTRHAB=rep(0, 1),
        DLINK=rep(0, 1), ST_GRAD=rep(0, 1), DIST_CON=rep(0, 1)))
with(data.predict, lines(ACREAGE, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        col="brown", lty=2))
# create data set and plot with medium instream habitat, dlink high,
# and drainage area varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9, 9, .1), INSTRHAB=rep(0, 1),
        DLINK=rep(2, 1), ST_GRAD=rep(0, 1), DIST_CON=rep(0, 1)))
# plot of effects of drainage area on percent geomiv when
# dlink is high
with(data.predict, lines(ACREAGE, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        col="red", lty=3))
legend(3, 40, legend=c("low d-link", "medium d-link", "high d-link"),
        col=c("blue", "brown", "red"),
        lty=c(1, 2, 3), bty="n", y.intersp=.2, cex=.6)
# Looking at interaction between distance to confluence and dlink
# create data set and plot with average instream habitat scores, low dlink,
# and distance to nearest confluence varied from small to large
data.predict<-as.data.frame(cbind(DIST_CON=seq(-9, 9, .1), INSTRHAB=rep(0, 1),
        DLINK=rep(-2, 1), ST_GRAD=rep(0, 1), ACREAGE=rep(0, 1)))
par(fig=c(.25, .75, 0.05, .40), new=T)
with(data.fish.rich.2, plot(DIST_CON, PGEOMIV,
        cex.axis=.7, cex.lab=.7,
        xlim=c(with(data.fish.rich.2, min(DIST_CON)),
        with(data.fish.rich.2, max(DIST_CON))),
        ylim=c(0, 100),
        col="lightgray",
        xlab="Standardized Distance to Confluence (Isolation)",
        ylab="", las=1, tck=-0.04, cex=.8))
with(data.predict, lines(DIST_CON, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        pch=1, col="blue", cex=.8))
# create data set and plot with average instream habitat scores, dlink average,
# and distance to confluence varied from low to high
data.predict<-as.data.frame(cbind(DIST_CON=seq(-9, 9, .1), INSTRHAB=rep(0, 1),
        DLINK=rep(0, 1), ST_GRAD=rep(0, 1), ACREAGE=rep(0, 1)))
with(data.predict, lines(DIST_CON, (predict(g.geomiv@objects[[1]],
        newdata=data.predict, type="response")*100),
        col="brown", lty=2))
# create data set and plot with average instream habitat scores, dlink high,
# and distance to confluence varied from low to high

```

```
data.predict<-as.data.frame(cbind(DIST_CON=seq(-9,9,.1),INSTRHAB=rep(0,1),
                                DLINK=rep(2,1),ST_GRAD=rep(0,1),ACREAGE=rep(0,1)))
# plot of effects of distance to confluence scores on percent geomiv when
# dlink is high
with(data.predict,lines(DIST_CON,(predict(g.geomiv@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       col="red",lty=3))
legend(2.5,40,legend=c("low d-link","medium d-link","high d-link"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)
mtext("Percent Generalists, Omnivores, and Invertivores",2,-5,out=T,cex=.8)
```

```

setwd("~/Grad School/Thesis/Data Analysis/Benthics")
data.invert.taxa<-read.csv("Benthic_Variables.csv",header=T)
library(Hmisc)
library(rJava)
library(glmulti)

data.invert.taxal<-
  as.data.frame(cbind(data.invert.taxa[17:21],
                      data.invert.taxa[23],
                      scale(data.invert.taxa[2:6],center=T,scale=T),
                      scale(log(data.invert.taxa[7]),center=T,scale=T),
                      scale(data.invert.taxa[8:10],center=T,scale=T)))

data.invert.taxal[1:3,]

# Running the source model using rarified taxa richness

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.rich.source <- glmulti(log(NTAXA_RAR)~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                        fitfunction=glm.redefined,
                        data=data.invert.taxal,
                        level=2,
                        marginality=T,
                        method="h",
                        always="+EPI_SUB + ST_GRAD + ACREAGE + DLINK + ACREAGE:EPI_SUB + ACREAGE:ST_GRAD +
DLINK:ACREAGE")
print(g.rich.source)
sum(summary(g.rich.source)$modelweights[1:6])
summary(g.rich.source)$modelweights[1]
round(coef(g.rich.source,select=2), 4)
summary(g.rich.source@objects[[1]])$r.squared
extractAIC(g.rich.source@objects[[1]])[1]+1
extractAIC(g.rich.source@objects[[1]])[2]
summary(g.rich.source@objects[[1]])
confint(g.rich.source@objects[[1]])

# Running the source model using percent chironomidae

x<-with(data.invert.taxal,round((PCHIRON/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCHIRON/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
             glm(xy~ST_GRAD*DIST_CON*DLINK*NUM_IMP_US*DIST_IMP_US*DIST_IMP_DS
                ,family=binomial)))
options("glmulti-cvalue"=9475.2/282)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.pchiron.source <- glmulti(xy~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                           data=data.invert.taxal,
                           fitfunc=glm.redefined,
                           family="binomial",
                           crit="qaicc",
                           level=2,
                           marginality=T,
                           always="+ACREAGE+DLINK+DIST_CON")

print(g.pchiron.source)
sum(summary(g.pchiron.source)$modelweights[1:4])
summary(g.pchiron.source)$modelweights[1]
round(coef(g.pchiron.source,select=5), 4)
(summary(g.pchiron.source@objects[[1]])$null.deviance-
 summary(g.pchiron.source@objects[[1]])$deviance)/
 summary(g.pchiron.source@objects[[1]])$null.deviance
extractAIC(g.pchiron.source@objects[[1]])[1]+1
extractAIC(g.pchiron.source@objects[[1]])[2]
summary(g.pchiron.source@objects[[1]])
confint(g.pchiron.source@objects[[1]])

# Running the source model using percent clingers

x<-with(data.invert.taxal,round((PCLING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCLING/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*DIST_CON*NUM_IMP_US*DIST_IMP_US*DIST_IMP_DS
                ,family=binomial)))
options("glmulti-cvalue"=11077/314)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.pcling.source <- glmulti(xy~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                          data=data.invert.taxal,
                          fitfunc=glm.redefined,
                          family="binomial",
                          crit="qaicc",

```

```

        level=2,
        marginality=T,
        always="+EPI_SUB+DIST_CON")

print(g.pcling.source)
sum(summary(g.pcling.source)$modelweights[1:3])
summary(g.pcling.source)$modelweights[1]
round(coef(g.pcling.source,select=3), 4)
(summary(g.pcling.source@objects[[1]])$null.deviance-
 summary(g.pcling.source@objects[[1]])$deviance)/
 summary(g.pcling.source@objects[[1]])$null.deviance
extractAIC(g.pcling.source@objects[[1]])[1]+1
extractAIC(g.pcling.source@objects[[1]])[2]
summary(g.pcling.source@objects[[1]])
confint(g.pcling.source@objects[[1]])

# Running the source model using percent shredders

x<-with(data.invert.taxal,round((PSHRED/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PSHRED/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*DLINK*NUM_IMP_US*DIST_IMP_US*DIST_IMP_DS
                 ,family=binomial)))
options("glmulti-cvalue"=5293.7/282)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.pshred.source <- glmulti(xy~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                          data=data.invert.taxal,
                          fitfunc=glm.redefined,
                          family="binomial",
                          crit="qaicc",
                          level=2,
                          marginality=T,
                          always="+EPI_SUB+ST_GRAD+
                                  EPI_SUB*ST_GRAD")

print(g.pshred.source)
sum(summary(g.pshred.source)$modelweights[1:7])
summary(g.pshred.source)$modelweights[1]
round(coef(g.pshred.source,select=7), 4)
(summary(g.pshred.source@objects[[1]])$null.deviance-
 summary(g.pshred.source@objects[[1]])$deviance)/
 summary(g.pshred.source@objects[[1]])$null.deviance
extractAIC(g.pshred.source@objects[[1]])[1]+1
extractAIC(g.pshred.source@objects[[1]])[2]
summary(g.pshred.source@objects[[1]])
confint(g.pshred.source@objects[[1]])

# Running the source model using percent flying insects

x<-with(data.invert.taxal,round((PFLYING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PFLYING/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB+ACREAGE+DLINK+DIST_CON
                 +EPI_SUB*ACREAGE
                 +EPI_SUB*DLINK
                 +ACREAGE*DLINK
                 +DIST_CON*DLINK
                 +NUM_IMP_US*DIST_IMP_US
                 +NUM_IMP_US*DIST_IMP_DS
                 +DIST_IMP_US*DIST_IMP_DS
                 ,family=binomial)))
options("glmulti-cvalue"=6930.8/331)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...)
}
g.pflying.source <- glmulti(xy~NUM_IMP_US+DIST_IMP_US+DIST_IMP_DS,
                          data=data.invert.taxal,
                          fitfunc=glm.redefined,
                          family="binomial",
                          crit="qaicc",
                          level=2,
                          marginality=T,
                          always="+EPI_SUB+ACREAGE+DLINK+
                                  EPI_SUB*ACREAGE+EPI_SUB*DLINK+ACREAGE*DLINK")

print(g.pflying.source)
sum(summary(g.pflying.source)$modelweights[1:5])
summary(g.pflying.source)$modelweights[1]
round(coef(g.pflying.source,select=2), 4)
(summary(g.pflying.source@objects[[1]])$null.deviance-
 summary(g.pflying.source@objects[[1]])$deviance)/
 summary(g.pflying.source@objects[[1]])$null.deviance
extractAIC(g.pflying.source@objects[[1]])[1]+1
extractAIC(g.pflying.source@objects[[1]])[2]
summary(g.pflying.source@objects[[1]])
confint(g.pflying.source@objects[[1]])

```

```

setwd("~/Grad School/Thesis/Data Analysis/Benthics")
data.invert.taxa<-read.csv("Benthic_Variables.csv",header=T)
library(Hmisc)
library(rJava)
library(glmulti)

data.invert.taxal<-
  as.data.frame(cbind(data.invert.taxa[17:21],
                      data.invert.taxa[23],
                      scale(data.invert.taxa[2:6],center=T,scale=T), data.invert.taxa[11],
                      scale(log(data.invert.taxa[7]),center=T,scale=T),data.invert.taxa[13]))
data.invert.taxal[1:3,]

# Running the isolation model using rarified taxa richness

glm.redefined = function(formula, data, always="", ...) {
  lm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.rich.isolate <- glmulti(log(NTAXA_RAR)~ROADS_DS+IMP_DS,
                          fitfunction=glm.redefined,
                          data=data.invert.taxal,
                          level=2,
                          marginality=T,
                          method="h",
                          always="+EPI_SUB + ST_GRAD + ACREAGE + DLINK + ACREAGE:EPI_SUB + ACREAGE:ST_GRAD +
DLINK:ACREAGE")
print(g.rich.isolate)
sum(summary(g.rich.isolate)$modelweights[1:2])
summary(g.rich.isolate)$modelweights[1]
round(coef(g.rich.isolate,select=2), 4)
summary(g.rich.isolate@objects[[1]])$r.squared
extractAIC(g.rich.isolate@objects[[1]])[1]+1
extractAIC(g.rich.isolate@objects[[1]])[2]
summary(g.rich.isolate@objects[[1]])
confint(g.rich.isolate@objects[[1]])

# Running the isolation model using percent chironomidae

x<-with(data.invert.taxal,round((PCHIRON/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCHIRON/100)*TOTAL_IND),0))
xy<-cbind(x,y)
#Is the below model correct? Are all of the variables supposed to be multiplied or added together? Or should this
be the best fit model added to RoadsDS*IMP DS?
summary(with(data.invert.taxal,
             glm(xy~ACREAGE+DLINK+DIST_CON
                ,family=binomial)))
options("glmulti-cvalue"=12484/342)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.pchiron.isolate <- glmulti(xy~ROADS_DS+IMP_DS,
                             data=data.invert.taxal,
                             fitfunc=glm.redefined,
                             family="binomial",
                             crit="qaicc",
                             level=2,
                             marginality=T,
                             always="+ACREAGE+DLINK+DIST_CON")

print(g.pchiron.isolate)
sum(summary(g.pchiron.isolate)$modelweights[1:3])
sum(summary(g.pchiron.isolate)$modelweights[1])
(summary(g.pchiron.isolate@objects[[1]])$null.deviance-
 summary(g.pchiron.isolate@objects[[1]])$deviance)/
  summary(g.pchiron.isolate@objects[[1]])$null.deviance
round(coef(g.pchiron.isolate,select=2), 4)
extractAIC(g.pchiron.isolate@objects[[1]])[1]+1
extractAIC(g.pchiron.isolate@objects[[1]])[2]
summary(g.pchiron.isolate@objects[[1]])
confint(g.pchiron.isolate@objects[[1]])

# Running the isolation model using percent clingers

x<-with(data.invert.taxal,round((PCLING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCLING/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*DIST_CON*ROADS_DS*IMP_DS
                ,family=binomial)))
options("glmulti-cvalue"=10596/322)
glm.redefined = function(formula, data, always="", ...) {
  glm(as.formula(paste(deparse(formula), always)), data=data, ...) }
g.pcling.isolate <- glmulti(xy~ROADS_DS+IMP_DS,
                             data=data.invert.taxal,

```

```

fitfunc=glm.redefined,
family="binomial",
crit="qaicc",
level=2,
marginality=T,
always="+EPI_SUB+DIST_CON")

print(g.pcling.isolate)
sum(summary(g.pcling.isolate)$modelweights[1:1])
sum(summary(g.pcling.isolate)$modelweights[1])
(summary(g.pcling.isolate@objects[[1]])$null.deviance-
summary(g.pcling.isolate@objects[[1]])$deviance)/
summary(g.pcling.isolate@objects[[1]])$null.deviance
round(coef(g.pcling.isolate,select=2), 4)
extractAIC(g.pcling.isolate@objects[[1]])[1]+1
extractAIC(g.pcling.isolate@objects[[1]])[2]
summary(g.pcling.isolate@objects[[1]])
confint(g.pcling.isolate@objects[[1]])

#plot of the interaction of road downstream and impoundments down stream
model<-with(data.invert.taxal,glm(xy~ROADS_DS+IMP_DS+EPI_SUB+DIST_CON+ROADS_DS*IMP_DS,
family=binomial))

summary(model)
predict.data1<-
as.data.frame(cbind(EPI_SUB=rep(0,6),
DIST_CON=rep(0,6)))

predict.data1
predict.data2<-
as.data.frame(cbind(ROADS_DS=with(data.invert.taxal,rep(levels(ROADS_DS),2)),
IMP_DS=with(data.invert.taxal,c(rep(levels(IMP_DS)[1],3),
rep(levels(IMP_DS)[2],3))))))

predict.data2
predict.data<-cbind(predict.data1,predict.data2)
predict.data
plot.data<-as.data.frame(predict(model,newdata=predict.data,se.fit=T))
plot.data<-cbind(mean=plot.data[,1],
plus=plot.data[,1]+(1.96*plot.data[,2]),
minus=plot.data[,1]-(1.96*plot.data[,2]))
plot.data<-exp(plot.data)/(1+exp(plot.data))
plot.data
par(fig=c(0.1,.5,0,1))
par(mar=c(5,1.5,1,.5))
errbar(c(0,1,2),plot.data[1:3,1],
plot.data[1:3,2],
plot.data[1:3,3],
xlab="",ylab="",
ylim=c(0,1),xaxt="n")
lines(c(0,1,2),plot.data[1:3,1],lty=2)
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("Percent Clingers",2,line=3)
text(-0.1,.03,"No downstream",pos=4,cex=.8)
text(-0.1,0,"impoundments",pos=4,cex=.8)
par(fig=c(0.5,.9,0,1),new=T)
par(mar=c(5,1.5,1,.5))
errbar(c(0,1,2),plot.data[4:6,1],
plot.data[4:6,2],
plot.data[4:6,3],
xlab="",ylab="",
ylim=c(0,1),yaxt="n",xaxt="n")
lines(c(0,1,2),plot.data[4:6,1],lty=2)
axis(1,at=c(0,1,2),labels=c("0","1","2 or more"))
mtext("No. of roads downstream",1,line=3,at=-.3)
text(-0.1,0.03,"Downstream",pos=4,cex=.8)
text(-0.1,0,"impoundments",pos=4,cex=.8)

# Running the isolation model using percent shredders

x<-with(data.invert.taxal,round((PSHRED/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PSHRED/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
glm(xy~EPI_SUB*ST_GRAD*DLINK*ROADS_DS*IMP_DS
,family=binomial)))
options("glmulti-cvalue"=5527.5/298)
glm.redefined = function(formula, data, always="", ...) {
glm(as.formula(paste(deparse(formula), always)), data=data, ...)}
g.pshred.isolate <- glmulti(xy~ROADS_DS+IMP_DS,
data=data.invert.taxal,
fitfunc=glm.redefined,
family="binomial",
crit="qaicc",
level=2,
marginality=T,
always="+EPI_SUB+ST_GRAD+EPI_SUB*ST_GRAD")

print(g.pshred.isolate)

```

```

sum(summary(g.pshred.isolate)$modelweights[1:4])
sum(summary(g.pshred.isolate)$modelweights[1])
(summary(g.pshred.isolate@objects[[1]])$null.deviance-
summary(g.pshred.isolate@objects[[1]])$deviance)/
summary(g.pshred.isolate@objects[[1]])$null.deviance
round(coef(g.pshred.isolate,select=2), 4)
extractAIC(g.pshred.isolate@objects[[1]])[1]+1
extractAIC(g.pshred.isolate@objects[[1]])[2]
summary(g.pshred.isolate@objects[[1]])
confint(g.pshred.isolate@objects[[1]])

# Running the isolation model using percent flying insects

x<-with(data.invert.taxal,round((PFLYING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PFLYING/100)*TOTAL_IND),0))
xy<-cbind(x,y)

summary(with(data.invert.taxal,
glm(xy~EPI_SUB*ACREAGE*DLINK*ROADS_DS*IMP_DS
,family=binomial)))
options("glmulti-cvalue"=5047.7/298)
glm.redefined = function(formula, data, always="", ...) {
glm(as.formula(paste(deparse(formula), always)), data=data, ...)}
g.pflying.isolate <- glmulti(xy~ROADS_DS+IMP_DS,
data=data.invert.taxal,
fitfunc=glm.redefined,
family="binomial",
crit="qaicc",
level=2,
marginality=T,
always="+EPI_SUB+DLINK+EPI_SUB*ACREAGE+
EPI_SUB*DLINK+ACREAGE*DLINK")

print(g.pflying.isolate)
sum(summary(g.pflying.isolate)$modelweights[1:1])
sum(summary(g.pflying.isolate)$modelweights[1])
round(coef(g.pflying.isolate,select=2), 4)
(summary(g.pflying.isolate@objects[[1]])$null.deviance-
summary(g.pflying.isolate@objects[[1]])$deviance)/
summary(g.pflying.isolate@objects[[1]])$null.deviance
extractAIC(g.pflying.isolate@objects[[1]])[1]+1
extractAIC(g.pflying.isolate@objects[[1]])[2]
summary(g.pflying.isolate@objects[[1]])
confint(g.pflying.isolate@objects[[1]])

```

```

setwd("~/Grad School/Thesis/Data Analysis/Benthics")
data.invert.taxa<-read.csv("Benthic_Variables.csv",header=T)
library(Hmisc)
rcorr(as.matrix(data.invert.taxa[,3:7]))
library(rJava)
library(glmulti)
library(MASS)

# creating data sets with standardized variables. Note that we include only those variable
# that we need. Scale function here takes columns 2 through 7 of the data.fish.taxa.R data
# set and centers the values (ie subtracts the mean) and scales them (ie divides by the
# standard deviation). The reason for this is so the parameter estimates are all on the same
# scale and can be compared to assess importance.

data.invert.taxal<-
  as.data.frame(cbind(data.invert.taxa[17:21],
    data.invert.taxa[23],
    scale(data.invert.taxa[2:6],center=T,scale=T),
    scale(log(data.invert.taxa[7]),center=T,scale=T)
  ))
data.invert.taxal[1:3,]

install.packages('pastecs')
library(pastecs)
stat.desc(data.invert.taxa[2:7])
stat.desc(data.invert.taxa[17:23])
-----

# Running the base model using rarified taxa richness

with(data.invert.taxal,hist(NTAXA_RAR,seq(0,30,1)))
g.rich.base <- glmulti(log(NTAXA_RAR)~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+DLINK,
  fitfunction="lm",
  data=data.invert.taxal,
  level=2,
  marginality=T)

print(g.rich.base)
sum(summary(g.rich.base)$modelweights[1:10]) # weight of model within 2 AICc of best model
summary(g.rich.base)$modelweights[1] # weight for best model
summary(g.rich.base@objects[[1]])$r.squared # produce r-squared for best model
round(coef(g.rich.base,select=2, # mean parameter estimate and unconditional
  icmethod="Burnham", # variances over models within 2 AICc units
  varweighting="Johnson"), 3) # of the best model
summary(g.rich.base@objects[[1]])$coef
extractAIC(g.rich.base@objects[[1]])[1]+1 # k for the best model (note 1 has been added)
extractAIC(g.rich.base@objects[[1]])[2] # AIC for best modle
confint(g.rich.base@objects[[1]]) # 95% CI for paramter estimates
summary(g.rich.base@objects[[1]])$r.squared # produce r-squared for best model

#Looking at interaction between epibenthic substrate and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-12,12,.1),
  ST_GRAD=rep(0,1),ACREAGE=rep(-2,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is small
par(oma=c(0,0,1,0),fig=c(.25,.75,.65,1),mar=c(3,3,0,0),mgp=c(1,0.25,0))
with(data.invert.taxal,plot(EPI_SUB,(NTAXA_RAR),
  cex.axis=.7,cex.lab=.7,pch=1,
  xlim=c(with(data.invert.taxal,min(EPI_SUB)),
    with(data.invert.taxal,max(EPI_SUB))),
  col="lightgray",
  xlab="Standarized Epibenthic Substrate Score",
  ylab="",las=1,tck=-0.02,cex=.8))
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-5,6,1),
  ST_GRAD=rep(0,1),ACREAGE=rep(0,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is average
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-5,6,1),
  ST_GRAD=rep(0,1),ACREAGE=rep(2,1),
  DLINK=rep(0,1)))
# plot of effects of epifaunal substrate on rarified taxa richness when
# drainage area is high
with(data.predict,lines(EPI_SUB,exp(predict(g.rich.base@objects[[1]],
  newdata=data.predict)),
  col="red",lty=3))

```

```

legend(-0.75,18,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

#Looking at interaction between stream gradient and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-12,12,.1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(-2,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is low
par(fig=c(.25,.75,.325,.675),new=T)
with(data.invert.taxal,plot(ST_GRAD, (NTAXA_RAR),
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(ST_GRAD)),
                                   with(data.invert.taxal,max(ST_GRAD))),
                           col="lightgray",pch=1,
                           xlab="Standarized Stream Gradient",
                           ylab="Rarified Taxa Richness",las=1,tck=-0.02,cex=.8))
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-5,8,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(0,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is average
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(ST_GRAD=seq(-5,8,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(2,1),
                                  DLINK=rep(0,1)))
# plot of effects of gradient on rarified taxa richness when
# drainage area is high
with(data.predict,lines(ST_GRAD,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="red",lty=3))
legend(2,41,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

#Looking at interaction between D-link and watershed size
# create data set for plot with small watershed
data.predict<-as.data.frame(cbind(DLINK=seq(-12,12,.1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(-2,1),
                                  ST_GRAD=rep(0,1)))
par(fig=c(.25,.75,0,.35),new=T)
with(data.invert.taxal,plot(DLINK, (NTAXA_RAR),
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(DLINK)),
                                   with(data.invert.taxal,max(DLINK))),
                           col="lightgray",pch=1,
                           xlab="Standarized Log D-link",
                           ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        pch=1,col="blue",cex=.8))
# create data set for plot with average drainage area
data.predict<-as.data.frame(cbind(DLINK=seq(-5,5,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(0,1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of d-link on rarified taxa richness when
# drainage area habitat is average
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="brown",lty=2))
# create data set for plot with high drainage area
data.predict<-as.data.frame(cbind(DLINK=seq(-5,5,1),
                                  EPI_SUB=rep(0,1),ACREAGE=rep(2,1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of d-link on rarified taxa richness when
# drainage area is high
with(data.predict,lines(DLINK,exp(predict(g.rich.base@objects[[1]],
                                             newdata=data.predict)),
                        col="red",lty=3))
legend(1.9,40,legend=c("small watershed","medium watershed","large watershed"),
      col=c("blue","brown","red"),
      lty=c(1,2,3),bty="n",y.intersp=0.08,cex=.6)

# Running the base model using percent chironomidae
with(data.invert.taxal,hist(PCHIRON,seq(0,100,5)))

```

```

x<-with(data.invert.taxal,round((PCHIRON/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCHIRON/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=11468/314)
g.pchiron <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                    data=data.invert.taxal,
                    fitfunc="glm",
                    family="binomial",
                    crit="qaicc",
                    level=2,
                    marginality=T)

print(g.pchiron)
sum(summary(g.pchiron)$modelweights[1:22])
summary(g.pchiron)$modelweights[1]
round(coef(g.pchiron,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pchiron@objects[[1]])$null.deviance-
 summary(g.pchiron@objects[[1]])$deviance)/
summary(g.pchiron@objects[[1]])$null.deviance
extractAIC(g.pchiron@objects[[1]])[1]+1
extractAIC(g.pchiron@objects[[1]])[2]
summary(g.pchiron@objects[[1]])
confint(g.pchiron@objects[[1]])

# Running the base model using percent clingers
with(data.invert.taxal,hist(PCLING,seq(0,100,5)))
x<-with(data.invert.taxal,round((PCLING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PCLING/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=11114/314)
g.pcling <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pcling)
sum(summary(g.pcling)$modelweights[1:9])
summary(g.pcling)$modelweights[1]
round(coef(g.pcling,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pcling@objects[[1]])$null.deviance-
 summary(g.pcling@objects[[1]])$deviance)/
summary(g.pcling@objects[[1]])$null.deviance
extractAIC(g.pcling@objects[[1]])[1]+1
extractAIC(g.pcling@objects[[1]])[2]
summary(g.pcling@objects[[1]])
confint(g.pcling@objects[[1]])

# Running the base model using percent shredders
with(data.invert.taxal,hist(PSHRED,seq(0,100,5)))
x<-with(data.invert.taxal,round((PSHRED/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PSHRED/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=5944.6/314)
g.pshred <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pshred)
sum(summary(g.pshred)$modelweights[1:9])
summary(g.pshred)$modelweights[1]
round(coef(g.pshred,select=2,icmethod="Burnham",varweighting="Johnson"), 4)
(summary(g.pshred@objects[[1]])$null.deviance-
 summary(g.pshred@objects[[1]])$deviance)/
summary(g.pshred@objects[[1]])$null.deviance
extractAIC(g.pshred@objects[[1]])[1]+1
extractAIC(g.pshred@objects[[1]])[2]
summary(g.pshred@objects[[1]])
confint(g.pshred@objects[[1]])

#Looking at interaction between epibenthic substrata and stream gradient
# create data set for plot with high gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                  ST_GRAD=rep(2,1)))
# plot of effects of epibenthic substrate on percent shredders when
# gradient is high

```

```

with(data.invert.taxal,plot(EPI_SUB,PSHRED,
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                                   with(data.invert.taxal,max(EPI_SUB))),ylim=c(0,100),
                           col="lightgray",
                           xlab="Standardized Epibenthic Substrata Score",
                           ylab="Percent Shredders",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       pch=1,col="blue",cex=.8))
# create data set for plot with average gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                  ST_GRAD=rep(0,1)))
# plot of effects of epifaunal substrate on percent shredders when
# gradient is average
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       col="brown",lty=2))
# create data set for plot with low gradient
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),
                                  ST_GRAD=rep(-2,1)))
# plot of effects of epifaunal substrate on percent shredders when
# gradient is low
with(data.predict,lines(EPI_SUB,(predict(g.pshred@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       col="red",lty=3))
legend(-2.5,100,legend=c("high gradient","average gradient","low gradient"),
       col=c("blue","brown","red"),
       lty=c(1,2,3),bty="n",y.intersp=0.5,cex=.6)

# Running the base model using percent flying
with(data.invert.taxal,hist(PFLYING,seq(0,100,5)))
x<-with(data.invert.taxal,round((PFLYING/100)*TOTAL_IND,0))
y<-with(data.invert.taxal,round(TOTAL_IND-((PFLYING/100)*TOTAL_IND),0))
xy<-cbind(x,y)
summary(with(data.invert.taxal,
             glm(xy~EPI_SUB*ST_GRAD*ACREAGE*DIST_CON*DLINK,family=binomial)))
options("glmulti-cvalue"=6516.6/314)
g.pflying <- glmulti(xy~EPI_SUB+ST_GRAD+ACREAGE+DIST_CON+(DLINK),
                   data=data.invert.taxal,
                   fitfunc="glm",
                   family="binomial",
                   crit="qaicc",
                   level=2,
                   marginality=T)

print(g.pflying)
sum(summary(g.pflying)$modelweights[1:5])
summary(g.pflying)$modelweights[1]
round(coef(g.pflying,select=2,icmethod="Burnham",varweighting="Johnson"),4)
(summary(g.pflying@objects[[1]])$null.deviance-
 summary(g.pflying@objects[[1]])$deviance)/
 summary(g.pflying@objects[[1]])$null.deviance
extractAIC(g.pflying@objects[[1]][1]+1)
extractAIC(g.pflying@objects[[1]][2])
summary(g.pflying@objects[[1]])
confint(g.pflying@objects[[1]])

# Looking at interaction between epibenthic substrata and watershed area
# create data set and plot with small watershed size, dlink average
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(-2,1),
                                  DLINK=rep(1,1)))
par(oma=c(0,3,0,0),fig=c(.25,.75,.65,1),mar=c(3,0,1,0),mgp=c(1,.4,0))
with(data.invert.taxal,plot(EPI_SUB,PFLYING,
                           cex.axis=.7,cex.lab=.7,
                           xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                                   with(data.invert.taxal,max(EPI_SUB))),
                           ylim=c(0,100),
                           col="lightgray",
                           xlab="Standardized Epibenthic Substrata Score",
                           ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB,(predict(g.pflying@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       pch=1,col="blue",cex=.8))
# create data set and plot with medium watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                                  DLINK=rep(1,1)))
with(data.predict,lines(EPI_SUB,(predict(g.pflying@objects[[1]],
                                         newdata=data.predict,type="response")*100),
                       col="brown",lty=2))
# create data set for plot with large watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(2,1),

```

```

                DLINK=rep(1,1))
# plot of effects of epibenthic substrata scores on percent flying inverts when
# watersheds size is high
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(-0.7,30,legend=c("small watershed","medium watershed","large watershed"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=0.2,cex=.6)
# Looking at interaction between epibenthic substrata and dlink
# create data set and plot with average watershed size, low dlink,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(-2,1)))
par(fig=c(.25,.75,.35,.70),new=T)
with(data.invert.taxal,plot(EPI_SUB,PFLYING,
                cex.axis=.7,cex.lab=.7,
                xlim=c(with(data.invert.taxal,min(EPI_SUB)),
                with(data.invert.taxal,max(EPI_SUB))),
                ylim=c(0,100),
                col="lightgray",
                xlab="Standardized Epibenthic Substrata Score",
                ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                pch=1,col="blue",cex=.8))
# create data set and plot with average watershed size, dlink average,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(0,1)))
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="brown",lty=2))
# create data set and plot with average watersheds size, dlink high,
# and epibenthic substrate scores varied from low to high
data.predict<-as.data.frame(cbind(EPI_SUB=seq(-9,9,.1),ACREAGE=rep(0,1),
                DLINK=rep(2,1)))
# plot of effects of epibenthic substrata scores on percent flying inverts when
# dlink is high
with(data.predict,lines(EPI_SUB, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(-.5,32,legend=c("low d-link","average d-link","high d-link"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)
# Looking at interaction between watershed and dlink
# create data set and plot with average epibenthic substrate scores, low dlink,
# and water size varied from small to large
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(-2,1)))
par(fig=c(.25,.75,0.05,.40),new=T)
with(data.invert.taxal,plot(ACREAGE,PFLYING,
                cex.axis=.7,cex.lab=.7,
                xlim=c(with(data.invert.taxal,min(ACREAGE)),
                with(data.invert.taxal,max(ACREAGE))),
                ylim=c(0,100),
                col="lightgray",
                xlab="Standardized Watershed Size",
                ylab="",las=1,tck=-0.04,cex=.8))
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                pch=1,col="blue",cex=.8))
# create data set and plot with average epifaunal substrate, dlink average,
# and watershed size varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(0,1)))
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="brown",lty=2))
# create data set and plot with average epifaunal substrate, dlink high,
# and watershed size varied from low to high
data.predict<-as.data.frame(cbind(ACREAGE=seq(-9,9,.1),EPI_SUB=rep(0,1),
                DLINK=rep(2,1)))
# plot of effects of watershed size on percent flying inverts when
# dlink is high
with(data.predict,lines(ACREAGE, (predict(g.pflying@objects[[1]],
                newdata=data.predict,type="response")*100),
                col="red",lty=3))
legend(2.5,32,legend=c("low d-link","average d-link","high d-link"),
        col=c("blue","brown","red"),
        lty=c(1,2,3),bty="n",y.intersp=.2,cex=.6)
mtext("Percent Flying Invertebrates",2,-5,out=T,cex=.8)

```

CURRICULUM VITAE

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NAME: Sean D. Sipple

DEGREE AND DATE TO BE CONFERRED: Master of Science, 2016

EDUCATION:

- Towson University, Towson, Maryland, Master of Science in Environmental Science, 2016
- Towson University, Towson, Maryland, Bachelor of Science in Biology, 2002
- Anne Arundel Community College, Arnold, Maryland, Associate of Environmental Science, 1999

PROFESSIONAL POSITIONS HELD:

- Senior Environmental Scientist, Coastal Resources, Inc., Annapolis, Maryland
Dates Employed: 3/15/11 – Present
- Project Environmental Scientist, Wetland Studies and Solutions, Inc., Gainesville, Virginia
Dates Employed: 7/1/04 – 3/15/11
- Environmental Specialist III, Maryland Department of Environment, Baltimore, Maryland
Dates Employed: 12/17/02-6/30/04
- Field/Lab Technician, Smithsonian Environmental Research Center, Edgewater, Maryland
Dates Employed: 6/1/02-12/13/02
- Field/Lab Technician, Anne Arundel Community College Environmental Center, Arnold, Maryland
Dates Employed: 10/1/96-1/1/00

PROFESSIONAL TITLES/CERTIFICATIONS:

- 2012, 2015 MBSS Benthic Macroinvertebrate Sampling Certification
- 2012 MBSS Laboratory Certification
- 2012-2013 MBSS Fish Crew Leader Certification
- 2012-2015 MBSS Fish Taxonomist Certification
- 2012 Society of Freshwater Science (SFS) Certified Chironomidae Taxonomist
- 2010 SFS Certified EPT Taxonomist
- 2007,2014 Professional Wetland Scientist/1730/National
- 2008, 2014 Professional Wetland Delineator/3402000096/Virginia
- 2008 SFS Certified Family-level Taxonomist for Aquatic Invertebrates
- 2010, 2015 SFS Certified Other Arthropods Taxonomist
- 2009 Certified Ecologist/Ecological Society of America (inactive)
- USFWS Qualified Surveyor for small whorled pogonia (*Isotria medeoloides*)

TEACHING/PRESENTATIONS:

- Environmental Concern, Inc., “Ecology and Identification of Freshwater Macroinvertebrates in Wetlands”
- Environmental Concern, In., “Basic Wetland Delineation”
- Virginia Master Naturalist Program, “Ecology and Management of Wetlands”
- Wetland Studies and Solutions, Inc., “Introduction to the Taxonomy of Ephemeroptera, Plecoptera and Trichoptera”
- Wetland Studies and Solutions, Inc., “Tidal Wetland Plant Identification”
- Wetland Studies and Solutions, Inc., “Identification of the Grasses, Sedges, and Rushes”
- Association of Mid-Atlantic Aquatic Biologists Conference, “Population Dynamics and Habitat Preference of Wood Turtles (*Glyptemys insculpta*) at Fraser Preserve, Fairfax County, Virginia”
- Association of Mid-Atlantic Aquatic Biologists Conference, “Distribution and Abundance of the comely shiner (*Notropis amoenus*) in the Upper Northwest Branch”
- Mid-Atlantic Stream Restoration Conference, “Using the Stream Condition Index to Evaluate the Condition of Virginia Non-coastal Stream Restoration”
- ICC Inter-agency Work Group (IAWG), “Pre-Construction Condition Assessment for Channel Enhancement: Indian Creek”
- Maryland Water Monitoring Council Annual Conference, “Assessment of Northwest Branch Stream Restoration (NW160/170): Two Years After Restoration”
- Maryland Water Monitoring Council Annual Conference, “Factors Considered for Conducting a Fish Crossing Analysis for Culvert Projects in Maryland”

