

ABSTRACT

Title of Document: CUMULATIVE IMPACTS OF
STREAM BURIAL ON NETWORK
STRUCTURE AND FUNCTIONAL
CONNECTIVITY IN HEADWATER
STREAM SYSTEMS

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Stream burial is common during urbanization, and disproportionately affects headwater streams. Burial undermines the physical, chemical, and spatial processes governing aquatic life, with consequences for water quality and biodiversity, both within headwaters and in downstream waters. Network changes associated with headwater burial have not been explored, limiting our understanding of changes in biotic composition with urbanization of these critical ecosystems. To address this need, I predicted stream burial across the Potomac River Basin (PRB) from impervious cover data and training observations from high-resolution aerial photography. Results across the PRB urban gradient reveal consistent burial patterns related to catchment area and topographic slope. I discuss these results in the context of physiographic constraints on stream location and urban development, including implications for management of aquatic resources. Second, I examined burial-related

changes to headwater network structure and habitat connectivity, using a series of topological and distance measures, and a novel application of circuit-theoretical modeling to stream networks. Results show stream burial significantly affects both the number and size of remnant stream segments and their spatial orientation. Significant decreases in landscape connectivity were observed with burial, around ecologically important features such as confluences, and for urbanized headwater systems as a whole. Third, I used biological data to compare environmental and spatial controls on species turnover in fish and insect communities across headwater systems. Turnover was analyzed using generalized dissimilarity modeling, which accommodates variation in rates of species turnover along and between gradients, and two novel measures of resistance distance, which combine aspects of space and environment, specifically the spatial extent, orientation, and relative favorability of habitat across the landscape. Results show headwater species are more sensitive to environmental parameters, with less mobile species more sensitive to habitat fragmentation and required dispersal distances. Rapid compositional turnover occurred within short distances from the sampled reaches, suggesting headwater taxa disperse only short distances, with even small obstructions or habitat loss having potential to impact diversity within headwater systems. Knowledge gained from this research is critical for understanding the cumulative impact to stream networks, and for future decision-making allowing for urban development while protecting stream ecosystem function.

CUMULATIVE IMPACTS OF STREAM BURIAL ON NETWORK
STRUCTURE AND FUNCTIONAL CONNECTIVITY IN
HEADWATER STREAM SYSTEMS

By

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Preface

This dissertation contains an overall abstract and five chapters. Chapter II, III, and IV are presented in manuscript form; therefore, the study area may be repeated, pronouns reflect manuscript authorship, and tables and figures appear at the end. A single reference section occurs at the end for literature cited throughout the dissertation.

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Chapter 1: Introduction

Headwater (zero-3rd order) streams are unique and critical components of aquatic networks, providing valuable ecosystem services to adjacent and downstream environments (Lowe and Likens 2005, Alexander et al. 2007, Meyer et al. 2007, Wipfli et al. 2007; Figure 1). While headwater stream channels themselves are small and may go dry seasonally, they serve as the main conduit for the flow of energy and matter to downstream ecosystems (Likens and Bormann 1974). The complexity of the aquatic-riparian interface in headwater systems creates high levels of habitat heterogeneity that supports diverse biotic assemblages, with many “specialists” uniquely adapted to headwater life (Lowe and Likens 2005, Meyer et al. 2007). The unique functional and structure attributes of headwater systems also render them extremely sensitive to natural and anthropogenic disturbance within their watersheds (Smith and Lamp 2008), and such impacts can have substantial, but largely underappreciated downstream effects (Meyer et al. 2007, Nadeau and Rains 2007).

Due to their prevalence on the landscape, constituting more than 2/3 of stream length in a typical river drainage (Leopold et al. 1964, Meyer et al. 2007, Nadeau and Rains 2007), headwater streams have been disproportionately affected by urbanization as compared to larger systems. For example, reduced infiltration and increased runoff from extensive urbanization of headwater catchments in Cincinnati, OH, has altered headwater base flows to such an extent, that ephemeral and intermittent flow origins have been reduced by 93% and 46%, respectively, and replaced by new, perennial reaches (Roy et al. 2009). Furthermore, Nelson and Palmer (2007) have

postulated that urban-related runoff has affected water temperatures in headwater streams more pervasively than will future climate change.

Stream burial, the process of directing streams into culverts, pipes, concrete-lined ditches, or simply paving them over during urbanization, has resulted in the removal of up to 70% of headwater stream length in some areas (Elmore and Kaushal 2008). As with other forms of stream modification, burial alters the primary physical, chemical, and biological processes in headwater systems, contributing to a state of degradation commonly referred to as “urban stream syndrome” (Walsh et al. 2005). With the percentage of the world’s population living in urban areas continuing to grow (United Nations 2010), a greater emphasis has been placed on understanding the structure and function of urban streams, and associated impacts to human health, and that of downstream ecosystems. The identification of stream burial as a critical and pervasive driver of the “urban stream syndrome” (Walsh et al. 2005), and the recognition that key questions remain in regards to ecosystem structure and function within piped ecosystems (Wenger et al. 2009), has led to increased research activity, and the explicit consideration of stream burial in formulation of long-term research agendas (e.g., the Baltimore Long Term Ecological Research (LTER) site; Sujay Kaushal, *personal communication*).

While not extensive to date, research on the phenomenon of stream burial has demonstrated a consistent set of interrelated ecosystem impacts, including modified flow velocities, altered carbon and nutrient inputs, and amplified nitrogen transport (Wenger et al. 2009), loss of habitat and decreased nutrient subsidies (Meyer et al. 2005a), and barriers to dispersal of aquatic organisms (Meyer et al. 2005b). More

recently, (Kaushal and Belt 2012) have recognized stream burial as part of an “urban stream continuum”, whereby extensive engineering of headwater systems has expanded natural flowpaths (“urban karst”);(Kaushal et al. 2014), leading to increased hydrologic connectivity within watersheds , thereby influencing the flux and transformation of nutrient, contaminants, and energy across both space and time. Leveraging this novel conceptual framework, subsequent research has focused largely on biogeochemical cycles within buried headwater streams, documenting significant reductions in nitrogen (N) uptake, gross primary production (GPP), and ecosystem metabolism (ER), with potential to influence watershed nutrient exports to downstream waters(Beaulieu et al. 2014, Hope et al. 2014, Pennino et al. 2014) .

Despite the importance of headwater streams, and the degree to which they have been impacted by urbanization, the cumulative impacts of stream burial on headwater network structure and the function of downstream and adjacent aquatic ecosystems remain largely unstudied. For example, although extensive research has explored spatial patterns in impervious surface generally, including incorporating these observations into predictive models (Jantz et al. 2004, 2010) , little is known about stream burial patterns, or how stream burial impacts stream network structure. Further, although it is well known that maintenance of habitat patches and dispersal between patches is critical for sustaining aquatic populations (Fagan 2002, Grant et al. 2007), it is not clear whether these findings scale to entire watersheds, nor have studies considered stream burial as the specific driver of fragmentation of aquatic populations.

Knowledge of the cumulative impacts of altered network structure and how it relates to functioning within buried stream networks is crucial for informing management of stream ecosystems in light of continued growth in urban areas (Grimm et al. 2008) and the uncertain response of freshwater ecosystems to the stresses of global climate change (Poff et al. 2002). Until recently, progress on understanding the impacts of stream burial was hindered by a lack of analytical approaches for mapping headwater streams and for quantifying stream burial. These obstacles have largely been overcome by new developments in Geographic Information Science (GIS) and remote sensing-based methodologies (Elmore and Kaushal 2008) such that we can now accurately measure the former extent of headwater streams and the severity of burial across large areas. These data can be coupled with existing techniques for modeling landscape connectivity, such as circuit theory (McRae et al. 2008), to model aquatic networks and to quantify how burial may alter the potential flow of organisms and materials within and among urbanized systems. In turn, models of network connectivity can be considered in light of long-term biological and environmental datasets to quantify the ecosystem effects of stream burial at multiple spatial scales. Taken together, the combined analyses of fragmentation of headwater systems, undertaken as the focus of this dissertation, will provide critical information on cumulative impacts of buried streams necessary for monitoring and regulating development pressures on aquatic resources.

1.1 Research objectives and dissertation format

The main goal of my dissertation was to enhance understanding of the phenomenon of stream burial during urbanization, and the associated impacts to headwater stream ecosystems of the Potomac River Basin (PRB). My research is organized around three general themes: (1) the distribution of headwater stream burial across gradients in stream size, topography, and land use, (2) stream burial impacts to stream network structure and habitat connectivity, and (3) the role of these measures in structuring headwater fish and insect communities. The measures of cumulative impact developed for this project will consider headwater stream systems as habitat networks potentially connected by both longitudinal (along the flow direction) and lateral (perpendicular to the flow direction) dispersal events. Recent work (Grant et al. 2010) highlights the critical importance of network connectivity on dispersal and maintenance of salamander diversity in small streams. I hypothesize that the same is true for aquatic insect and fish assemblages living in highly isolated, headwater systems.

CHAPTER 2 focuses on mapping the distribution of stream burial across gradients in stream size, topography, and land use. The primary question was *what are the cumulative impacts of burial on headwater stream systems of the PRB?* Headwater streams are critical areas for biodiversity, and have been shown to be disproportionately affected by stream burial. I combined training observations from high-resolution aerial photography, spatial analysis of impervious surface data, and decision-tree classification to predict stream burial probabilities for every stream segment in the PRB. I then quantified the relationship between buried stream

reaches, their size, and slope, factors we theorize should influence the rate of stream burial across the landscape. My units of analyses were counties and independent cities, as decisions governing land use occur almost exclusively at this level. County-level comparisons were stratified across the urban gradient, to gain insight into the progression of burial with increasing levels of urban development. Finally, I compared county-level burial rates to total impervious cover, attempting to identify counties where stream protection policies might be more, or less effective, given a certain level of impervious cover. Quantifying the extent and nature of stream burial across the PRB informs us about the pressures that headwater streams are facing, in light of continued urbanization of the basin.

CHAPTER 3 assesses burial related impacts to stream network structure and habitat connectivity within headwater stream networks. The principle question was *what are the potential implications of stream burial for aquatic biodiversity in critical headwater ecosystems?* Stream burial eliminates discrete habitat patches, directly undermining the movement of organisms and materials both within and between aquatic systems. Through spatial comparison of buried and intact stream networks, I quantified burial related habitat loss and fragmentation for headwater systems across the PRB, using a suite of topological and distance measures. I specifically addressed the loss of and changes to critical habitat components including confluences and channel head areas, shown to be important areas for aquatic biodiversity. Additionally, I developed and implemented a novel application of circuit-theoretical modeling to quantify changes to habitat connectivity within headwater systems based on increased resistance of landscape to movement by

organism following stream burial and upland urban development. Understanding how stream burial alters the geometry of headwater networks provides will aid in the effective management of headwater systems for biodiversity conservation and the provision of ecological goods and services.

CHAPTER 4 investigates the relative roles of space and environment on species turnover (beta diversity) in headwater communities. The essential question here was *how might urban-related changes in land use and habitat connectivity impact the ability of organisms to move within and between headwater streams?*

While relatively species-poor in comparison to larger, downstream ecosystems, headwater streams exhibit high degrees of species turnover (beta diversity) within and between systems, thereby contributing disproportionately to regional species pools (gamma diversity). I applied generalized dissimilarity modeling to quantify the degree of compositional turnover in fish and insect communities in relation to environmental and spatial gradients between headwater bio-monitoring sites in Maryland. For the spatial component of the analyses, I developed two novel measures of resistance distance that incorporate information on the spatial extent, orientation, and relative favorability of habitat across the landscape, and along stream networks. The resistance measures, along with Euclidean distance, were then tested against a suite of field-measured and GIS-derived environmental variables, to quantify the amount of compositional turnover explained by each. These analyses provide insight into the specific mechanisms driving species turnover in headwater systems, and the scales at which they operate.

CHAPTER 5 summarizes the results, discusses general implications, and suggests future research directions.

Chapter 2: Extent and severity of stream burial across the Potomac River Basin, USA, and its relationship to local slope and catchment area

2.1 Abstract

Stream burial – the routing of streams through culverts, into pipes and concrete-lined channels, or simply paving them over – is common during urbanization. Headwater streams are particularly vulnerable, due to their small size, their ubiquity, and relatively low cost of burial versus that of protection or restoration. Burying streams undermines the physical and chemical processes that govern life in streams, with consequences for water quality and quantity and aquatic biodiversity, which have the potential to amplify from headwaters to downstream receiving waters. Knowledge of the extent and severity of stream burial is critical for understanding the cumulative impact to stream networks, and for future decision-making that allows for urban development while protecting stream ecosystem function. With this in mind, we predicted stream burial across the urbanizing Potomac River Basin (PRB) for each 10-m stream segment in the basin from medium-resolution impervious cover data and training observations obtained from high-resolution aerial photography. We compared results across 16 counties and independent cities representing the PRB urban gradient, and discovered consistent, reoccurring patterns in stream burial predictions related to catchment area and topographic slope. In areas with low stream burial, burial is detected in stream reaches characterized by low slopes and small catchment areas, with the steepest slopes and largest streams exhibiting no detectable burial. Stream size is less constraining in counties that are more urbanized, with

heavily urbanized city centers exhibiting high rates of burial across all but the largest or steepest streams. We discuss these results in the context of physiographic constraints on stream location and urban development, including implications for environmental management of aquatic resources.

2.2 Introduction

Stream burial is common in urbanized areas. In many regions, the majority of buried reaches are headwater (1st and 2nd order) streams, including ephemeral and intermittent reaches (Elmore and Kaushal 2008, Roy et al. 2009). The straightening of channels, routing through pipes, and lining of streams with concrete reduces in-channel complexity, and eliminates or permanently alters the availability of in-stream habitat. In addition to immediate destruction of habitat, burial of headwater streams contributes to downstream impacts via increased flow velocities and altered nutrient and material imports and exports, universal symptoms of urban streams (Walsh et al. 2005). While the cumulative effects to ecosystem processes wrought by stream burial have important ramifications for regulation under the U.S. Clean Water Act (Leibowitz et al. 2008), the extent of burial, has not been assessed for most urban areas. Knowledge of the extent and severity of burial events is critical for effective resource management, including preservation of remaining intact streams, restoration of urban streams, and assessing cumulative impacts of urbanization to water quantity and quality.

Research has demonstrated a consistent negative effect of increasing levels of urbanization on various indicators of stream health (Booth and Jackson 1997, Paul and Meyer 2001, Walsh et al. 2005). Most studies have relied on total

imperviousness (TI; the proportion of a watershed that is covered in impervious surface) as the primary measure of urbanization impacts on freshwater ecosystems as TI is viewed as an integrative and comprehensive indicator (Allan 2004) that can be readily incorporated into land use planning (Meyer et al. 2005a, Schueler et al. 2009, Theobald et al. 2009) . However, impervious cover alone has proven an insufficiently sensitive measure of river health (Booth et al. 2004), as significant aquatic assemblage degradation has been observed across a wide range of watershed imperviousness (Cuffney et al. 2010).

Recognition that the spatial configuration of impervious cover relative to stream channels may be an important moderator of the magnitude of stream ecosystem response to urbanization (King et al. 2005, Moore and Palmer 2005) has led to development of alternative metrics for measuring urbanization effects on stream ecosystems. Measures of effective imperviousness (EI, impervious cover directly adjacent to a stream channel; (Wang et al. 2001, Schiff and Benoit 2007) and directly connected impervious area (DCIA, impervious surfaces that route stormwater runoff directly to streams via stormwater pipes; (Roy and Shuster 2009) have been shown to better integrate the multiple stressors of urban development, relative to TI. However, these methods also have shortcomings; they either fail to explicitly capture piped and concrete-lined stream channels (e.g., EI) or necessitate detailed information on stormwater conveyances and intensive field surveys to determine runoff routing and specific on-lot drainage patterns (DCIA). Most importantly, neither approach directly quantifies the impact of urbanization on stream habitat, and instead relies on indirect measures such as changes in sedimentation and hydrology.

Stream habitat is most directly impacted when impervious surface completely covers the stream channel, termed stream burial. Previous research has shown a relationship between stream size and the probability of burial, with the smallest, headwaters streams of the urbanized Gunpowder-Patapsco watershed, Maryland, exhibiting disproportionately high rates of burial in relation to larger streams (Elmore and Kaushal 2008). Whether this pattern remains consistent in other watersheds or across broader geographic scales is unknown. Local topographic patterns, such as slope, are also known to affect the probability of urbanization (Claggett et al. 2004, Jantz and Goetz 2005), by making some places inaccessible or unstable for building (Jenerette and Wu 2001). It remains unclear whether these same physiographic constraints may limit, or necessitate, the burial of streams. Insights into both the spatial and temporal patterns of stream burial, particularly with respect to stream size and topographic slope, are critical for gauging the effectiveness of land-use policies meant to foster development, while protecting the health of stream ecosystems. Historical patterns of stream burial also provide insight into the characteristics of stream that remain, information that is potentially useful for describing and understanding patterns of remaining aquatic biodiversity.

Recent advancements in stream mapping, remote-sensing of impervious cover, and predictive models now make it possible to map stream burial at a relatively high level of detail and accuracy across large areas. To enhance our understanding of the phenomenon of stream burial, we developed a novel analytical approach (using improved headwater stream maps (Elmore et al. 2013), moderate resolution impervious cover data (Fry et al. 2011), and recursive partitioning models (Hothorn et

al. 2006) to map the extent and magnitude of burial across an urban gradient in the Mid-Atlantic United States. We expect these new burial maps, paired with spatially continuous maps of physiographic parameters, to provide a fresh perspective into land use decision-making processes, and the development pressures facing critical headwater stream ecosystems, past, present, and future.

2.3 Methods

2.3.1 Study Area

The primary study region spans the Potomac River Basin (PRB; Figure 1), second largest tributary to the Chesapeake Bay (supplying 17% of the Bay's mean annual freshwater input), and the fourth largest river along the U.S. Atlantic Coast (Claggett et al. 2004, Lookingbill et al. 2009). Draining an area of approximately 38,000 km² across five geological provinces (Appalachian Plateau, Ridge and Valley, Blue Ridge, Piedmont and Coastal Plain), the PRB constitutes a landscape continuum from mountains to sea characterized by gradients in topography and climate that support an array of aquatic ecosystems and a diverse biota (Lookingbill et al. 2009). Spanning portions of 4 states (Maryland, Pennsylvania, Virginia, and West Virginia) and the entire District of Columbia, the PRB is also home to more than 5.3 million people (United States Census 2000). The long history of cultural and economic development in the basin has rendered a diversity of land uses, ranging from rural forested and agricultural landscapes, to high-density, completely urbanized municipalities. The distinctive physiographic, ecological, and socio-economic characteristics of the PRB make it a model system for studying the cumulative impacts of stream burial on aquatic ecosystem function in urbanizing landscapes.

2.3.2 Mapping potential stream burial

Our predictions of stream burial for the entire PRB used recently generated “potential” stream maps (10-m resolution, Elmore et al. 2013, henceforth referred to as “streams” or “stream maps”), which represent a much more complete coverage of streams (including ephemeral and intermittent streams) than is represented by the more commonly used National Hydrography flow lines. The term “potential streams” arises from the fact that these stream maps were generated from topographic modeling and trained from observations of streams in forested settings. Therefore, they show our best understanding of where streams would be if the entire basin had the same land use history as modern forested lands. Therefore, the stream maps provided by Elmore et al. (2013) allow identification of the potential stream network in areas that have been urbanized for many decades, including those streams that were buried prior to any available stream maps. Details on the methodology used to generate potential stream maps are available, including a detailed analysis of classification omission and commission error (Elmore et al. 2013).

A remote-sensing derived impervious surface (ISA) product was acquired from the 2006 National Land Cover Dataset (Fry et al. 2011) and was used to represent hard, urban surfaces. The overall approach we used was to identify buried streams as stream segments that intersect ISA above a defined threshold. The purpose of predictive modeling (next section) is to identify the threshold that most accurately separates the training data into buried and intact stream segments. In practice, the stream and ISA layers are created at different resolutions and geolocation accuracy. It is entirely possible for a stream to appear to flow through a high-ISA pixel, but to in

fact be protected by a riparian buffer that is represented by a series of low ISA pixels adjacent to the stream. To address these and similar spatial co-registration issues between stream and impervious datasets, we calculated a selection of statistics intended to represent the spatial variability (e.g., mean, standard deviation, range, minimum, maximum) of ISA surrounding each 10m stream segment. The results of these statistical calculations were associated with each stream segment for use in subsequent burial modeling. Additionally, the flow accumulation area (FAC, discussed below) for each segment was calculated for use with predictive modeling, which serves as a proxy for stream size. We expected stream size to affect critical thresholds in the ISA statistics used to predict the probability of burial.

To build a training dataset for mapping stream burial, representative, high spatial resolution (30-cm) aerial photographs (c.2001, 2006), were obtained for 17 sample areas (mean area $\sim 50\text{km}^2$, sum $>2\%$ basin area) across the PRB, chosen to capture a diversity of environments, including the full gradient in land use from forest to urban. From the stream segments located within the bounds of the aerial photos, a stratified- random set of reaches (n=1620) was selected, with 10% of the points located within each 10% increment of ISA. Additional streams in the highest ISA category (90-100%) were selected to ensure the training data included roughly equal numbers of buried and intact streams. The aerial photos were examined to determine the status of each reach as either buried or intact. If a stream was visible in the air photograph the stream was labeled as intact. If the stream flowed through a forested area, but the trees obscured the stream, the stream was also labeled as intact. However, if the stream was not visible due to urban land cover (pavement, buildings,

or bare earth) the stream was labeled as buried. This technique is not sensitive to other types of stream burial in urban environments (e.g., buried streams piped and covered by vegetation under lawns or agricultural lands, or inundated by man-made impoundments). When confronted by these situations, streams were designated as intact, likely leading us to slightly underestimate the total length of affected stream across the study area.

A recursive partitioning decision tree ('Party' package, Hothorn et al. 2006) was built in R (R Core Development Team 2013), using the training data (buried or intact) as the dependent variable. The ISA neighborhood statistics for the 8-neighboring pixels to each stream pixel and the flow accumulation area were used as independent variables. The fraction of buried streams in each terminal node of the resulting decision tree (Figure 2) was used as the probability of burial for every 10m stream segment across the PRB. Each split in the tree structure was determined by conditional inference to reduce the remaining variance in the data and was associated with a p-value <0.05. Comprehensive maps of each ISA statistic used in the decision tree were then used to project stream burial across the entire study region.

2.3.3 Accuracy analysis of burial classification

Accuracy analysis of burial probability classifications were performed using components of the "party" package, and a series of custom functions, in R (R Core Development Team 2013). Two "model sets" were created utilizing burial training data developed from 17 areas across the PRB (described in detail, above), consisting of a stream status class (intact or buried) and impervious cover statistics for 2216

stream reaches. First, a series of 100 recursive partitioning decision trees were generated by iteratively and randomly selecting 70% of the data to train each model, with the remaining 30% of the data held in reserve for model validation. Modeled accuracy of the trees was compiled and averaged for an overall accuracy score for the burial probability classification. The second accuracy assessment utilized the same functions to create a single decision tree, using the full dataset for model training and validation. A receiver operating characteristic (ROC) analysis was then performed on the full model results to identify the burial probability threshold that would minimize false positive and maximize true positive fractions resulting from the classification.

2.3.4 Analysis of stream burial patterns in relation to slope and catchment area

The completed stream burial probability layer was imported into a GIS (ESRI 2012), and the extent and severity of stream burial evaluated in the context of urbanization intensity (total impervious cover), catchment area (FAC; flow accumulation area), and local topographic slope. Analysis units consisted of counties and independent cities, the jurisdictional level where most development decisions are made. Urban development across the PRB largely began in and around Washington, DC, and has since radiated outward in concentric rings from the urban center (Morrill 2006). A series of 16 counties and independent cities were selected to capture the full development gradient, from rural to densely urban (Figure 3), and their boundaries (National Boundary Dataset 2014; <http://nationalmap.gov/boundaries.html>) used to quantify the extent of predicted burial and total impervious cover (Fry et al. 2011) within each. For the purposes of comparison, counties were assigned to one of four

“development tiers”, based on their relative level of total impervious cover and distance from Washington, DC (Figure 3).

Catchment area values for stream pixels within each county were derived from 10-m National Elevation Data (Gesch et al. 2002) using the TauDEM (Tarboton et al. 2009) suite of tools, to generate flow direction and flow accumulation (FAC) area maps. Values for catchment area represent the areal sum of all 100 m² pixels upstream from each stream pixel. Slope values for each stream pixel were derived directly from the DEM using the average landscape gradient (rise/run) in a nine-cell window surrounding each pixel.

Data for county-level burial rates, catchment area, and slope were examined to determine the relationship between burial and each of the two other variables. For comparisons with predicted stream burial, catchment area and slope were each individually treated as the independent variable. To summarize the large variability in predicted stream burial rates, stream reaches were grouped into ‘bins’ of equally spaced catchment area and the mean stream burial was calculated for streams in each bin. Mean, predicted stream burial was then plotted against catchment area and slope and the resulting relationships were analyzed. To understand collinearity in the independent variables (catchment area and slope), we also analyzed slope against binned catchment area.

Initial examination of the plotted relationships revealed a consistent pattern between average predicted burial rates and catchment area, with burial exhibiting a characteristic “hump-shaped” distribution (e.g., Figure 4). For each county, there is a local burial ‘maximum’ evident in the mid-range of catchment area, with a

characteristic ‘ascending limb’ and ‘descending limb’ in the burial distribution to either side (red and green boxes in Figure 4). To analyze how the shape of the distribution of values on either side of this maximum changed with the level of development, we subset the data, and ran separate regressions for each limb. High rates of collinearity between slope and catchment area across all levels of development precluded reliable analysis of the interaction between the two, so separate analyses were run to determine the relationship between predicted burial rates and the two independent variables individually within each limb. Due to similarities in development history and resulting patterns in burial predictions, and to ensure sample sizes for analysis across catchment area bins, the 5 independent cities of Virginia were analyzed as a single unit. All statistical analyses were performed in the statistical programming package R (R Core Development Team 2013).

To investigate the potential effects of analysis scale on the relationship between stream burial and impervious surface area (ISA), a series of 3 additional analysis units covering the study area were devised at varying scales smaller than counties (Figure 5): Subwatersheds, 45 km² grid cells, and 22.5 km² grid cells. Subwatersheds consisted of 12-digit hydrologic catalog units (HUCs) from the USGS Water Boundary Dataset (<http://nhd.usgs.gov/wbd.html>), and were selected as a representation of naturally-derived management units, considering that relationships between burial and ISA observed at the county-level might be purely based on local decision-making within political boundaries. Scales for the two, grid-based analysis units were determined by halving the average area of the subwatersheds (~90 km²) to create 45 km² units, and again, halving the area of these units to create finer-scaled,

22.5 km² units. Grid cell layers were generated in ArcGIS 10.1 (ESRI, 2011) at the extent of the county layer, and along with the subwatershed polygons, were overlaid with 2006 burial estimates and ISA data (as described above) to calculate burial and impervious cover statistics for each analysis unit. Analyses of the relationships at each scale were performed in R (R Core Development Team 2013).

2.4 Results

Stream burial occurred across all counties and independent cities within the study area, with prediction rates ranging from 1.6% - 51.1% ($\mu = 20.5\%$; Table 1). The City of Alexandria, Virginia, exhibited the greatest degree of predicted burial (51.1%), followed closely by Washington, DC (47.3%), and then Arlington County, Virginia (39.4%). Predicted burial rates generally decrease with distance from the urban center (Figure 6), with the exception of the independent cities of Virginia, which, with the exception of Manassas Park, exhibited values above 23.0% burial. Clarke County, Virginia, by far the most rural and relatively undeveloped county, has experienced the least amount of stream burial, with only 1.6% of its streams predicted as buried by 2006. These figures for predicted stream burial are averaged across all streams, with the average weighted by the burial probability.

2.4.1 Relationship between predicted burial rates and impervious cover

Predicted, county-level stream burial increases linearly with total impervious cover (Figure 7), in an approximately 1:1 relationship ($y=1.135x-0.572$, p -value <0.0005), with a few exceptions (i.e., deviations from the 1:1 line). Several Tier

1 counties (Figure 3) and independent cities exhibited a higher proportion of stream burial than expected based on the relationship between predicted burial and impervious cover. Also compared with this relationship, counties that have developed more recently but still exhibiting high levels of development (mostly Tier 2), were seen to have lower levels of predicted burial. The largest discrepancies exist in the oldest municipalities with the greatest levels of urban development, including Washington, DC (1.26), the independent cities of Falls Church (1.22), and Alexandria (1.19), and Arlington County, VA (1.17). As a unit, the Virginia independent cities follow the same pattern as counties, where cities that developed earlier have higher predicted rates of burial per unit of impervious cover than do the newer-developing cities. All the Virginia cities exhibit very high predicted burial rates per unit imperviousness, with the exception of Manassas, which falls directly on the 1:1 line, and Manassas Park, which is the only independent city to show a significantly lower burial to impervious ratio (0.79).

2.4.2 Relationship between burial and catchment area

Stream burial-catchment area relationships exhibit a generally consistent pattern across all counties, regardless of development stage (Figures 8 & 9). Predicted burial rates are elevated for the very smallest streams, decreasing sharply to a local minimum (corresponding with maximum slope values, discussed below) around catchment areas of 0.1-0.2 \log_{10} ha, after which they increase linearly to a maximum burial rate in the mid-range of catchment area (~0.8-2.5 \log_{10} ha, depending on development stage). After this local maximum, burial rates generally

decrease with increasing catchment area, until approximately $3.5 \log_{10}$ ha, where predicted burial rates tend to level off and remain very low (\sim zero) as catchment area continues to increase.

The magnitude of the maximum predicted burial rate, and thereby the slope of the distribution of burial data on either side of the local maximum, becomes steeper (more positive to the left, and more negative to the right of the maximum) with increasing rates of urban development (Table 2, Figures 8 & 9). In the cities and counties with the highest levels of development (e.g., Tier 1, Figure 8), rather than decreasing sharply as catchment area increases past the initial maximum rate, predicted burial remains high across a wide range, before decreasing sharply approaching catchment areas of $3.5 \log_{10}$ ha. The maximum line generally occurs in the neighborhood of $1.0 \log_{10}$ ha (range 0.8 - $1.4 \log_{10}$ ha, with exception of three counties - Washington, MD and Clarke, VA - where the maximum is shifted far to the right ($\sim 2.5 \log_{10}$ ha), and Clarke County, where the maximum lies at $2.1 \log_{10}$ ha catchment area.

The relationship between predicted burial rates and catchment area was highly significant for the majority of counties, and across both ascending and descending limbs of the burial curve (Table 3). Where catchment area did not explain a significant degree of variability in predicted burial rates, it tended to be for the descending limb of the burial distribution, e.g., the Independent Cities of Virginia and for Frederick County, MD. Catchment area did not explain predicted burial rates at any point in the distribution for Jefferson County, West Virginia.

2.4.3 Relationship between burial and slope

The very smallest watersheds in all counties exhibit moderate levels of predicted burial (compared to overall rates within a jurisdiction), corresponding with low to moderate slope values of up to 7-8 degrees. Predicted burial rates then decrease sharply to their local minimum as slope increases to its maximum (range = 6.2-24.16 degrees, $\mu = 9.47$, Figures 8 & 9), which occurs in all counties at approximately $0.2 \log_{10}$ ha catchment area, as discussed above. Predicted burial rates then increase sharply to their maximum, as slope values decrease from their maximum, with maximum burial rates occurring in the range of 2.37-6.36 ($\mu = 3.38$) degrees of slope across all counties. Beyond the point of maximum burial rate, both predicted burial and slope decrease linearly until both approach values of 0 at approximately $3.5 \log_{10}$ ha catchment area (Figures 8 & 9).

The degree to which slope explained the variability in predicted burial rates across counties and development tiers was mixed, except for the Tier 2 counties, where slope was significant for both ascending and descending limbs in all counties (Table 3). Where slope was significant, it was highly so (p -values < 0.001), but there were several counties across the development gradient for which slope was not related to predicted rates of burial for either the ascending or descending limbs, including the Virginia Independent Cities (Tier 1), Frederick County, MD (Tier 3), and both Jefferson County, WV, and Clarke County, VA, in Tier 4). Slope was a significant factor in predicted burial rates for the ascending burial limbs in both

Washington, DC, and Washington County, MD, but insignificant for the descending limbs in these two areas.

2.4.4 Effects of scale on burial/ISA relationships

Relationships between percent stream burial and ISA for the 4 scales of analysis units (Table 4) are shown in Figure 10. In each case, units exhibit a roughly 1:1 relationship below a threshold of approximately 30% ISA, above which most, if not all analysis units exhibit a greater amount of stream burial per unit ISA. This general relationship between burial and ISA is consistent for all analysis units, regardless of scale, across the full range in ISA cover, though not surprisingly, analyses with smaller-scaled units yield a larger number of units above the 30% ISA barrier.

At the county-level, units above 30 percent ISA (Panel A, Figure 10) include Washington, D.C., Arlington County, and the independent cities of Alexandria and Manassas, Virginia. These regions of the study area (Figure 11) have the longest history of urban development, spanning back to mid-late 18th century, and have experienced continuous development and redevelopment to the present time. Of these units, only Manassas has maintained a roughly 1:1 ratio of burial to ISA, while the others exhibit significantly higher levels of burial per unit ISA. Only two subwatersheds (Panel B, Figure 10) exhibit greater than 30% ISA, their area corresponding with the most densely-developed regions of Washington, D.C., and its first tier suburbs (Figure 11). In general, burial-ISA relationships for subwatersheds vary little from 1:1, perhaps due to limitations imposed by natural features within

each watershed that preclude urban development, thereby controlling the ratio of developed and undeveloped landcover within these more naturally-derived analysis units.

At an analysis scale of 45 km² units, those grid cells with the highest ratio of burial to ISA (Panel C, Figure 10, orange ovals) still center on Arlington County, Alexandria, and the heart of Washington, D.C. (Figure 11). Also exhibiting >30 ISA, and elevated burial/ISA ratios at this analysis scale are significant areas of the first-tier D.C. suburbs in Maryland and Virginia. Interestingly, there are two grid units with just over 30% ISA (Figure Y, Panel C, green oval) that exhibit significantly lower ratios of burial to ISA, centering on the cities of Herndon and Sterling in the western Suburbs of Virginia, and in suburban Prince George's County, Maryland, to the southeast of Washington, D.C. Surprisingly, these areas are characterized by dense residential and commercial development centered on the local transportation corridors of VA Route 28 and the Dulles Airport Access Road (Rt. 267), and on the Interstate 95/495 corridors, respectively (Figure 11).

Finally, at the smallest analysis scale of 22.5 km², the greatest number of analysis units exhibit increased burial/ISA ratios above the threshold of 30% ISA (Panel D, Figure 10). Those with the greatest deviation from 1:1 again include grid units spanning areas of Arlington, Alexandria, and the core of Washington, D.C. (orange ovals). There is also a large cluster of units above the 1:1 line, consisting of additional portions of D.C. and close suburbs with a longer history of development and infill. Those cells falling just above, and on the 1:1 line include large portions of the Potomac River, and other park areas with significant undeveloped area. Several

additional areas in the suburbs of Maryland and Virginia appear at this analysis scale, largely centered on more recent suburban and commercial development around significant transportation corridors (Figure 11), and exhibiting a wide range in deviation from the 1:1 line. Falling just above the 30% ISA threshold, one grid cell centers on Hagerstown, MD (Figure 11), where recent and rapid development around the intersection of Interstates 70 and 81 has led to a very high ratio of burial per unit ISA (Panel D, Figure 10, yellow oval). Falling right on the 1:1 line are additional cells including Springfield, VA (I-95 corridor), Manassas, VA (I-66 corridor), and in Prince George's County, MD (I-495 corridor), which, despite centering on significant transportation corridors, have managed to maintain significant natural land cover (Figure 11). Exhibiting burial/ISA ratios just below 1:1 is an additional grid cell in Prince William County, VA, adjacent to Manassas, and one cell centered on the I-270 corridor in Montgomery County, MD. Two additional grid cells with >30% ISA fall well below the 1:1 line (Panel D, Figure 10, green oval), and include the areas around Herndon, VA, and suburban Prince George's County, MD, that exhibited similarly low ratios at the 45km² scale, as discussed above.

2.4.5 Burial prediction accuracy

Model prediction accuracy values for the iterative and full models can be found in Table 5. Iterative models, reserving 30% of available data for validation, yield average prediction accuracy scores of 92.7% (87-98%) and 55.8% (36-72%) for intact and buried stream segments, respectively, with a mean model accuracy of 83.1%. Accuracy scores for the full model, utilizing all available data for both

training and accuracy, were 88% and 71% for intact and buried segments, respectively, with a similar overall accuracy of 83%. ROC analysis identified a burial probability threshold of 0.35 as the optimum level that minimizes false positives for the burial classification (Figure 12).

2.5 Discussion

2.5.1 Extent of predicted stream burial

Predicted stream burial rates for the study counties follow a consistent pattern across all levels of development, with burial proceeding in a roughly one-to-one relationship with increasing impervious cover. There is no indication that any county or independent city development policies have succeeded in preventing potential stream burial, regardless of development stage. Neither does there appear to be any significant difference between state-level planning policies, as indicated by the lack of significant variation from the 1:1 line (Figure 7) for the majority of counties across the three states examined: Maryland, Virginia, and West Virginia.

2.5.2 Relationship of predicted burial to ISA across multiple scales

The main goal in analyzing predicted burial/ISA relationships across different scales was to determine if the size of the analysis unit influenced the outcome of the analysis. Initial observations at the county-level (Figure 3) suggested an approximate 1:1 relationship between predicted burial and ISA, until a threshold value for ISA of roughly 30% is achieved (Panel A, Figure 10). County units with greater than 30% ISA exhibited greater ratios of burial/ISA, and included 5 independent cities in

Virginia, Arlington County, VA, and Washington, D.C. I originally hypothesized that this was due principally to the longevity of development in these areas (mid- late-18th century), and their long term roles as commercial and government centers, leading to a greater degree of predicted stream burial through sustained and dense development and redevelopment over time. But these units are quite small (48.3 km² mean area), whereas the rest of the county units are much larger (1095.4 km² mean area). There exist similarly small-sized, dense areas of urban development within these larger counties, and it was unclear if the 1:1 relationship between burial/ISA would pertain to these areas as well, or if the true relationship was being masked, or ‘averaged out’, by including large amounts of non-urban land cover present in these larger analysis units in the calculations.

The expanded analyses included units ranging from the scale of Counties (631.2 km² mean area), to small grid cells with a uniform area of 22.5 km² (Table 4), and yielded some interesting results. Larger numbers of smaller units covering the same area led, generally speaking, to a higher number of analysis units above the 30% threshold. The subwatershed analysis was an exception, with only two units exhibiting ISA values greater than 30% (Panel B, Figure 10). This may have been due to the extent and distribution of the subwatershed units, being natural, and encompassing entire stream systems, and therefore not comparable in that sense to arbitrary government boundaries or regularly sized and spaced grid analysis units that only capture a portion of any watershed. Nevertheless, across all units and scales, we observed similar relationships between predicted burial and ISA, both above and below the 30% threshold. In general, it appears that streams are buried in proportion

to ISA to a level of approximately 30% ISA, after which streams are buried at a higher rate per unit ISA. This phenomenon is most likely due to the lack of remaining developable land that is not directly adjacent to streams, with continued development... a.k.a. “infilling”... leading to stream impacts.

Across all scales, again with the exception of subwatersheds, we see that there are examples of a few analysis units that buck the trend, exhibiting much lower burial/ISA ratios, even above the 30% ISA threshold. However, these examples tend to be extremely close to the 30% threshold, and we don’t see this at levels of ISA above 30%-40%. Areas with elevated burial/ISA ratios tend to be older developments, either in the D.C. core, or near-suburbs that have been developing and redeveloping for decades, though there are a couple of newer-developing areas with elevated ratios (e.g., Hagerstown, MD). Areas above 30% ISA that fall along the 1:1 line include a mixture of both old and new development, and tend to be areas that include significant non-urban cover areas, such as parks or agriculture, or are centered on large bodies of water such as the tidal portions of the Potomac River. Areas with lower burial/ISA ratios tend to be new suburban and commercial centers, including those surrounding important transportation hubs and corridors. Whether this is due to policies more effective at preventing stream burial, or whether they have simply not developed to their full density, is as yet unclear.

As the analyses moved from larger to smaller units, we generally saw a larger percentage of the total study area that fell above the 30% ISA threshold (Table 4), suggesting that the size of the analysis unit does have some effect on the results. The simple explanation is that because of the larger number and smaller size of the

analysis units, the units are more efficient in capturing portions of the study area with a higher percentage of ISA, and therefore potential stream burial. Nevertheless, the approximate 30% ISA threshold, and corresponding increase in burial/ISA ratio appears to hold across analysis units of any shape and scale, with the most appropriate dimensions determined by the nature of the questions being asked.

2.5.3 Predicted burial patterns by development stage, and relationship to catchment area and slope

Headwater streams across the study area are predicted to be buried more extensively than are larger streams at all levels of urban development, with maximum predicted burial rates for all but the most urbanized counties peaking at catchment areas of approximately $1.0 \log_{10}$ ha, after which burial rates decrease linearly with increasing catchment area. In the more urban counties, streams are predicted as buried at high rates (spatially distributed evenly) between approximately 1.0 and 2.5 \log_{10} ha catchment areas, after which predicted burial rates decrease fairly rapidly as catchment size increases. Both of these findings are consistent with those of Elmore & Kaushal (2008) from the Gunpowder-Patapsco watershed of Maryland, suggesting similar initial constraints to stream burial across basins and management entities. In the case of heavily urbanized areas, it appears the initial burial constraint consistent with the $1.0 \log_{10}$ ha catchment area can be overcome. This “soft constraint” is most likely related to some aspect of the landscape affecting the ‘favorability’ of a particular area to urban development (e.g., topographic slope, discussed below), and becomes less of a constraint once an area becomes developed enough that the most favorable (e.g., low slope) lands are unavailable for further development. The upper

limit to maximum predicted burial, occurring at roughly $2.5 \log_{10}$ ha catchment area appears to be universally observed, suggesting a ‘hard constraint’, beyond which burial is largely impossible. As suggested by Elmore & Kaushal (2008), streams above this threshold may simply be too large for burial to be economically feasible, or the limit may be set by regulatory statute, such as the floodplain development restrictions imposed by the Federal Emergency Management Agency (FEMA).

Long-term, time-series data on stream burial rates and patterns are currently unavailable, therefore, our analysis utilizes a space-for-time (SFT) substitution (Pickett 1989) across the study counties, whereby the urban-rural gradient, as indicated by total impervious cover (IC), serves as a proxy for predicting trends in stream burial over time. Space-for-time substitutions are often used in urban ecology to assess the consequences of increasing urbanization intensity (Valiela et al. 1992, Grimm et al. 2000, Brown et al. 2009, Stranko et al. 2012, Diaz-Porras et al. 2014), with more heavily urbanized areas serving as a reference for the future of other, less-developed places (Netzband et al. 2007). Relying on SFT substitution assumes that spatial and temporal variation across sampling units are equivalent (Pickett 1989), that is, study locations differing in land use are essentially similar in all other respects, and, will therefore experience an equivalent progression over time as that of any single location experiencing urbanization (Allan 2004).

Given the long history (200+ years) of urban development in the region, there is a risk that the relationship between stream burial and impervious cover has changed over time, with the shifting socio-economic context leading to changes in development

practices. Nevertheless, our results adequately incorporate any changes in this relationship over time, but do not speak to the potential for change in the future.

We found consistent patterns in stream burial predictions between counties with a similar development history (Figure 13). Local burial minima ($\sim 0.2 \log_{10}$ ha) are established immediately, as initial development (Tier 4), and, therefore, stream burial is generally confined to areas with the lowest slopes. Catchments with area $< 0.5 \log_{10}$ ha are generally located on flatter areas on ridge tops, and are generally among the first areas to be developed, along with lower slope areas in river valleys (Riebsame et al. 1996). During this stage, predicted burial rates are relatively low ($\sim 2\%$ - 5%) and across all catchment sizes, and the local maximum in burial rates ($\sim 1.0 \log_{10}$ ha) characteristic of later development stages is not yet clearly delineated (Figure 9, Tier 4), though there does appear to be a shift in the distribution of burial at this point that may become more distinct as development progresses.

It appears that for two of the counties in this development tier (Washington Co., MD, and Clarke Co., VA) the point of maximum predicted burial is shifted to the right relative to counties in later development stages, towards the $2.5 \log_{10}$ hectare 'hard constraint' (discussed above). This trend is especially obvious in Washington County, MD, the most heavily developed of the three, and may indicate a conscious effort to guide development away from the steeper slopes, thereby concentrating burial on streams of moderately larger catchment size. Jefferson County, WV, differs from the other two in exhibiting relatively even levels of predicted stream burial across all catchment areas (as indicated by non-significant slopes for both ascending and descending burial limbs (Table 2)), very high rates of predicted burial ($\sim 4x$ - $6x$)

across the smallest watersheds, and a higher rate of predicted burial per unit impervious cover to the others within its tier. Considering all three counties in this tier straddle The Great Valley, and are roughly equivalent in topography and the distribution of streams, these differences most likely indicate a more permissive decision-making process in Jefferson County, allowing stream burial to proceed regardless of the constraints limiting development of streams in other counties.

In more recently developed counties, (Tier 3, Figure 9), the predicted burial ‘curve’ tends to rise within a narrow range in catchment size, creating an evident local maximum (~ 1.0 - $1.4 \log_{10}$ ha catchment area, Table 2), and the characteristic ‘humped’ distribution (with steeper slopes for ascending and descending limbs, Table 2) of predicted stream burial rates in relation to catchment size that is maintained throughout later development stages. The local minimum in burial, established at the outset of development, is maintained, though its value increases as streams within and surrounding this size class are buried to a greater degree. Within Tier 3 (Figure 9), Frederick County, MD, exhibits a slightly different predicted burial pattern than the other two counties. While predicted burial rates in the smallest size classes ($< 0.4 \log_{10}$ catchment area) are comparable to that of Loudon and Prince William counties in Virginia, the characteristic “burial hump” is less evident, with burial rates rising only slightly, and remaining relatively consistent ($\sim 4\%$ - 5%) across larger size classes (slopes of the ascending and descending burial limbs are insignificant (Table 2)), before decreasing beyond the $2.5 \log_{10}$ ha catchment area constraint. It is not clear at this point whether this anomaly is due to differences in planning policies across state

lines, or some other unique factor driving the distribution of development within Frederick County.

Farther along the development spectrum, Tier 2 counties maintain the humped burial distribution, with higher overall rates of burial across all size classes. With maximum predicted burial rates approaching 20%, Fairfax County exhibits a greater amount of potential stream burial (Figure 8) across all size classes than do the two Maryland counties in this tier. Prince George's County, MD, however, appears to have moved towards the burial patterns exhibited by Tier 1 counties, as described below. Maximum predicted burial rates continue to occur in the range of 1.0-1.4 \log_{10} ha catchment area in this Tier, reinforcing the idea of some sort of burial constraint imposed in this general size range.

The urban centers (Tier 1, Figure 8), including Washington, DC, Arlington, VA, and the Virginia Independent Cities, exhibit drastically higher rates of predicted stream burial than lesser-developed tiers, with burial rates of 60% or more in certain catchment-area classes. Rather than a single, peak burial rate, jurisdictions in this size class exhibit uniformly high rates of predicted burial across a wide range of catchment sizes. While the initial slope constraint remains intact, burial rates increase rapidly and significantly thereafter, remaining at high levels until about 2.5 \log_{10} ha catchment area. At some point in their long development history, the 'soft constraint' on stream burial rates occurring at approximately 1.0 \log_{10} ha catchment areas was relaxed, most likely due to the 'in-filling' of areas previously protected as the need for developable area within these jurisdictions continued to rise. The roughly 30%-50% of headwater streams still existing above ground within these areas, is most

likely due to the maintenance of parks and other protected natural areas (Elmore and Kaushal 2008), and will likely remain at or near these levels in the future, barring future changes to protection policies for riparian zones and other open areas.

2.5.4 Accuracy analysis of burial predictions

Both the iterative model set and the full model yield essentially the same overall classification accuracy (~83%, Table 5), yet the models differed in their calculated accuracy values for the binary classification factors, that is, the models' ability to accurately classify streams as intact or buried. The iterative models, on average, were better able to correctly classify intact streams (92.7% vs. 88%), while the full model was far superior at correctly classifying buried streams (71% vs 55.8%). In addition to the lower average classification accuracy for buried segments as compared to the full model, the iterative models exhibited much higher variability in their ability to accurately classify buried segments. This variability may be due to the relatively low number of training points classified as buried (576) versus intact (1640) from which to randomly select for model input. Additional factors may include the wide variation the types of stream burial evident across the basin (e.g., bridges vs. parking lots vs. concrete-lined channels), and therefore the values for impervious cover statistics generated for the 'neighborhood' of each classified segment, or various and inconsistent coregistration errors between classified points and the impervious cover layers. A higher burial accuracy value for the full model suggests that the model is overfitting the data. Results from the iterative model set show that particular combinations of training data influence the models more than

others, with changing results every time the data is resampled leading to lower overall accuracy values for the buried fraction.

The ROC analysis identified a burial probability value of 0.35 as the ideal threshold, given the data, for accurately classifying sites as intact or buried (Figure 12). While numerically distant from the threshold of 0.50 we applied for our burial classification (see description above), 50% burial probability is the next highest node in our decision tree, and is, therefore, the most appropriate probability value for our dataset. There was a terminal node in our decision tree classification with a probability value of .34, extremely close to the optimum threshold, but had we selected this node as our threshold probability, we would have significantly increased the false positive fraction of buried points within the classification. Ideally, we the ROC curve would be less sparse, and we would have more numerous threshold values from which to select. A different set of explanatory variables may have been more diagnostic, but given the nature of our indicator data, and the finite number of terminal node values generated by the decision tree classification we employed, we are confident that we chose the optimum probability threshold for the PRB burial dataset.

2.5.5 Mapping approach and uncertainties

The combination of new methods outlined above, including improved stream maps, moderate resolution impervious cover data, and non-linear modeling allow for the successful mapping of burial probability for every stream reach within the PRB, overcoming obstacles presented by previous mapping attempts requiring intensive, on-the-ground investigations (Roy et al. 2009). There are several instances, however,

where error may have been introduced into the burial classification. For example, the improved stream maps of Elmore et al. (2013) were modeled using training data gathered from forested watersheds as a reference, and using digital elevation models to place streams where they should occur naturally, based on the topographic flow of water across the landscape. These methods may be less accurate in heavily urbanized landscapes, where land cover and topographic relief have been highly altered, and streams may have never existed or been diverted significantly from their original course. In many of these areas, there may be no maps to confirm the pre-development status and location of streams, thereby preventing confirmation of their previous existence, or lack thereof.

The methods for calculating the probability of burial for stream reaches cannot account for slight variations in stream path caused by natural shift of channels over time, or other co-registration errors between the stream and impervious cover data layers, potentially leading to inaccuracies in the calculation of values for the average level of impervious cover in the neighborhood of each stream pixel, which was used to classify burial potential. Additionally, while creating the training data for classifying burial potential, only burial related to impervious cover was considered. In reality, other forms of burial can also be prevalent across a watershed, including streams routed into pipes, and buried under residential lawns, in agricultural fields (Stammler et al. 2013), or inundated by man-made impoundments, and even large reservoirs. As we were primarily interested in urban-related stream burial, these cases were not classified as buried, leading to the probability that stream burial is underestimated for counties across the gradient from rural to urban. Finally, a high

degree of variability was present in the predicted burial data at larger catchment areas (approximately $2.5 \log_{10}$ ha and larger) across some counties. This is due largely to the fact that there are very few streams in these larger size classes, with average burial rates for these bins potentially being artificially heightened or lowered by a one or more extreme values within the bin. Despite these uncertainties, we see robust, repeated patterns in the data, with very little variability across most catchment sizes.

2.6 Conclusions and management implications

Our work indicates that stream burial is an ongoing phenomenon, with predicted burial increasing linearly with total impervious cover across all levels of development, bringing into question the efficacy of existing stream protections. The close relationship with total impervious cover limits the utility of predicted stream burial as an overall indicator of watershed health and function, that is, simply summing to achieve the total amount of burial does not provide additional information above and beyond the value for total impervious cover across our study area. What it does provide is a spatially-explicit measure of potential stream-specific impacts, accounting for the effects of impervious cover immediately adjacent to and covering stream channels, including direct habitat loss, and the probable effects of contiguous impervious cover on physical and hydrologic regimes in stream ecosystems. Predicted stream burial data could be used to identify high impact watersheds for targeting restoration, to address riparian and network connectivity issues, and to integrate effects of hydrological change into efforts to manage downstream water quality, including the Federally-regulated TMDL process.

We know that loss of in-stream and riparian habitat holds potential implications for aquatic organisms, and their ability to move both within and between headwater systems. Subsequent chapters of this dissertation deal with the effects of predicted stream burial on network geometry (the size and spatial orientation of remaining stream reaches), and the effects on habitat connectivity within and between headwater systems on biodiversity patterns in aquatic communities. Future work may also include examining predicted burial rates across time, to better discern how burial has proceeded in relation to physiographic and policy constraints, and related effects to ecosystem structure and function across large, developing watersheds.

Headwater stream burial is prevalent across the study area, even within watersheds with very little urban development. Predicted burial increases linearly with total impervious cover across all levels of development, bringing into question the efficacy of existing stream protections. Both slope and catchment area combine to limit stream burial during development, but these constraints were largely overcome in the most intensely urbanized jurisdictions. Headwater stream systems are critical to the maintenance of downstream water quality and hydrologic regimes (Freeman et al. 2007), and yet, continue to be disproportionately affected relative to larger streams. Clearly, more rigorous and uniform protection policies and other strategies to reduce the impacts of burial are needed to preserve the ecological function of these vital ecosystems.

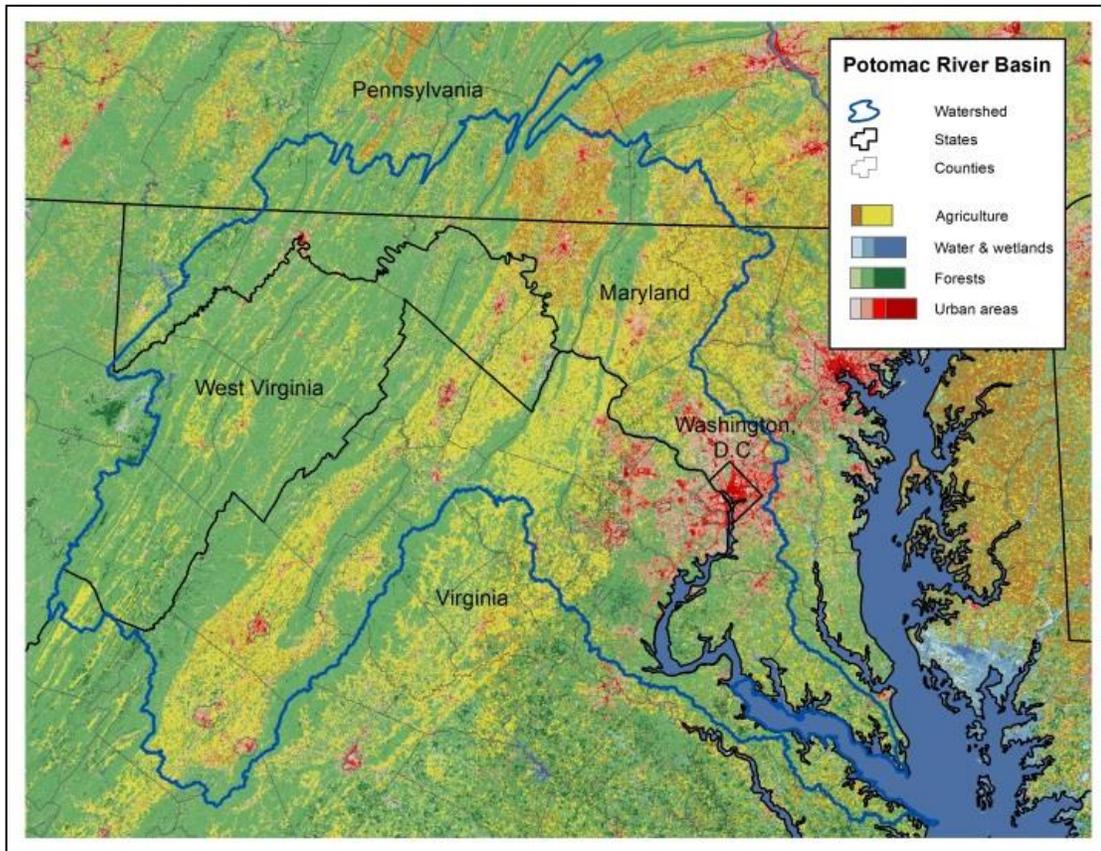


Figure 2.1 The extent and severity of stream burial was modeled for streams across the entire Potomac River Basin (PRB), which spans portions of four states (MD, PA, VA, WV) and Washington, DC.

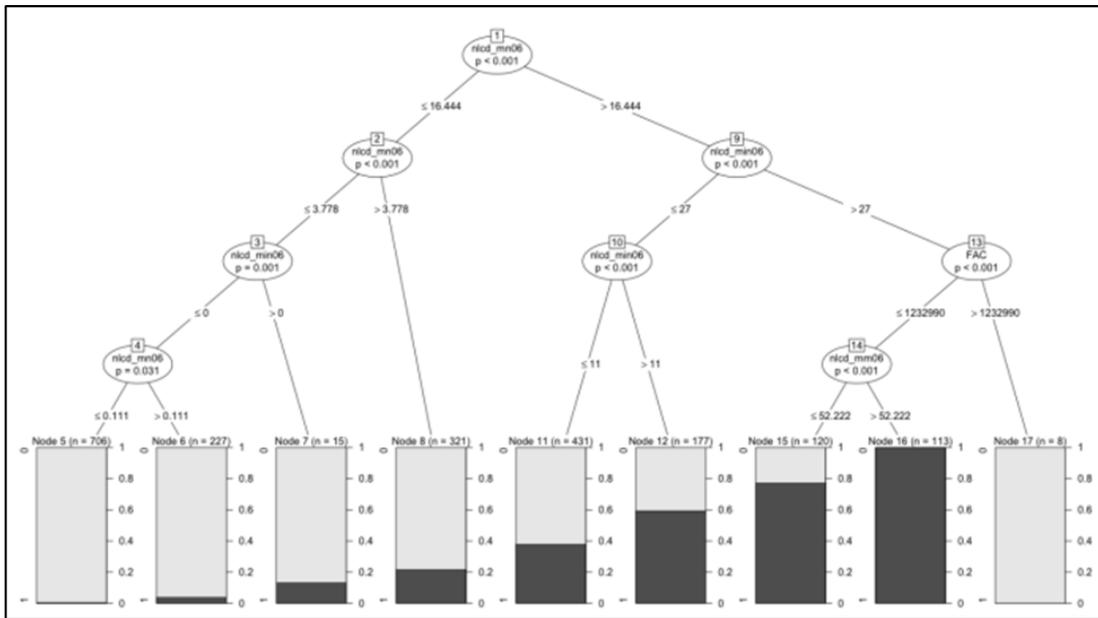


Figure 2.2 Decision tree for assignment of stream burial probability as determined by recursive partitioning of impervious cover statistics for each 10m stream reach across the PRB. Each split in the tree structure was determined by conditional inference to reduce the remaining variance in the data and was associated with a p-value < 0.05 .

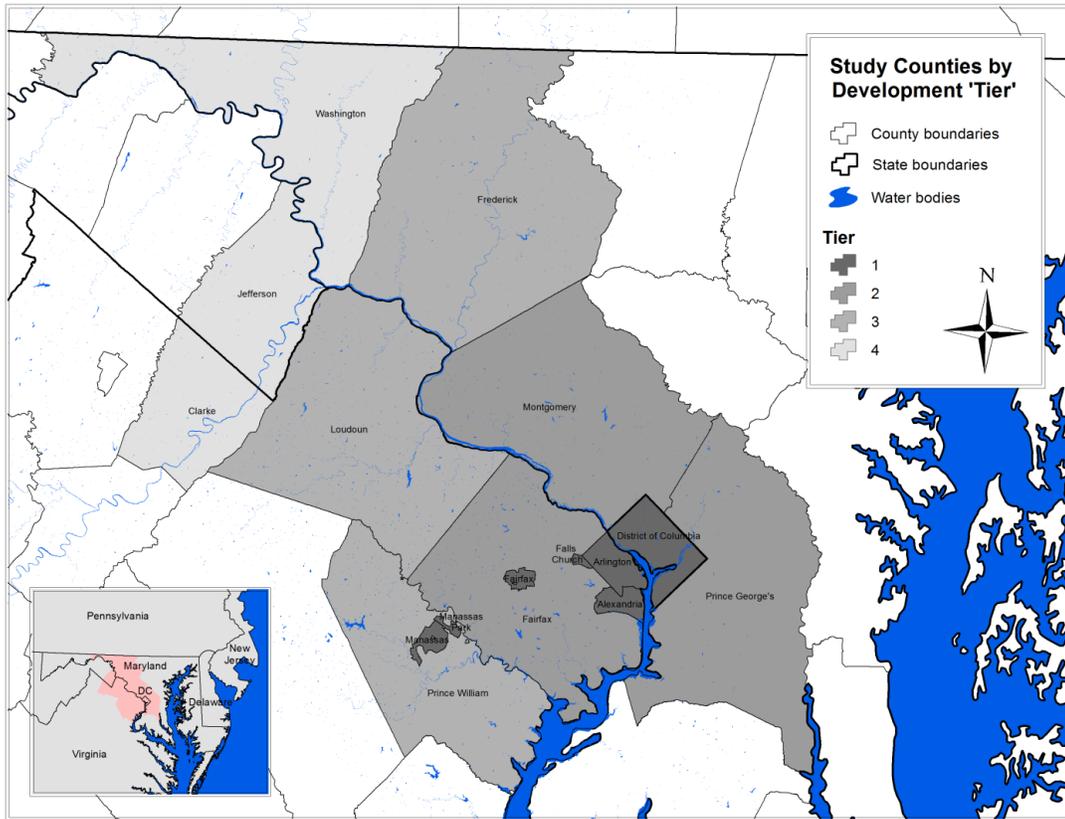


Figure 2.3 The sixteen study counties and independent cities colored by development “tier”, as determined by the total amount of impervious cover, and relative distance from the Washington, D.C., urban center.

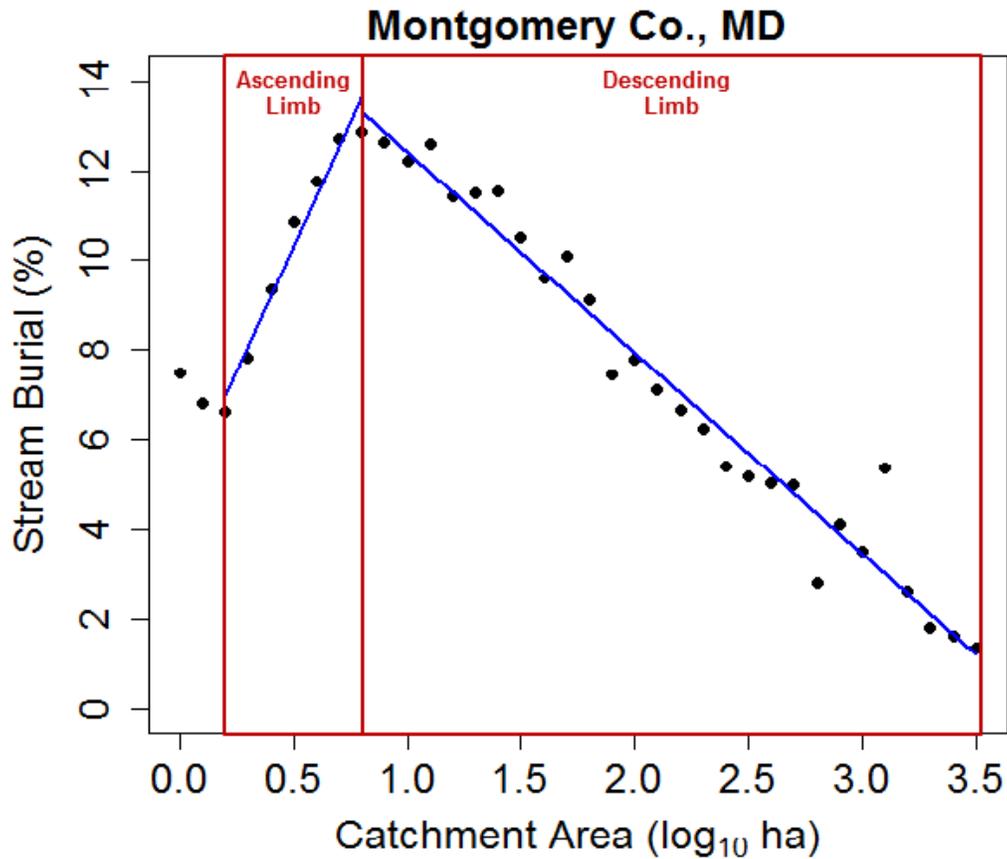


Figure 2.4 Distribution of burial by catchment area for Montgomery County, Maryland. Values of local minima and maxima are indicated by vertical, dashed lines. Fit lines for burial data on either side of the maxima are indicated in blue. Red boxes indicate the ascending and descending ranges of data on either side of the burial maximum, for which regression analyses were performed across all counties and development tiers.

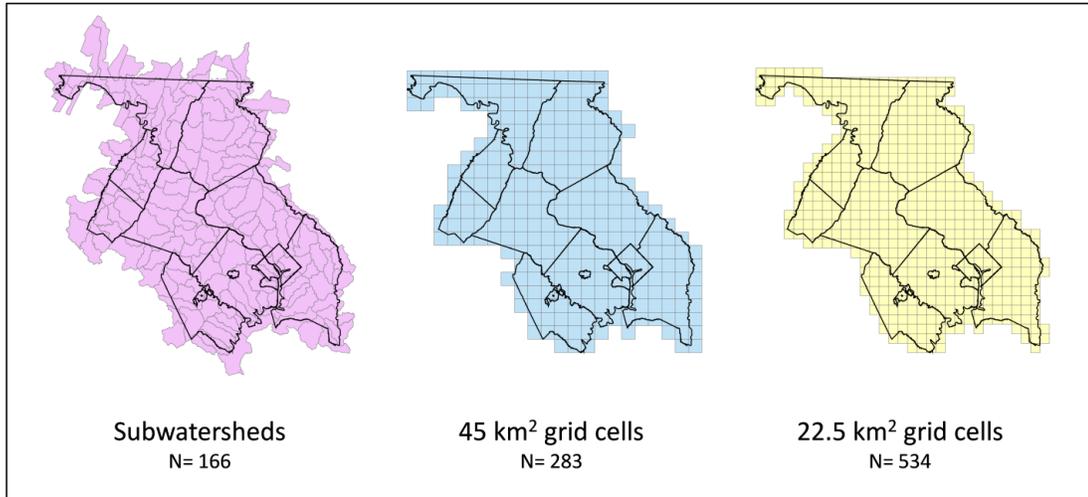


Figure 2.5 Extent and number of analysis units at three scales smaller scales across the 16 county study area. Subunit boundaries are indicated by grey lines, with county-scale boundaries are indicated by black lines.

Table 2.1 Area, stream length, impervious cover and stream burial statistics for the 16 study counties.

Counties and Independent Cities	Area (km²)	Potential Stream Length (km)	Impervious Cover (%)	Stream Burial (%)
Washington, D.C.	177.0	325.8	37.6	47.3
Arlington County, VA	67.3	170.9	33.6	39.4
City of Alexandria, VA	39.9	95.7	42.8	51.1
City of Fairfax, VA	16.3	40.9	28.9	31.3
City of Falls Church, VA	5.1	11.2	26.6	32.4
City of Manassas, VA	25.8	49.1	32.0	31.7
City of Manassas Park, VA	6.5	16.4	29.1	22.9
Prince George's County, MD	1291.0	2984.5	16.4	18.5
Montgomery County, MD	1313.5	3830.8	10.2	11.0
Fairfax County, VA	461.5	2803.9	15.2	14.3
Frederick County, MD	1728.4	4146.2	3.3	4.4
Loudon County, VA	1053.1	3555.3	5.5	4.9
Prince William County, VA	902.3	2566.7	8.0	7.5
Washington County, MD	1210.9	2151.0	3.7	4.4
Jefferson County, WV	548.0	733.0	2.5	4.5
Clarke County, VA	1349.6	658.4	0.9	1.6

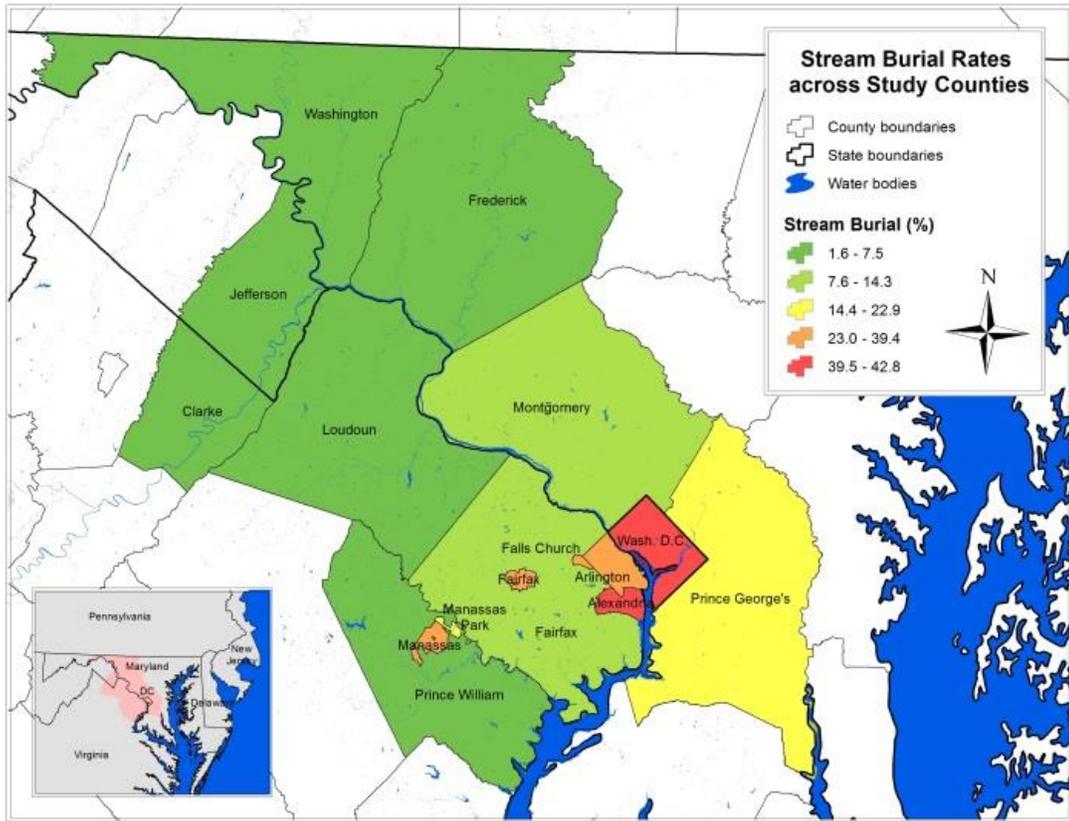


Figure 2.6 Stream burial rates across the 16 study counties and independent cities.

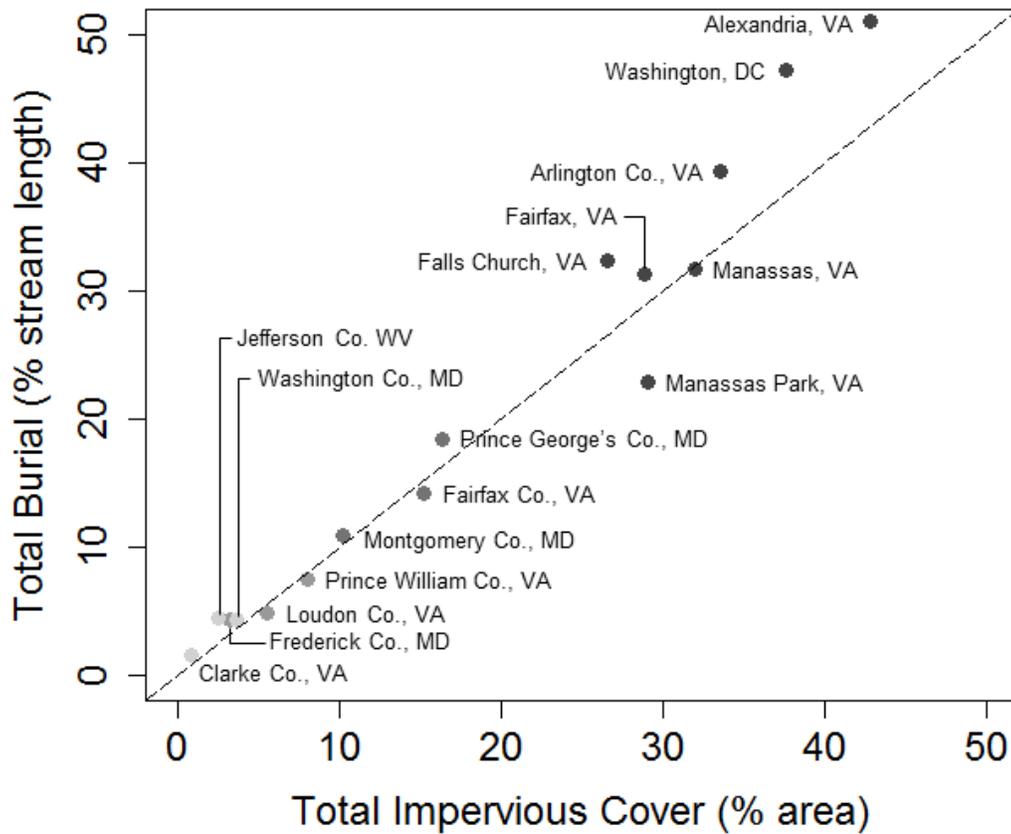


Figure 2.7 Percent burial as a function of impervious cover for the sixteen study counties. Colors of the points correspond with colors of development tiers in Figure 3. The dashed line represents the 1:1 line for burial and impervious cover.

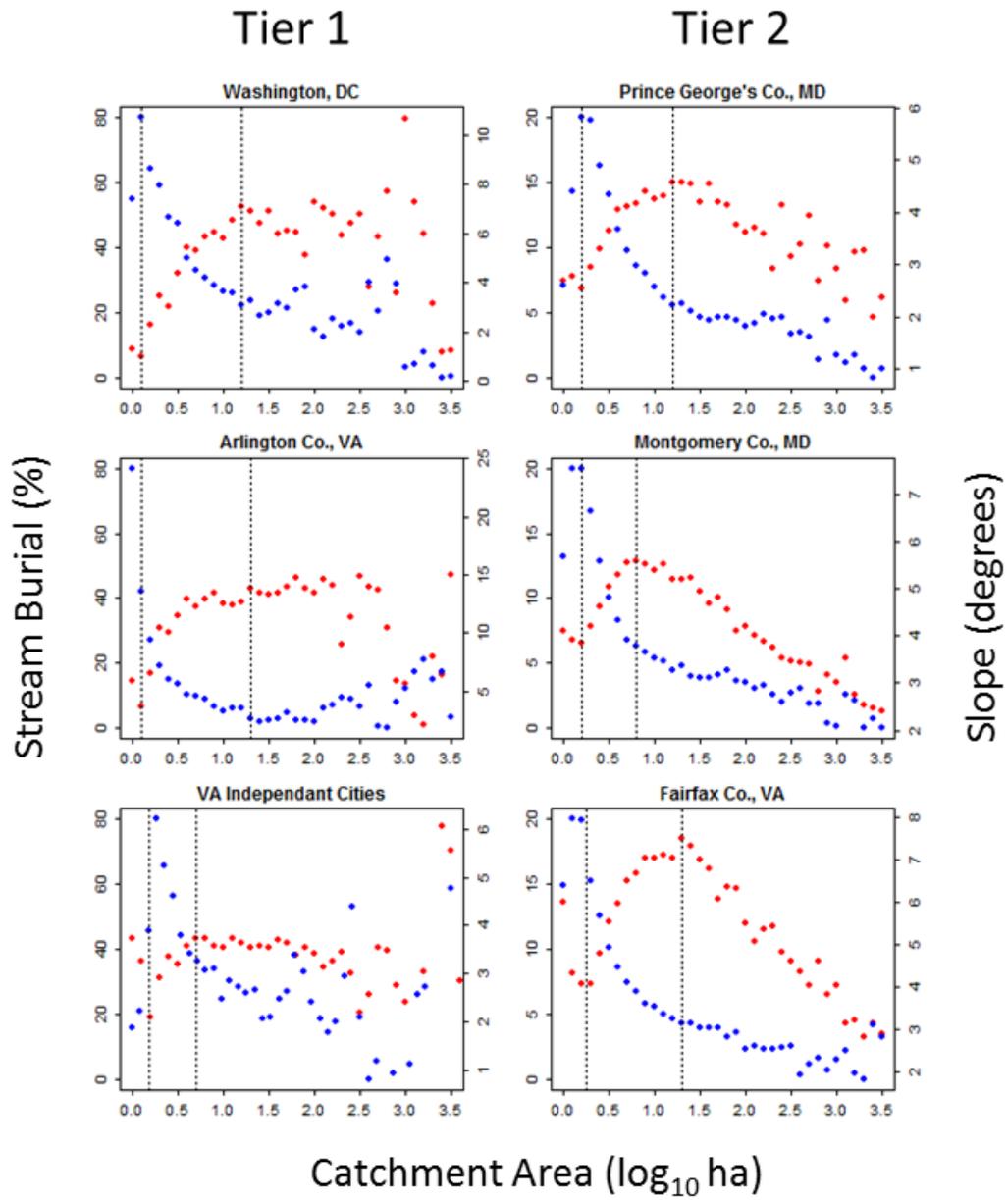


Figure 2.8 Stream burial (%) and slope (degrees) in relation to catchment area (log₁₀ ha) for Tier 1 and Tier 2 counties. Data for the independent cities of Virginia were analyzed as a single entity, and the results plotted together.

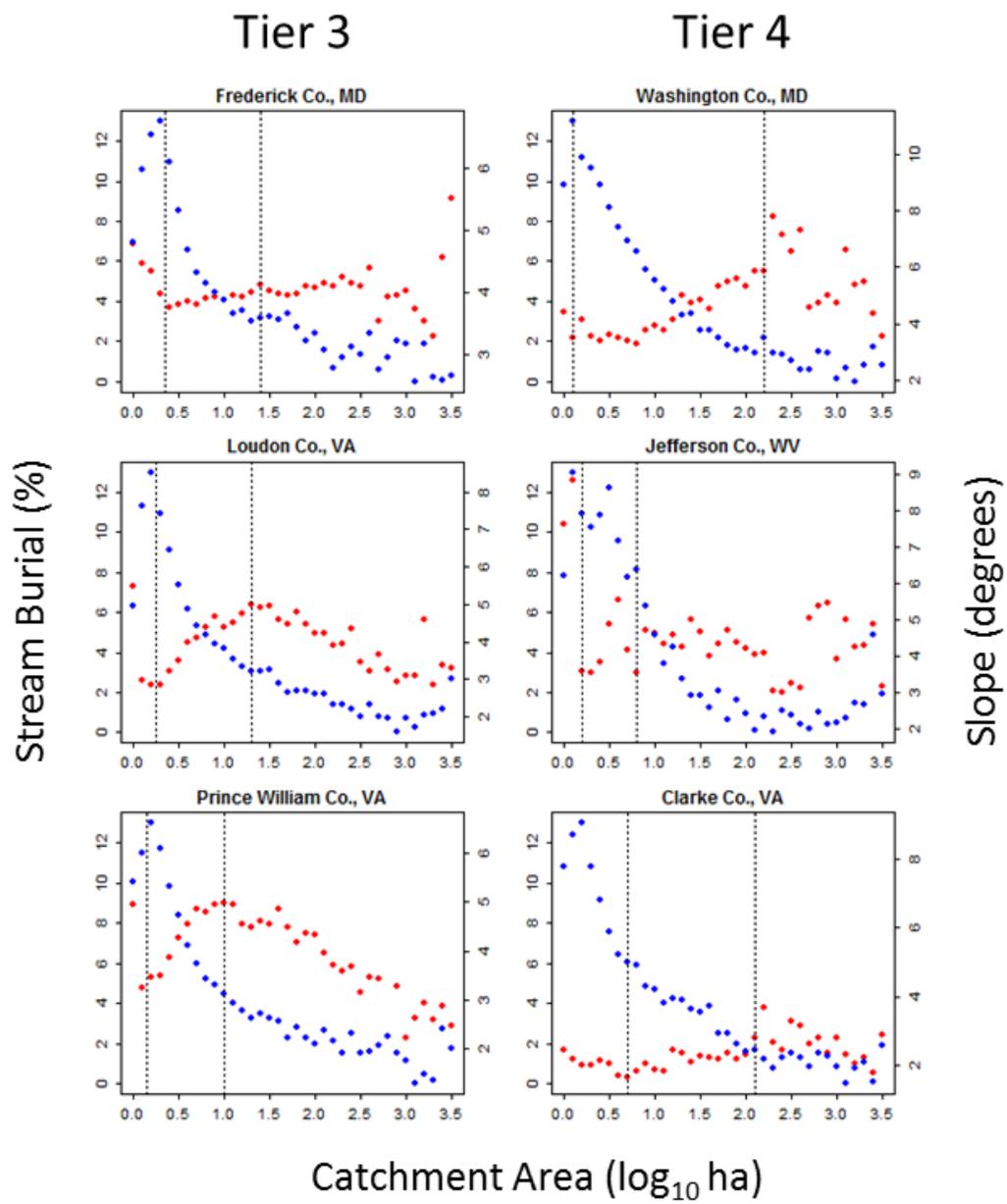


Figure 2.9 Stream burial (%) and slope (degrees) in relation to catchment area (log₁₀ ha) for Tier 3 and Tier 4 counties.

Table 2.2 Characteristics of the distribution of burial data in relation to catchment area for the sixteen study counties. Results include analyses for both the ascending and descending limbs of the burial distribution. All models were significant to at least $p < 0.5$, with many being even more highly significant. Results with daggers ([†]) are for models where the slope of the ascending and descending limbs was not significant.

Counties		Max Burial % (FAC)	Local Mimimum* (FAC)	Local Maximum* (FAC)	Ascending Slope	Ascending Intercept	Descending Slope	Descending Intercept
Tier 1	Washington, D.C.	79.4 (3.0)	0.1	1.2	37.20	10.10	-9.28	65.21
	Arlington County, VA	47.4 (3.5)	0.1	1.3	21.75	18.34	-13.30	65.60
	Independent Cities, VA	78.0 (3.4)	0.2	0.8	36.09	17.82	2.48 [†]	34.96 [†]
Tier 2	Prince George's County, MD	15.0 (1.3)	0.2	1.2	7.36	6.90	-3.71	19.59
	Montgomery County, MD	12.9 (0.8)	0.2	0.8	11.06	4.75	-4.48	16.88
	Fairfax County, VA	18.6 (1.3)	0.25	1.3	9.95	6.64	-6.93	26.89
Tier 3	Frederick County, MD	9.1 (3.5)	0.35	1.4	0.89	3.35	0.22 [†]	4.10 [†]
	Loudon County, VA	7.3 (0.0)	0.25	1.3	3.61	1.88	-1.62	8.30
	Prince William County, VA	9.0 (1.0)	0.15	1.0	5.25	4.34	-2.63	11.83
Tier 4	Washington County, MD	8.2 (2.3)	0.1	2.2	1.74	1.42	-2.90	13.46
	Jefferson County, WV	12.6 (0.1)	0.2	0.8	1.78 [†]	3.19 [†]	-0.08 [†]	4.45 [†]
	Clarke County, VA	3.8 (2.2)	0.7	2.1	0.85	-0.01	-1.12 [†]	5.16 [†]

Table 2.3 Results from linear models consisting of Burial~FAC, and Burial~SLOPE.

Counties		Limb	FAC	R ²	SST	SLOPE	R ²	SST
Tier 1	Washington, D.C.	Ascending	***	0.91	2183.87	***	0.95	2183.9
		Descending	*	0.18	5624.6	---	-	-
	Arlington County, VA	Ascending	***	0.65	1335.17	***	0.96	1335.17
		Descending	**	0.38	4672.4	***	0.62	4672.4
	Independent Cities, VA	Ascending	**	0.81	450.05	---	-	-
		Descending	---	-	-	---	-	-
Tier 2	Prince George's County, MD	Ascending	***	0.86	69.312	***	0.95	69.313
		Descending	***	0.75	210.571	***	0.71	210.57
	Montgomery County, MD	Ascending	***	0.96	35.493	***	0.99	35.492
		Descending	***	0.97	379.15	***	0.87	379.16
	Fairfax County, VA	Ascending	***	0.86	126.375	***	0.99	126.374
		Descending	***	0.96	503.26	**	0.45	503.27
Tier 3	Frederick County, MD	Ascending	***	0.86	1.01895	---	-	-
		Descending	---	-	-	---	-	-
	Loudon County, VA	Ascending	***	0.89	16.044	***	0.96	16.0435
		Descending	***	0.68	39.097	***	0.56	39.097
	Prince William County, VA	Ascending	***	0.92	18.042	***	0.98	18.0419
		Descending	***	0.88	114.503	***	0.60	114.502
Tier 4	Washington County, MD	Ascending	***	0.81	33.0171	***	0.64	33.017
		Descending	**	0.46	41.182	---	-	-
	Jefferson County, WV	Ascending	---	-	-	---	-	-
		Descending	---	-	-	---	-	-
	Clarke County, VA	Ascending	***	0.60	3.4154	---	-	-
		Descending	*	0.35	10.0001	---	-	-

Significance codes: 0 '***', 0.001 '**', 0.01 '*', no significance '---'

Table 2.4 Basic statistics for 4 scales of analysis unit across the study area.

Analysis Units	N	Mean Area (Range)	Area with >30% ISA
County level	16	632.1 km ² (5.19 – 1728.50)	292.01 km ²
Subwatersheds	166	89.9 km ² (33.75 – 170.44)	221.48 km ²
45 km ² grid cells	283	45 km ²	450.24 km ²
22.5 km ² grid cells	534	22.5 km ²	517.41 km ²

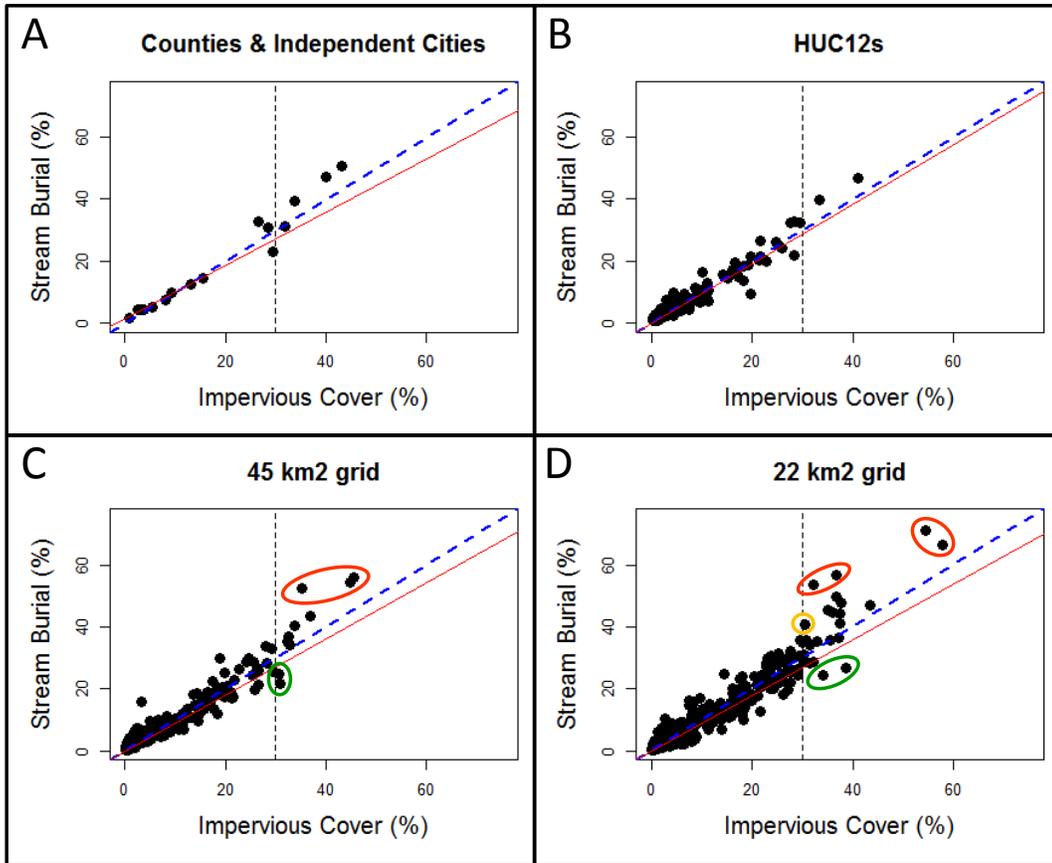


Figure 2.10 Relationship between estimated stream burial and percent ISA (NLCD 2006) for analysis units of different scales. Black dots represent individual analysis units. Blue, dashed line is 1:1 line. Red, solid line is the regression line for the data. Vertical, dashed line is the 30% ISA threshold. Colored ovals are referenced in ‘Results’ section of chapter text.

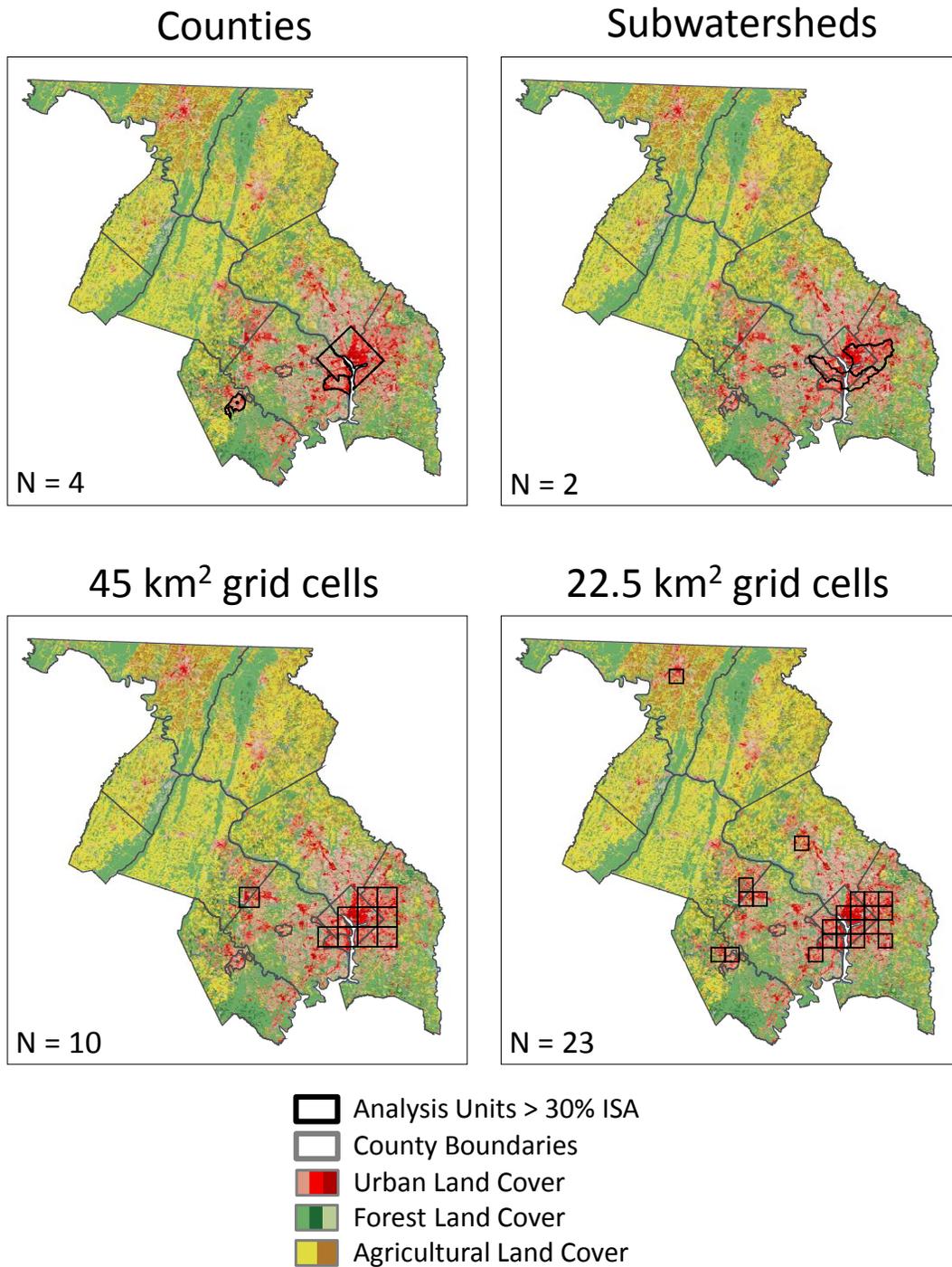


Figure 2.11 Maps of the study area showing the distribution of analysis units with >30% ISA, the threshold beyond which units exhibit an increasingly greater burial/ISA ratio with increasing %ISA. Analysis units with less than 30% ISA are excluded for clarity. Impervious and other land cover data consists of the 2006 NLCD.

Table 2.5 Accuracy values for iterative and full burial models.

Model	Accuracy (%)		
	Intact	Buried	Overall
Iterative	92.7	55.8	83.1
Full	88.0	71.0	83.0

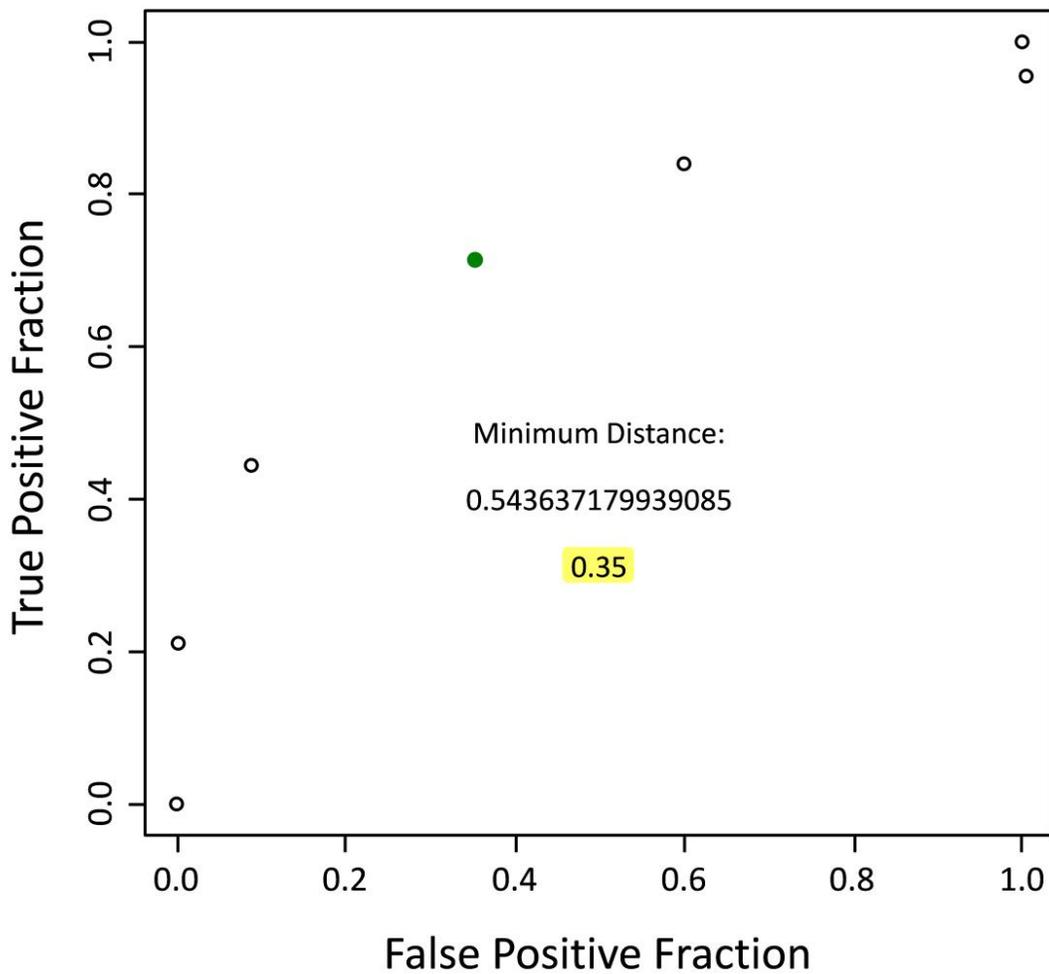


Figure 2.12 ROC curve of predictors stream burial across the Potomac River Basin. Green dot represents the probability threshold that minimizes false positives and maximizes true positive burial predictions (point that minimizes the distance to the upper left corner of the plot. The minimum distance is indicated within the plot, as is the ideal threshold value of 0.35.

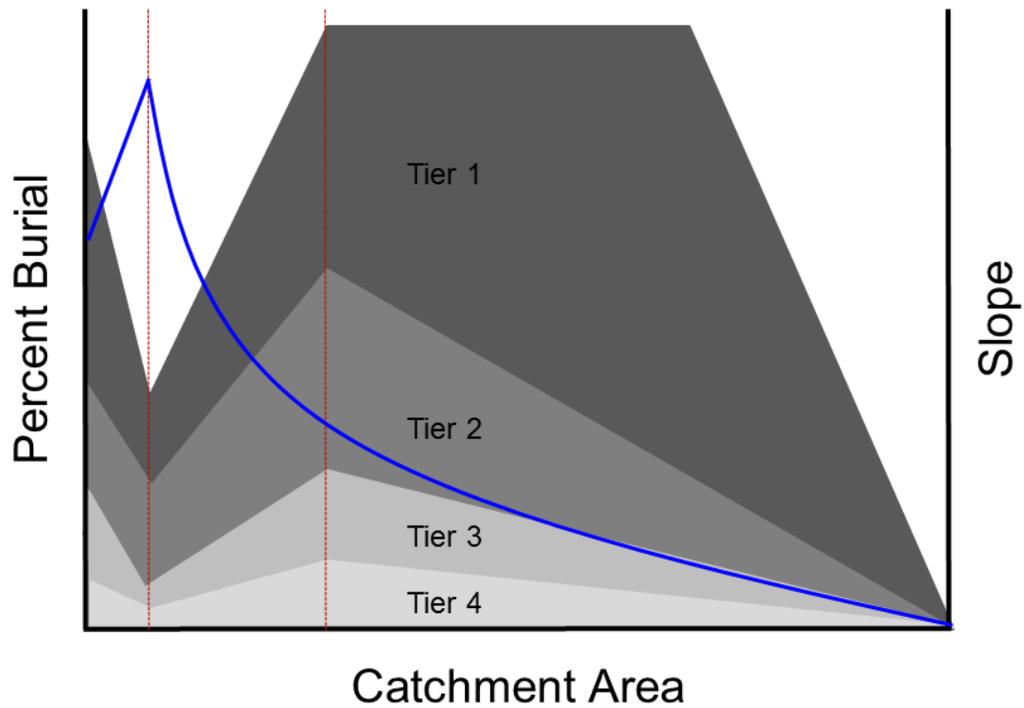


Figure 2.13 Conceptual diagram of the general progression of stream burial patterns as development proceeds from Tier 1 to Tier 4 across the study area. Red dashed lines represent local burial minima and maxima. The blue line represents the distribution of slope values in relation to catchment area. Axes are not to scale, but are meant to illustrate the general relationships between the variables.

Chapter 3: Cumulative effects of urban-related stream burial on network geometry and connectivity of headwater stream systems

3.1 Abstract

The spatial arrangement of habitat features in riverine systems interacts with species dispersal behaviors to influence patterns of aquatic diversity. The process of urban stream burial eliminates discrete habitat patches, directly undermining the movement of organisms within and between aquatic systems. Headwater systems have been disproportionately affected by stream burial, with removal of 70% or headwaters in some areas. The specific nature of network change associated with headwater burial has never been explored, limiting our ability to predict changes in biotic composition with urbanization of these critical ecosystems. We examined burial-related changes to network structure and habitat connectivity within headwater systems, using a series of topological and distance measures, and a novel application of circuit-theoretical modeling to stream networks. Results show that stream burial significantly affects both the number and size of remnant network components and their spatial orientation, with potential to disrupt ecological flows within headwaters, and to downstream receiving waters. Significant decreases in landscape connectivity were observed with burial, both in areas surrounding ecologically important features, such as confluences, and for urbanized headwater systems as a whole. Despite significant effects of stream burial on the network structure and distance measures evaluated here, at each level of stream burial there was considerable variability

observed in each measure. This suggests all stream burial events are not equivalent in their impact to network structure and biotic diversity.

3.2 Introduction

The dendritic architecture of river systems supports myriad physical, chemical, and biological processes critical to ecosystem health and human well-being (Fisher 1997, Benda et al. 2004b, Fagan et al. 2007, Rodriguez-Iturbe et al. 2009). Network geometry governs the spatial and temporal heterogeneity of resources and habitat in riverine systems (Benda et al. 2004a), thereby controlling population dynamics by influencing colonization opportunities and extinction risk (Calabrese and Fagan 2004, Fagan et al. 2007). The numbers of tributaries, their respective size and location within the network (network depth), and junction (confluence) effects are all critical in ecosystem function (Fisher 1997, Rice et al. 2001, Fagan 2002, Benda et al. 2004a, Benda et al. 2004b, Rice et al. 2006). Stream burial (e.g., the paving over of streams, or placing streams in culverts and storm water systems) has the potential to modify stream networks, potentially with detrimental effects to the spatial processes that sustain biotic diversity. Network fragmentation resulting from stream burial degrades or eliminates discrete habitat patches, directly undermining the movement of materials and organisms within and between aquatic systems (Freeman et al. 2007, Wipfli et al. 2007). Macroinvertebrate populations in headwater streams may be particularly sensitive to disruptions in network connectivity, due to the high levels of habitat specialists restricted to these systems (Morse et al. 1993, Richardson and Danehy 2007, Clarke et al. 2008). Furthermore, low physical connectivity among

headwaters limits opportunities for colonization and population exchange to long distance dispersal paths through highly inhospitable habitats (Fagan 2002, Gomi et al. 2002, Richardson and Danehy 2007).

Network structure consists of more than just the identity of the structural elements of a system, but their size, orientation, configuration, and relative position (Fisher 1997), collectively known as network “geometry” (Fagan et al. 2007). The spatial structure of habitat features controls processes at several ecological levels (from genes to whole communities), with the specific spatial arrangement and hierarchical organization interacting with species’ dispersal behaviors to control patterns of aquatic diversity (Grant et al. 2007). As headwater systems constitute the vast majority of stream length and catchment area in any watershed (Leopold et al. 1964, Hansen 2001, Benda et al. 2005), understanding the cumulative effects of stream burial on the quantity and spatial arrangement of system components, and associated changes to habitat connectivity, is essential to the effective management of aquatic ecosystem health.

The aim of this study was to assess the cumulative impacts of urban-related stream burial to network geometry and habitat connectivity within headwater stream systems of the Potomac River Basin, with a particular focus on critical habitats and dispersal processes relevant to aquatic insect communities. We compared newly-modeled, comprehensive stream burial maps for the basin (2006; Chapter 2) with intact headwater stream maps (Elmore et al. 2013), to quantify changes to the number, size, and spatial orientation of critical habitat components within stream networks, and how these changes are distributed across headwater systems. The

buried stream data was then combined with moderate-resolution land cover data (Fry et al. 2011) in a novel application of circuit-theoretical models (McRae et al. 2008), to examine burial-related changes to habitat connectivity within headwater stream networks and their surrounding landscapes (systems, or watersheds). We expected that habitat loss and fragmentation from stream burial, coupled with associated urban land use change in upland areas, would lead to significant decreases in connectivity, and therefore, the potential for successful dispersal of aquatic organisms within and between headwater systems. This research provides new insight into the effects of urban development on stream ecosystem form and function, with potential application to understanding the consequences of continued loss of headwater streams to local and regional aquatic communities.

3.2.1 Measured stream network characteristics

Headwater reaches constitute the main point inputs of water, materials, and energy to aquatic systems (Gomi et al. 2002), therefore their number and distribution must be explicitly considered (Fisher 1997). The geometry (“branchiness”) of tributary networks determines the availability and spatial arrangement of habitat patches in riverine systems, governing population dynamics by influencing colonization opportunities and extinction risk (Calabrese and Fagan 2004, Fagan et al. 2007). Tributary *confluences* represent abrupt changes in physical and chemical regimes (Benda et al. 2004a), with increases in morphological heterogeneity providing refugia for sensitive life stages or species, and access to the mainstem for migratory individuals (Campbell Grant et al. 2007). Loss of these biological

“hotspots” (McClain et al. 2003) to stream burial can alter the flux of organisms and material to downstream waters (Benda et al. 2004b).

Channel head areas, including ephemeral, intermittent, and perennial reaches at the upstream termini of headwater networks, are known to be critical refugia for certain aquatic taxa (Progar and Moldenke 2002, Covich et al. 2009), and may be critical for aerial dispersal of winged adult insects in headwater systems where upstream sources of colonists are lacking (Williams and Hynes 1976, Wallace et al. 1986, Bunn and Hughes 1997, Flory and Milner 2000). Often representing the shortest distance between adjacent stream reaches, recent work has shown that adults may preferentially move between watersheds along a direct path through these upland areas, rather than along the stream corridor (Macneale et al. 2005, Chaput-Bardy et al. 2008). These out-of-network movements may be particularly important for maintaining genetic diversity within populations, and for population persistence following fragmentation of dendritic networks (Fagan 2002).

Even small amounts of burial-related *fragmentation* in dendritic stream landscapes can significantly decrease the chances for successful dispersal and colonization of new habitats by aquatic organisms (Fagan 2002). However, the cumulative impact of changes in form on ecological function depend on the hierarchical level at which they occur (Fisher 1997). For instance, branched river systems, and especially headwater stream systems, are intimately connected with the landscape, to lakes, wetlands, and both shallow and deep groundwater systems. Certain areas within headwater networks may be more critical than others in maintaining ecological integrity, both locally and in downstream areas. Therefore, a

measure of *network depth*, or location along the drainage network would be helpful in gauging whether burial-induced fragmentation occurs with equal probability throughout the network, or may be clustered in certain areas (Fagan 2002, Fagan et al. 2007).

Consideration of the cumulative effects of burial-related changes to *headwater stream connectivity* on the dispersal mechanisms of aquatic insects must include both longitudinal and lateral components. The majority of insect dispersal in aquatic networks occurs along stream channels and between adjacent riparian areas (Bilton et al. 2001). Longitudinal (downstream) drift of insect larvae, whether purposeful or passive, plays an important role in the colonization of downstream habitats (Williams and Hynes 1976) and represents an important food resource for higher trophic levels in aquatic habitats (Hershey et al. 1993, Hury and Wallace 2000, Malmqvist 2002). For insects with winged adult stages, movement is concentrated over the stream channel (Kovats et al. 1996, Petersen et al. 2004, Finn and Poff 2005) and biased towards an upstream direction (Hershey et al. 1993, Bilton et al. 2001), a behavior hypothesized by Müller (1982) to be a response to losses of larvae through downstream drift. Stream burial has been shown to impede *longitudinal movement* of insect larvae and adults, leading to demographic changes, loss of species diversity, and increased dominance of tolerant taxa within populations separated by such obstructions (Meyer et al. 2005b, Blakely et al. 2006).

While less common, lateral, overland dispersal of winged adults plays a critical role in the colonization of new habitats, and the exchange of individuals and genetic material between distant populations (Bunn and Hughes 1997, Bilton et al.

2001). *Lateral movement* is particularly critical in headwater systems as they lack upstream sources of drift and because long distance movements between watersheds along or within the stream channel are unlikely (Jackson et al. 1999). Winged adult insects are known to move across land, and while most remain within close proximity of the stream channel (Petersen et al. 2004), individuals of some species have been captured from one to five kilometers inland from their natal streams (Hershey et al. 1993, Kovats et al. 1996). Human alteration of land cover between streams may adversely affect the fitness, survival, and mating success of adult insects (Oke et al. 1989, Sweeney 1993, Pickett et al. 2001, Blakely et al. 2006), leading to population declines or localized extinctions by restricting overland dispersal.

3.3 Methods

3.3.1 Study systems

Our analysis of burial-related changes to stream networks focused on headwater systems of the Potomac River Basin (PRB; see Chapter 2 for full description). Headwater systems were delineated in ArcGIS (ESRI 2012) by extracting headwater stream reaches (Strahler 1957) from a spatially continuous stream network map for the PRB (Elmore et al. 2013), to form “networks,” consisting of groups of contiguous headwater reaches. “Pour points” were generated for networks at transitions in stream order (e.g., 1st – 2nd, and 2nd – 3rd), and at the downstream terminus of each 3rd order network (Figure 1), and assigned a value based on the stream order of the terminal stream segment (1, 2, or 3). The points were then spatially aligned with a hydrologic routing layer (Julian et al. 2012) derived

from a digital elevation model (Gesch et al. 2002), and all landscape pixels “upstream” of each pour point were identified. The collection of upstream pixels for each point represents the spatial extent of a single headwater system, and is synonymous with the drainage area, or watershed, of its component headwater network. The final products resulting from this exercise include a comprehensive set of spatially-nested system polygons (watersheds) and stream networks, used to characterize burial-related changes to every headwater system across the PRB.

3.3.2 Measures of change to network structure

Burial-related structural changes to critical headwater network components were quantified through comparative, spatial analysis of “intact” (pre-burial) and “buried” (post-burial) networks, using a suite of topological measures related to stream habitat loss and fragmentation (Table 1). The “intact” stream network for the PRB consists of the a newly-developed stream network layer for the PRB (Elmore et al. 2013), referred to as the “potential” stream network, as it represents the full distribution and connected nature of streams across the landscape as they would exist in the absence of land cover change. The “buried” network consists of the intact stream network, with all reaches exhibiting >50% burial probability removed (see Chapter 2 for discussion of burial probability layers). Analyses included all headwater stream networks (1st – 3rd), and examined changes both within and across scales of headwater systems.

Measures of change for 2nd and 3rd order systems included all lesser order segments (i.e., 1st order, and 1st & 2nd order segments, respectively) within their boundaries. First order streams, by definition (Strahler 1957), include only a single

segment. Changes to the number of confluences (points where two stream segments meet to form a larger order stream) within headwater networks were also examined, due to their importance as biodiversity hotspots, and in facilitating movement between multiple stream reaches). The difference between “intact” and “buried” structural measures for each system represent the cumulative impact of stream burial on network geometry for PRB headwater systems. Statistical analyses of treatment (stream burial) effects within and across headwater system sizes were performed in R (R Core Development Team 2013).

3.3.3. Changes to system connectivity

Burial-related changes to network connectivity *within* headwater systems were quantified using Circuitscape (McRae et al. 2008), a circuit-theoretical model that treats the landscape as an electrical circuit, passing ecological “current” through a series of landscape “resistors” between focal habitats units. In the model, landscapes are represented as conductive surfaces (Figure 2, left), with habitat more permeable to individual movement assigned low resistance, and less-permeable habitat types and barriers to movement assigned high resistance (Figure 2, center). Total (effective) resistance of the landscape (the “resistance distance”) between any two headwater stream reaches represents a measure of connectivity between those two reaches (McRae et al. 2008). In addition to numerical measures of effective resistance between individual stream reaches and/or systems, resulting “cumulative current maps” can be visualized in GIS (Figure 2, right), allowing users to effectively “see” the landscape through the eyes of a dispersing organism (current flows approximate “ecological flows”, or the movement of organisms).

A set of preliminary analyses were performed to explore the utility of Circuitscape to adequately model the movement of aquatic organisms, specifically adult aquatic insects, through the upland landscape. We began with a simple, rank order resistance classification, where each land cover type (Homer et al. 2007) was assigned a resistance value (0% - 100%; Figure 3) based on its relative favorability to movement of adult aquatic insects through the landscape (in-stream and through upland habitats) as identified from the literature. Burial events were simulated for a set of small, headwater streams in Prince William County, VA, and changes to effective resistance and current flow through the landscape, and critical network components were quantified by comparing pre- and post-burial model outputs. Stream channels, were buffered in 10 meter increments, to a distance of 100 meters from the feature, and the average resistance and current values, pre- and post-burial, were calculated. Results of these analyses (discussed below) gave us confidence that Circuitscape was an appropriate tool for modeling changes in landscape connectivity due to stream burial. Final circuit models were developed and run at the scale of individual system watersheds, with their component headwater stream reaches as focal habitat units. Source data for the resistance surface consisted of the 2006 National Land Cover Dataset (Fry et al. 2011), overlaid with headwater stream maps (10m) to create a seamless habitat raster. Once combined, each habitat pixel was assigned a resistance value (0% - 100%) based on its relative favorability to movement of adult aquatic insects through the landscape. Due to the lack of empirical data on movement/dispersal for most species across most habitats, additional expert input/review was solicited to assure the most accurate assignment of resistance values

across aquatic insect taxa. Experts were identified from the literature, and as recommended by their peers, and approached with a simple survey containing brief background information on the classification process, and asking for comments on the provisional resistance classification. They were asked to rank land cover classes in order, based on their knowledge of favorability to aquatic insects, and, where possible, to assign a relative resistance value (0%-100%) to each land cover class, including the ability to lump land cover types into similar resistance classes where applicable. A description of the survey method, the materials forwarded to potential reviewers, and a summary table of results from those who responded can be found in Appendix A.

Survey responses from the subject area experts were compared with the provisional classification, and a “consensus” classification was finalized (Table 2), consisting of 8 terrestrial resistance classes. Headwater streams were assigned low resistance (2%) relative to terrestrial classes, to favor movement in the model along and within streams and their near riparian areas. Larger rivers and open water habitats (lakes, ponds, estuaries) were assigned higher values (10%), to reflect their status as less-favorable habitat for headwater stream organisms.

Two resistance landscapes were created, one with stream habitat reflecting the “intact” network, as described above, and a second, reflecting the “buried” network. Where burial had removed streams segments from the landscape, missing streams were replaced with the landcover type that replaced them. Results of models using the two landscapes were compared to determine burial-specific changes to landscape connectivity within headwater systems. Due to computational issues with attempting

to analyze all systems across the PRB, we limited our analysis to a subset of systems (N=301) across the burial gradient within a single, 8-digit HUC (Hydrologic Unit Code; Water Boundary Dataset, <http://nhd.usgs.gov/wbd.html>).

We chose the Middle Potomac-Anacostia-Occoquan Watershed (HUC 02070010), due to the strong and complete urban gradient, ranging from completely forested natural areas to the dense urban development of Washington, DC, and the full complement of land cover types in the NLCD (Figure 4). Development of computer scripts (Van Rossum and Drake 2003) to automate resistance calculations across all headwaters of the PRB is ongoing. All analyses of burial-related changes to within-network resistance (connectivity) were performed in R (R Core Development Team 2013).

3.3.4 Gauging the sensitivity of circuit models to variations in landscape resistance

To gauge the sensitivity of our circuit models to the various decisions made while building and refining the resistance classification, we developed a series of 5 resistance ‘scenarios’ based on various iterations of the final ‘within-system’ classification, and review provided by subject area experts (Appendix A). Scenario 1 consists of the final classification used in the ‘within-system’ connectivity analysis for headwater systems, described above. Scenario 2 is based on the initial classification distributed to experts for review (Appendix A). Scenario 3 is the ‘rank order’ classification used in the preliminary analysis regarding the utility of circuit theoretical modeling to investigate landscape connectivity for aquatic insect taxa, described above, where resistance values are evenly spaced between 0% and 100%

resistance. Scenario 4 consists of the potential classification provided by Reviewer #2 (Appendix A), and, in addition to varying resistance values for each landscape class, the relative ranking of resistance classes is different than the previous 3 scenarios. Scenario 5 consists of the potential classification provided by Reviewer #4 (Appendix A), and is markedly different from the other scenarios, including fewer resistance classes, a different rank order, and classes considered 100% resistant to movement. Resistance values for land cover classes in each scenario can be found in Table 3.

As with our previous circuit models, resistance layers are based on the 2006 NLCD, with land cover classes reclassified to reflect resistance values in the various scenarios. Resistance values for all 5 scenarios are scaled from 0-100. The study area for this exercise consisted of all 2nd and 3rd order stream systems (N=2423) within the Middle Potomac-Anacostia-Occoquan Watershed (Figure 4). System polygons and input resistance layers for the various scenarios were developed in ArcGIS 10.1 (ESRI 2012), and models tested using Circuitscape, as described above. Variability in the distributions of output resistance values between scenarios were visualized in R (R Core Development Team 2013). The distributions of output resistance values for the scenarios were heavily skewed, and did not respond adequately to a data transformation (i.e., they could not be made to resemble a normal distribution), necessitating a non-parametric ANOVA (Kruskal-Wallis rank sum test) approach to test for differences in group means between scenarios.

3.4 Results

3.4.1. Headwater systems

A total of 234,772 headwater systems (1st – 3rd order) were delineated across the PRB (Table 4). Catchment area for headwater systems ranged from 0.0001 km² – 61.6 km², and collectively, account for 88.62% of the total land area of the PRB. Headwater stream length totals approximately 83,664 km, or 84.8% of total stream length for the basin. Nearly half of all streams in the PRB (45.2%) are represented by 1st order segments. As of 2006, PRB streams were buried at an overall rate of 1.4%, while total burial rates for headwater systems were slightly higher at 1.63%. Burial rates for individual systems can be much higher, however (discussed below), and generally occur in direct proportion to total impervious cover (discussed in Chapter 2).

3.4.2 Total burial rates for headwater systems

The vast majority of PRB headwater systems, regardless of order, are largely unaffected by stream burial. Of those systems experiencing burial, however, far more 1st order systems are affected than are higher order headwater systems, across all levels of network burial (Figure 5). Peak burial frequencies (~250 systems) for larger, 2nd and 3rd order systems occur at very low levels (~1-2% network burial), declining exponentially as order increases. Peak burial frequency for 1st order systems occur at slightly higher levels (~4-6% network burial), with frequencies declining at a much slower rate with increasing network burial, remaining relatively constant (~30-40 systems) across levels between 50-100% network burial. The

number of larger systems with burial rates approaching 100% is approximately zero. It is important to note, however, that even 2nd and 3rd order systems, which can be much larger in watershed area and total stream length, experience levels of burial approaching 100% in highly developed areas of the PRB.

3.4.3 Burial rates within systems

Second and 3rd order systems contain a single reach of the order by which they are defined, and varying numbers of lower order segments. Comparisons within 2nd and 3rd order systems (Figure 6) show 1st order streams are buried at higher average rates than 2nd order segments across all levels of system burial. Within 3rd order systems, both 1st and 2nd order stream segments are buried at higher average rates than are 3rd order streams. Differences in average burial rates by stream order within 2nd and 3rd order systems are all significant, with the same pattern (1st>2nd>3rd) holding across all levels of system burial. First order streams are buried at higher rates than are larger order streams, at all levels of stream burial.

3.4.4 Burial-related fragmentation of headwater systems

Burial in headwater networks leads to significant changes in both the number and size of remaining stream segments, with characteristic fragmentation patterns emerging along the gradient in burial (Figure 7, left panel). Of those 1st order systems that experience burial, many experience no change in the number of segments, indicating that burial is occurring at their distal extent, and not leading to fragmentation. Many experience numerous fragmentation events, as indicated by

change rates of up to 900% across the burial spectrum. The majority of 1st order systems, however, exhibit a 100% increase in the number of segments, with burial events occurring within-reach, leaving two, disconnected reaches. On average, 1st order systems experience an immediate increase in the number of segments with increasing burial ($\mu=70\%$ between 0-5% system burial), reaching a maximum mean change of approximately 100% by 15% system burial. As system burial rates increase, the mean change rate is relatively consistent until 50% system burial, after which the mean change in number of segments decreases as entire stream segments are eliminated from the landscape. The same general pattern is repeated for 2nd and 3rd order systems (Figure 7, middle and right panels), though the maximum mean change in number of segments is far less for 2nd order systems (~40%), and lesser still for 3rd order systems (~23%), perhaps indicating that most burial occurs within the 1st order portions of these headwater networks. The large increase in variability for percent change in the number of segments in 3rd order systems can be explained by very low numbers of 3rd order systems experiencing rates of total burial greater than 60%.

Stream burial also leads to significant reductions in average segment length within headwater stream networks. Across all system sizes, there is an immediate, significant decrease in mean segment length with increasing system burial (Figure 8). This is especially apparent in 1st order segments, with a mean decrease of over 30% in average segment length between 0-5% system burial, indicating that the majority of 1st order segments are being fragmented and losing significant reach length at very low levels of burial. Mean percent change continues to decrease faster than the rate

of burial until approximately 15% total burial, after which it decreases linearly with increasing burial as segments continue to lose length, but are not fragmented further. There are many 1st order segments that exhibit a one-to-one loss of segment length with increasing burial, indicative of burial proceeding from one end of the segment, without fragmentation. As with the burial-related changes to the number of stream segments, patterns for change in average segment length in 2nd and 3rd order systems are similar to 1st order systems, though the magnitude of change with increasing burial rates is lower.

3.4.5 Buried confluences

Percent change in the number of confluences with burial has no relevance to first order systems as they contain only a single segment. For both 2nd and 3rd order systems, there are a large number of systems experiencing no loss of confluences with increasing burial (Figure 9). For systems experiencing loss of confluences, however, confluence loss proceeds nearly linearly with percent burial, indicating that confluences, on average, are buried randomly, in proportion to total system burial. There are a number of 2nd order systems, across all levels of stream burial, with 100 percent loss of confluences, corresponding to those systems with only one confluence and it becomes buried.

3.4.6 Changes to connectivity within systems

Results of preliminary circuit models confirmed the utility of Circuitscape in quantifying changes in connectivity within headwater stream systems. Current flow

surrounding stream channels exhibited an exponential decay with distance (Figure 10), approximating similar patterns in the distribution of adult aquatic insects with distance from stream channels (Petersen et al. 2004, Macneale et al. 2005). Significant, post-burial increases in effective resistance between stream segments across the study landscape were observed, as were significant decreases in total current flow (Figure 11). Burial also affected current flow through confluence and channel head areas, with significant decreases in current flow observed through these critical components (Figure 12). Changes were not isolated to areas directly affected by burial, but affected areas of the landscape far removed from actual burial events.

At the system level, the cumulative effect of burial was summarized as the mean resistance distance among all pairwise comparisons of stream segments. These broader comparisons of burial-related changes to landscape resistance across headwater systems of the PRB provided complementary results. Across the 301 study systems, percent change in within-system resistance exhibited a significant, positive relationship with increasing burial (Figure 13, $P < 0.001$). A high degree of variability in the change of resistance with increasing burial led to low correlation ($R^2 = 0.067$) for the model, however, suggesting other factors are at play. Analysis of the relationship of changes in landscape resistance to measures of network structure pre and post burial showed no discernable relationships (scatter plots not shown). Further analyses regarding the relationship between burial-related changes in within-system resistance and changes in land cover within systems is warranted

3.4.7 Sensitivity of circuit analyses to change in landscape resistance input

The distributions of output resistance values for the 5 scenarios can be visualized in Figure 14. Overall, very little variability in resistance values was observed, with the highest degree of variability seen in the upper quartile of scenarios 3 and 5. The Kruskal-Wallis analysis yielded an insignificant model (Chi-square 236.97, $df = 4$, $p\text{-value} < 2.2e-16$), signifying there are no significant differences in means between any two scenarios included in the model.

3.5 Discussion

Headwater stream systems are ubiquitous on the landscape. The specific spatial arrangement and hierarchical organization of their structural elements control the flow of species and materials throughout the network and to downstream waters (Grant et al. 2007). We investigated the effects of stream burial on the number, size, and distribution of critical structural components within headwater networks, and explored the specific affects that stream burial, as part of a larger, urbanization component of watershed land use, affects the internal landscape connectivity of headwater systems. Results clearly show that small, headwater streams are affected by burial to a greater extent than larger streams, with significant reductions in overall stream length, varying levels of habitat fragmentation, and the loss of connectivity within systems as critical habitat elements are eliminated from the landscape.

Overall, stream burial rates for PRB headwaters are relatively low, with only about 1.6% of headwater stream length lost as of 2006. But stream burial is concentrated in developing areas of the basin, (Chapter 2), and these associated,

urban systems are affected at rates much higher than the average. Within the most heavily-developed regions (e.g., Washington, DC and close suburbs), many 1st order systems are entirely gone, and large portions of 2nd and 3rd order streams have also been buried. The complete loss of headwater systems across such large areas inhibits the maintenance of local and regional species assemblages, and challenges efforts to manage for water quality in downstream waters, including the Chesapeake Bay.

3.5.1 Burial patterns across headwater systems

Beyond simple totals of buried streams, it is critical to understand *where* burial is happening, as the effects on form and function of impacted systems will depend on the hierarchical level at which the disturbance occurs (Fisher 1997), and whether burial events occur with equal probability throughout the network, or are clustered (Fagan et al. 2002). Within systems, burial is concentrated in the smallest (1st order) headwater reaches, which is not surprising, as 1st order streams account for over 50% of headwater stream miles, drain nearly 60% of the basin's land area, and tend to flow over ground most amenable to development (Chapter 2). These smallest of streams are everywhere on the landscape, and are physically easy, and therefore inexpensive, to bury. Many of these segments may be ephemeral or intermittent (Hansen 2001), and therefore, not recognized as streams, per se, and therefore not regulated as strictly as streams with permanent flows. Many of these streams are missing from maps currently used to regulate land use change (Elmore et al. 2013), and are simply 'lost' in the process of urban development.

The concentration of burial within 1st order systems presents serious implications for the maintenance of biodiversity and ecosystem function at both local

and regional scales. Headwater streams are, by nature, highly isolated within larger stream systems (Gomi et al. 2002, Richardson and Danahy 2007), with 1st order segments, by definition, the most distal, isolated components. This relative isolation has led to high numbers of ecological specialists and endemic taxa within these systems (Lowe and Likens 2005, Meyer et al. 2007), and a high degrees of species turnover (β -diversity) between systems (Nekola and White 1999, Clarke et al. 2008). Therefore, though not typically species rich as compared to larger streams (Vannote et al. 1980), widespread loss of 1st order segments to stream burial may have a disproportionate effect on both local and regional species pools (α - & γ -diversity, respectively).

As the initial conduits of energy and matter from terrestrial uplands to downstream systems, the intimate and extensive linkage of 1st order stream channels with their surrounding landscapes, serve a critical role in the attenuation of nutrient, sediment, and hydrological flows to downstream systems (Meyer and Wallace 2001, Lowe and Likens 2005, Alexander et al. 2007). Channel simplification, or outright piping of 1st order segments short-circuits natural processes, shunting water and associated materials downstream in higher quantities and faster than larger systems are adapted to receive and assimilate (Walsh et al. 2005, Wenger et al. 2009). These effects are only compounded as 2nd and 3rd order segments, many of them buried as well, concentrate water and pollutants for efficient transfer to larger systems such as the Potomac River, and ultimately the Chesapeake Bay. In areas where large numbers of headwater streams are buried, and assimilation processes are heavily

degraded or completely lost, failure to effectively manage water quality in downstream receiving waters may be a foregone conclusion.

3.5.2 Burial-related fragmentation

How burial proceeds within a system, and the availability and spatial arrangement of remaining habitat patches, can strongly influence faunal patterns. Stream burial has severely fragmented PRB streams, reducing the size and increasing the distances between remaining headwater segments. Again, it appears to be 1st order systems where the majority of burial is occurring, with many reaches fragmented numerous times during the course of development. Because even a little fragmentation in dendritic landscapes can substantially reduce the potential for colonization (Fagan 2002), even systems with a minimum amount of burial can expect loss of species, shifting patterns in abundances, and reduced persistence of populations in the face of disturbance (Hansson et al. 1995, Schumaker 1996). The number and size ratios of tributary segments also controls morphological heterogeneity at confluences (Benda et al. 2004b), influencing local and downstream diversity and habitat heterogeneity (discussed below).

In PRB systems, we observe three distinct burial/fragmentation scenarios, each with negative implications for species and population viability. In the first scenario, there is no fragmentation, indicating that burial is occurring at the distal ends of streams, and proceeding in a downstream direction. In addition to direct habitat loss, critical channel head areas are altered or eliminated (discussed below), increasing distances between the distal tips of neighboring systems, and decreasing

the probability of cross-system dispersal through uplands, which in the case of headwater systems, might naturally be the most direct route for transfer of organisms between watersheds (Clarke et al. 2008). Most burial events across the PRB appear to have occurred within reaches, breaking streams into two or more disconnected segments, with varying degrees of initial habitat loss. Even small burial discontinuities, such as a single road culvert, have been shown to affect population viability in invertebrate taxa in remaining segments, through interruption of downstream drift of larvae, and the upstream dispersal of winged-adults (Blakely et al. 2006). Once fragmented, burial generally proceeds outward from the initial burial site, with remaining segments getting smaller and smaller, until they are entirely eliminated from the landscape. A third fragmentation scenario observed across the PRB is the burial of stream confluences, discussed below.

3.5.3 Burial-related loss of stream confluences

Within stream systems, confluences represent critical transition zones in physical and chemical processes. Abrupt increases in supply of water, sediment, and woody debris, lead to increased morphological heterogeneity, creating local “hotspots” of biodiversity and nutrient transformation (McClain et al. 2003, Benda et al. 2004a, Rice et al. 2006). Burial of confluences affects multiple stream segments at once, effectively isolating terminal reaches, and inhibiting the movement of organisms and material within stream networks. While 1st order systems consist of only a single reach, and therefore have no internal confluences, 2nd order systems, by definition, include at least one confluence where two 1st order reaches meet. Significant numbers of 2nd order systems across the PRB exhibit 100% confluence

loss, across all levels of system burial. This represents a complete loss of connectivity between stream segments within these systems, with serious implications for ecosystem function in local and downstream reaches. Altered fluxes of water and other materials due to lost confluences can affect habitat heterogeneity far downstream (Benda et al. 2004b), and eliminate the “spatially referenced cues” that some species use to navigate towards natal tributaries (Lowe and Bolger 2002). A clearer understanding of how and why confluences are affected by stream burial is vitally important for the development of local and basin-scale management strategies for these critical “hotspots.”

3.5.4 Changes to connectivity within stream network and surrounding uplands

Urban development across the PRB has led to significant decreases in habitat connectivity in aquatic systems, both through direct, burial-related changes to stream networks, and through land use change in upland areas. Decreased probability for movement of aquatic organisms through the affected systems is reflected in circuit models as significant increases to effective resistance and decreases in current flow between remaining stream segments. Remaining stream habitats are smaller and farther apart, and natural upland habitats, particularly critical for dispersal of adult aquatic insects, have largely been replaced by highly unfavorable urban land cover (e.g., impervious surfaces). Urbanized uplands present a number of “ecological traps” for dispersing insects, including altered temperature and humidity regimes (Collier and Smith 2000, Richardson and Danehy 2007), nighttime lighting that serves as an attractant (Horváth et al. 2009), and countless, hard surfaces such as

windows and roads (Kriska et al. 1998, Malik et al. 2008) that alter the natural frequencies and patterns of polarized light that cue different aspects of their life histories.

Burial within one portion of a stream network can have significant effects on areas quite removed from the actual burial event. We observed significant decreases in current flows in areas surrounding confluences and channel head areas remaining after burial, both critical habitat areas within headwater systems. The ecological importance of confluences is discussed above. Channel heads, the beginning of the stream network, for a direct link between terrestrial uplands and the stream system, and function as the main source for input of water, sediment, and organic matter to aquatic ecosystems (Nadeau and Rains 2007, Clarke et al. 2008, Julian et al. 2012). Furthermore, channel heads are critical areas for aerial dispersal of winged adult aquatic insects in headwater systems (Smith et al. 2009), where upstream sources of colonists are lacking (Wallace et al. 1986, Flory and Milner 2000). They are often the closest link between adjacent watersheds, facilitating out-of-network movements, which may be particularly important for maintaining genetic diversity and the persistence of populations in fragmented stream networks (Fagan 2002, Lowe 2002).

From a landscape perspective, we observed significant positive increases in total resistance within headwater systems experiencing stream burial. At very low levels of stream burial (0%-5%), there is little change in the average resistance of headwater landscapes, suggesting that ecological effects may be more localized, and confined largely within the network immediately surrounding burial events. As the percentage of burial increases, however, increases in landscape resistance, while

significant, exhibit a wide range of variability. We saw no discernable relationship between changes in system resistance and the network structural measures examined, suggesting that the lion's share of variability observed is more likely a result of the total amount and spatial distribution of high resistance land cover classes within individual systems. We did observe a significant, positive relationship between resistance distance and Euclidean distance however, suggesting that the distance between habitat segments remaining after burial will have some effect on total landscape resistance, regardless of the resulting proportion of land cover types within affected systems.

3.5.5 Sensitivity of circuit analyses to changes in landscape resistance classification

Overall, it does not appear that the circuit models are were sensitive to changes in resistance scenario, at least within the numerical bounds with which we examined potential variability. Resistance values in all scenarios were constrained between 0 and 100, and neither the differences in values between classes, nor the relative ranking of classes, were enough to cause significant differences in the outcomes of our models. We are confident, based on the existing literature on the relative favorability of various land cover classes for movement of aquatic insects across the landscape, and positive feedback from subject area experts, that the ranking of resistance classes are appropriate. We are also confident that the circuit models, themselves, adequately model organismal movement across the landscape, as confirmed through the preliminary work discussed above, where (ecological) current

flowed preferentially along streams and adjacent riparian corridors, with lateral distance decay curves that approximate those observed in nature.

3.5.6 Modeling uncertainties

As discussed in Chapter 2, basin-wide statistics for burial, including the number of systems affected and total amount of burial within systems are likely underestimates, as only streams with >50% probability of burial were excluded from the “buried” network. Additionally, slight co-registration errors between digital streams and land cover elements may affect burial probabilities for some reaches, and, therefore, the exact location of buried segments on the landscape and associated changes to network geometry. These errors may, in turn, affect the exact values for landscape resistance, as both the number and distribution of critical network components is crucial in consideration of connectivity within networks and the landscape as a whole.

Positive values for change in average segment length in 2nd and 3rd order systems experiencing stream burial (Figure 8) were unexpected, as this runs counter to the idea that segment length can only decrease as streams are fragmented. We feel this is an artifact the original stream mapping process (Elmore et al. 2013), whereby numerous, one or two pixel stream ‘tags’ were added to the stream network based on conditions within the DEM and classification data used to generate the maps. The only explanation for a positive change in average stream length is if these short segments are buried in the initial stages of system burial, leaving many, much longer stream segments intact. Such positive values can then persist for systems across the

gradient in burial, as long as further burial within the system proceeds in such a way that the average segment length remains greater than the initial value (e.g., long segments are slowly buried over time, with no fragmentation within their length).

The landscape resistance classification was developed, as possible, from the literature on habitat preferences and dispersal abilities of the target organisms (winged-adult aquatic insects). Empirical data for dispersal, especially across different land cover types, is fairly scant, and the classification may be enhanced with contribution of knowledge from other subject area experts, as was done in Chapter 4. Calculations for within-system resistance included in this chapter were performed prior to development of our final landscape classification, though there were only slight changes in resistance values following expert review for (5% increase in resistance for 3 land cover classes, as discussed in Chapter 4), giving us confidence that the resistance classification adequately captures the landscape elements affecting movement within stream systems. The exponential decay of current flow with distance from a stream emulates observed biological patterns, but it was not possible to calibrate the resistance layer to the actual magnitude of dispersal for multiple organisms with unknown dispersal abilities. The rate of exponential decay, however, approaches zero by approximately 100m from the stream, and is consistent with dispersal data collected for the few, known species, where the majority of dispersing organisms are captured within the same distance. Furthermore, cumulative current maps resulting from the analyses exhibited current patterns consistent with known ecological phenomena, specifically, a concentration of current flow along streams and adjacent riparian areas, and particularly high current values for confluences and

channel head areas, known to be hotspots of diversity and critical areas for dispersal of organisms within and between systems (discussed above).

Finally, the fact that no relationship was observed between changes in structural network measures and changes in landscape resistance after burial may be explained by the nature of current inputs in the Circuitscape model. At the time of the analysis above, input values for current to focal habitats (stream segments) were limited to a consistent value of 1 amp per node, resulting in roughly the same amount of current input to both natural and buried networks, regardless of changes in network components. In some cases, the amount of current may have been higher in buried networks, due to increases in the number of stream fragments with burial. Future analyses could benefit from new functionality within Circuitscape, whereby variable current can be ‘injected’ into focal habitats based on the nature of habitat loss through stream burial. For instance, the input current can be made a factor of the length of the focal segment, ranging from 0-1 in buried networks, based on decreases in segment length, with the assumption that populations within these reaches would exhibit lower population viability after burial of a portion of the original habitat.

3.6 Conclusions

This research represents the first attempt to quantify the effects of stream burial on network structure and habitat connectivity within headwater stream systems. Our findings clearly show that stream burial causes significant changes to network geometry, eliminating within-channel and upland habitats critical to aquatic species, with the potential to disrupt dispersal and other ecological processes vital proper

ecosystem function and the persistence of headwater populations. First order stream systems are disproportionately affected as compared to larger systems, across all levels of system burial. In addition to habitat loss and fragmentation within stream reaches, burial eliminates stream confluences, shown to be biodiversity hotspots and important areas for nutrient assimilation. Stream burial and associated urban development in the upland landscape conspire to increase landscape resistance to movement by aquatic organisms, and therefore, the relative connectivity of available habitat patches remaining post-burial. Further research investigating the relationships between landscape resistance and the total amount and spatial distribution of land cover/resistance classes is warranted. Collectively, these findings lay the groundwork for a more complete understanding of the consequences of stream burial on the structural aspects of stream networks, and the potential ramifications for biodiversity and ecosystem function within headwater systems and downstream waters.

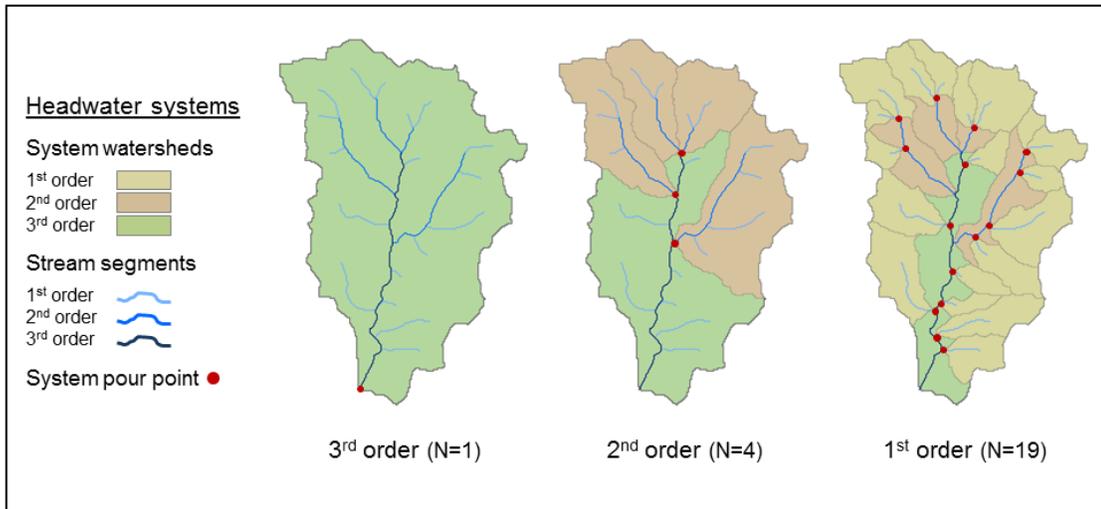


Figure 14.1 Representation of a headwater system for the PRB, containing 1st – 3rd order stream networks (collection of stream segments). Pour points, where streams transition between order, were used to delineate system boundaries (watersheds). The pictured system consists of a single, 3rd order network and system, with three, nested 2nd order systems, and nineteen, 1st order systems. Many (12) 1st order streams are nested within 2nd order systems, but several (7) are “non-nested”, flowing directly into the 3rd order reach.

Table 3.1 Measures calculated for “natural” and “buried” stream networks for analysis of structural changes to headwater networks following stream burial.

Structural measures
Total system stream length
Stream length (by order)
Number of stream segments (by order)
Average segment length (by order)
Number of confluences (by order)

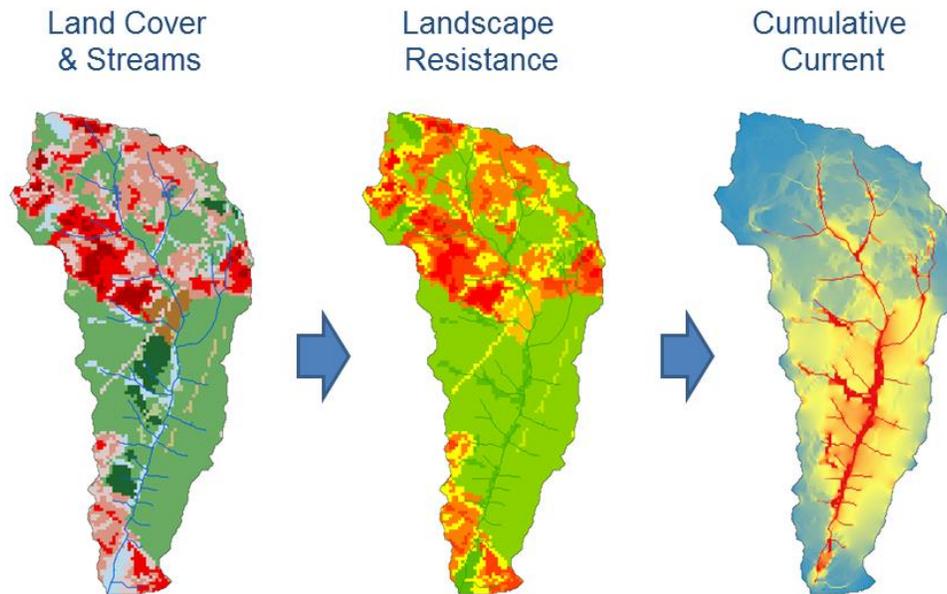


Figure 15 Land cover (NLCD 2006) and streams (left), are assigned resistance values based on their relative permeability to organism movement (center). Greener areas represent low resistance habitats (largely streams and forest cover) while hotter colors represent areas with higher resistance (e.g., urban areas). Circuitscape treats the landscape like an electrical circuit (center, adapted from McRae *et al.* (2008).), passing current through a series of variable resistors (land cover pixels) between two or more focal habitat patches (black circles). Cumulative current flow through the landscape can be mapped (right), with current densities through cells indicating the probability of an organism passing each cell as it moves between patches. Warmer colors (red and yellow) highlight critical movement corridors between focal patches.

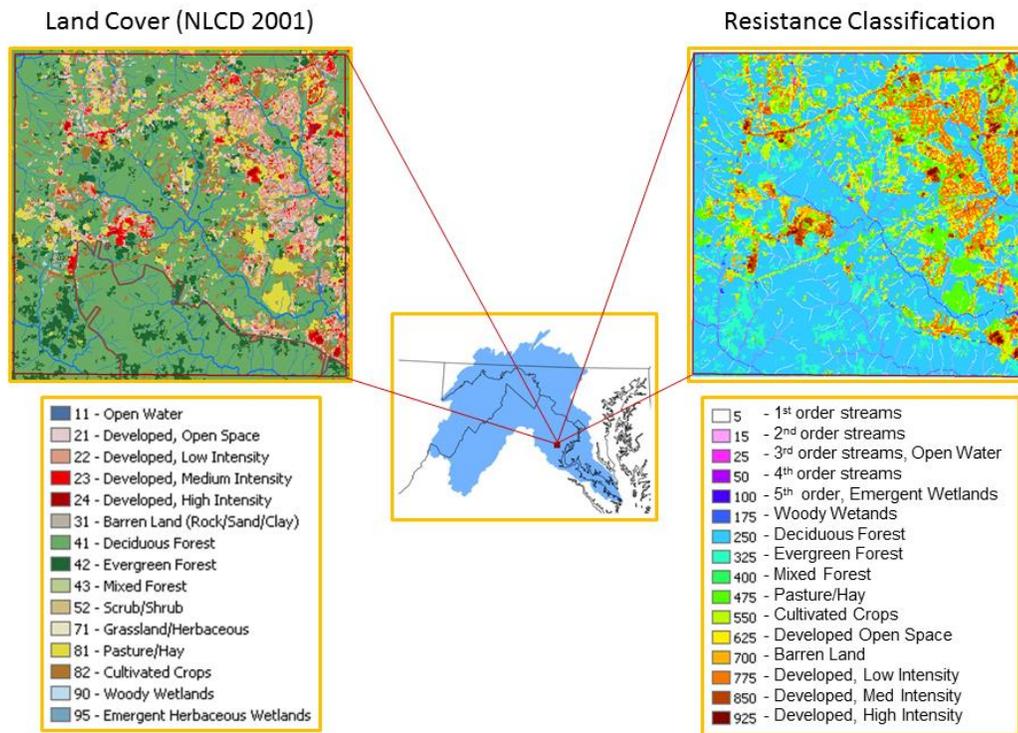


Figure 16 Preliminary rank order classification of landscape resistance for a 75km² pilot landscape in Prince William County, Virginia (red square, inset map). The study area spanned the full range in land use/land cover, from natural forest to densely urban environments, and straddled the Piedmont and Coastal Plain physiographic regions. Land cover classes (left) were assigned a resistance value (right) at equal intervals between 0 and 1000. Streams were assigned minor, yet positive, resistance values relative to upland land cover classes.

Table 3.2 Final resistance classification used to calculate within-system connectivity for headwater systems. Individual results from expert surveys used to formulate this final classification can be found in Table 2 of Appendix A.

Stream Size		Resistance (%)
Headwater stream (1 st – 3 rd order)		2
Mainstem stream (>3 rd order)		5
NLCD Land Cover Class	NLCD Code	
Open water	11	10
Emergent herbaceous wetland	95	10
Woody wetlands	90	10
Deciduous forest	41	25
Evergreen forest	42	25
Mixed forest	43	25
Grassland/Herbaceous	71	30
Shrub/Scrub	52	30
Barren land	31	40
Pasture/hay	81	40
Cultivated crops	82	50
Developed/open space	21	50
Developed/low intensity	22	65
Developed/medium intensity	23	75
Developed/high intensity	24	90

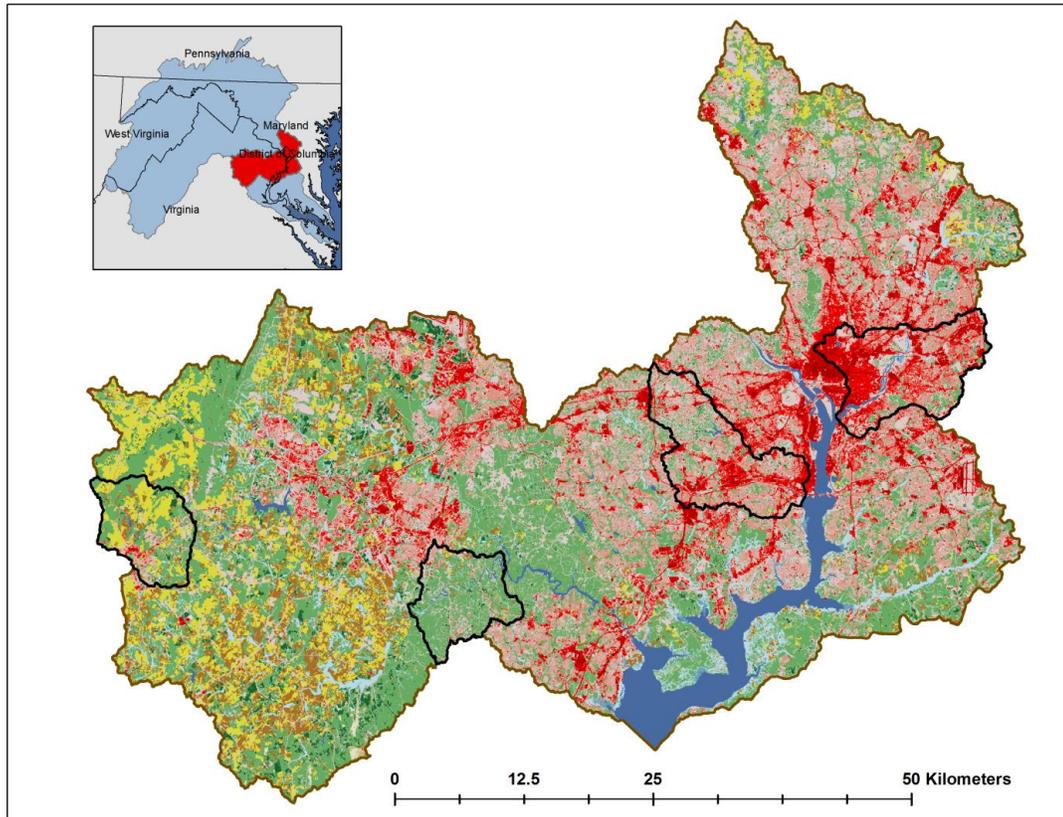


Figure 17 The Middle Potomac-Anacostia-Occoquan Watershed (HUC 02070010; Water Boundary Dataset, <http://nhd.usgs.gov/wbd.html>), showing the 4 sub-basins containing the 301 headwater systems analyzed for within-system connectivity. We chose this basin due to its strong and complete urban gradient, from completely forested natural areas to the dense urban development of Washington, DC, and the full complement of land cover types in the NLCD. In the figure, land cover classes include: urban development (reds and pinks), forest (greens), wetlands and open water (blues), and agriculture (yellow and brown). The inset map shows the watershed in relation to the Potomac River Basin (blue) and the states spanning the study region.

Table 3.3 Input values for 5 landscape resistance scenarios.

Landcover Class	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
	Final	Initial	Rank Order	Reviewer #2	Reviewer #4
Open Water	10	5	6.25	5	29
Emergent Herbaceous Wetlands	10	10	12.50	15	29
Woody Wetlands	10	10	18.75	12	14
Deciduous Forest	25	25	25.00	20	43
Evergreen Forest	25	25	31.25	25	43
Mixed Forest	25	25	37.50	17	43
Grassland/Herbaceous	30	30	43.75	15	57
Shrub/Scrub	30	30	50.00	16	57
Barren Land	40	40	56.25	51	57
Pasture/Hay	40	40	62.50	40	71
Cultivated Crops	50	50	68.75	50	71
Developed/Open Space	50	50	75.00	52	86
Developed/Low Intensity	65	70	81.25	58	100
Developed/Medium Intensity	75	80	87.50	60	100
Developed/High Intensity	90	90	93.75	65	100

Table 3.4 Network and burial statistics for headwater systems of the PRB.

Headwater Systems	Number of Systems	System Area (km²)	Land area (% PRB)	Total stream length (km)	HWS stream length (%)	PRB stream length (%)	2006 Burial (%)
1 st order	185,470	0.0001-9.9	58.73	44553.0	53.3	45.15	1.70
2 nd order	40,234	0.0006-16.6	60.20	26518.5	31.7	26.87	1.77
3 rd order	9,068	0.1281-61.6	60.51	12592.2	15.1	12.76	1.08
Total	234,772	0.0001-61.6	88.62	83663.8	100	84.78	1.63

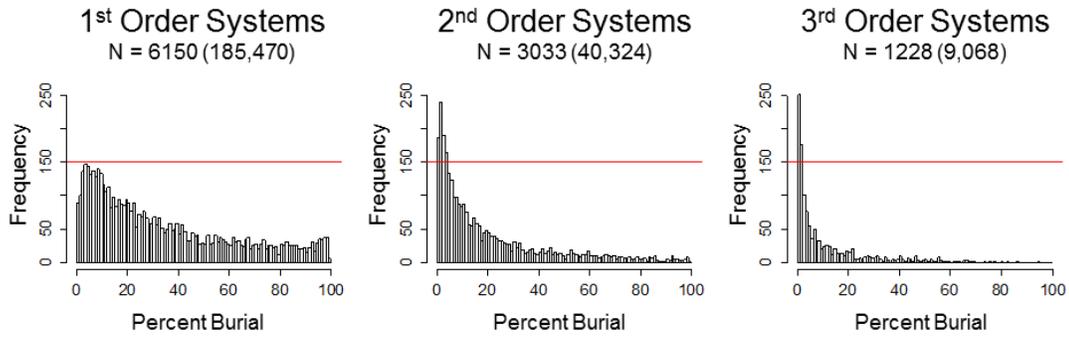


Figure 18 Frequency of 1st, 2nd, and 3rd order headwater systems by the total percent of their network stream length that is buried. Each bar represents a 1% burial class. Systems with less than 0.2% burial have been removed for clarity. The numbers of systems removed by order are: 1st order (n=179320, 96.7%); 2nd order (n=37,291, 92.5%); and, 3rd order (n=7849, 86.5%). N=number of systems remaining in the plot, with the total number of PRB systems of that order in parentheses. The red line at the system frequency of 150 corresponds with the maximum displayed burial rate for first order systems, and is consistent across all three plots, serving as a standard level against which the relative frequency of buried systems in each burial class can be compared.

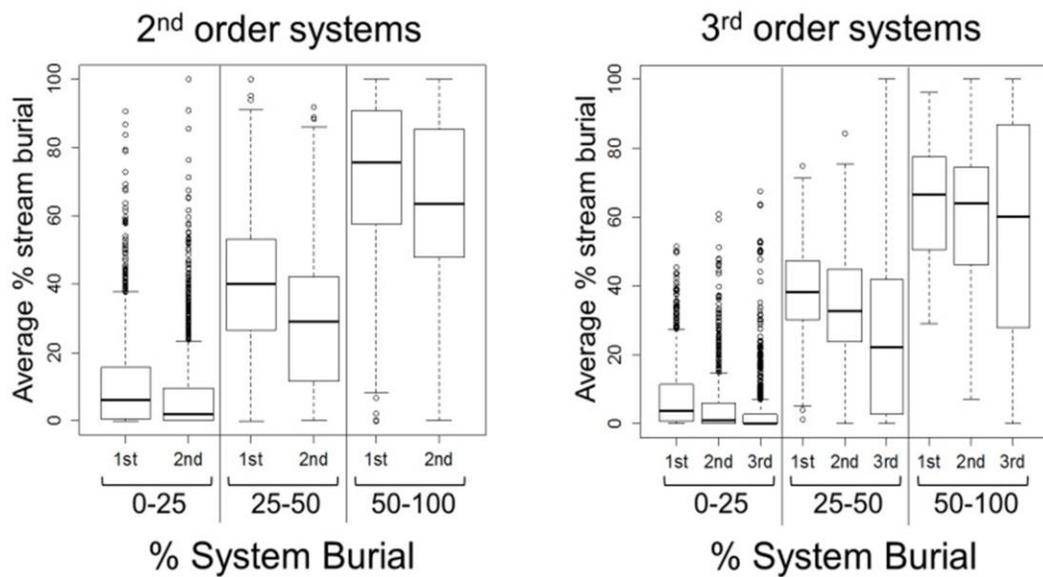


Figure 19 Percent stream burial within systems by stream order. Percent system burial is divided into burial “bins”, with the level of burial for streams of each order within the bin indicated.

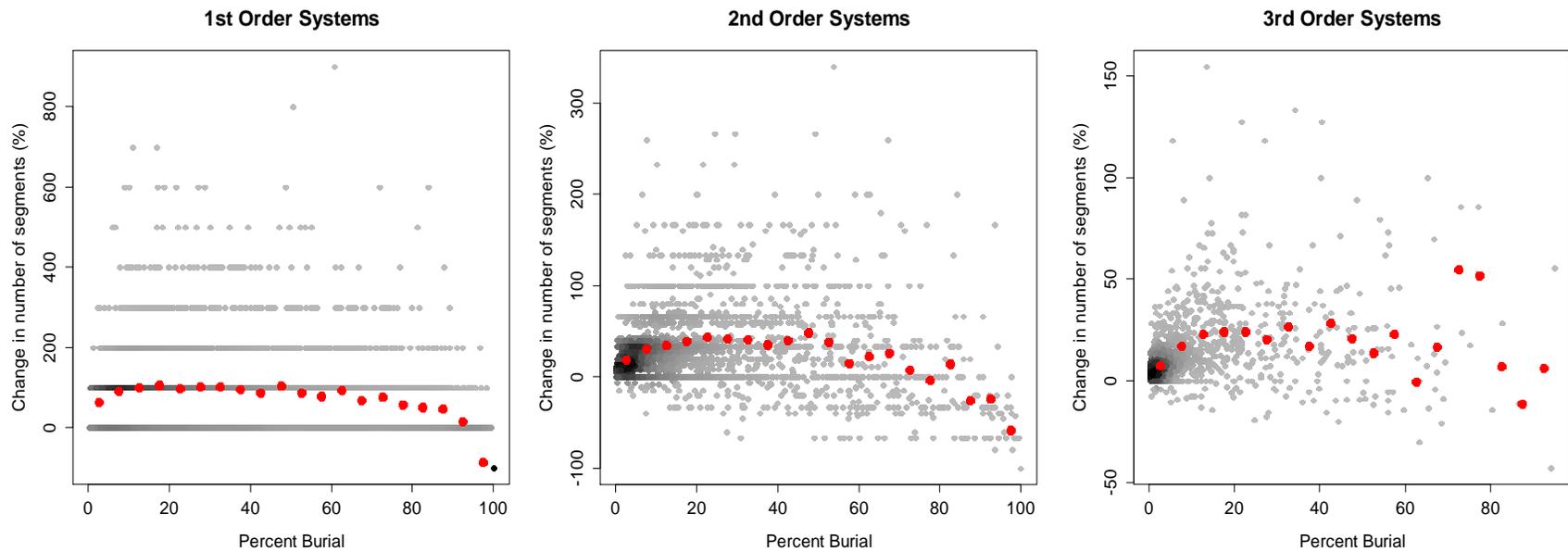


Figure 20 Percent change in the number of stream segments with increasing percent burial within systems. Points represent individual systems, with the degree of gray shading representing the density of systems with a particular change value along the gradient in percent burial. Red dots represent the mean value for all systems within each 5% burial bin.

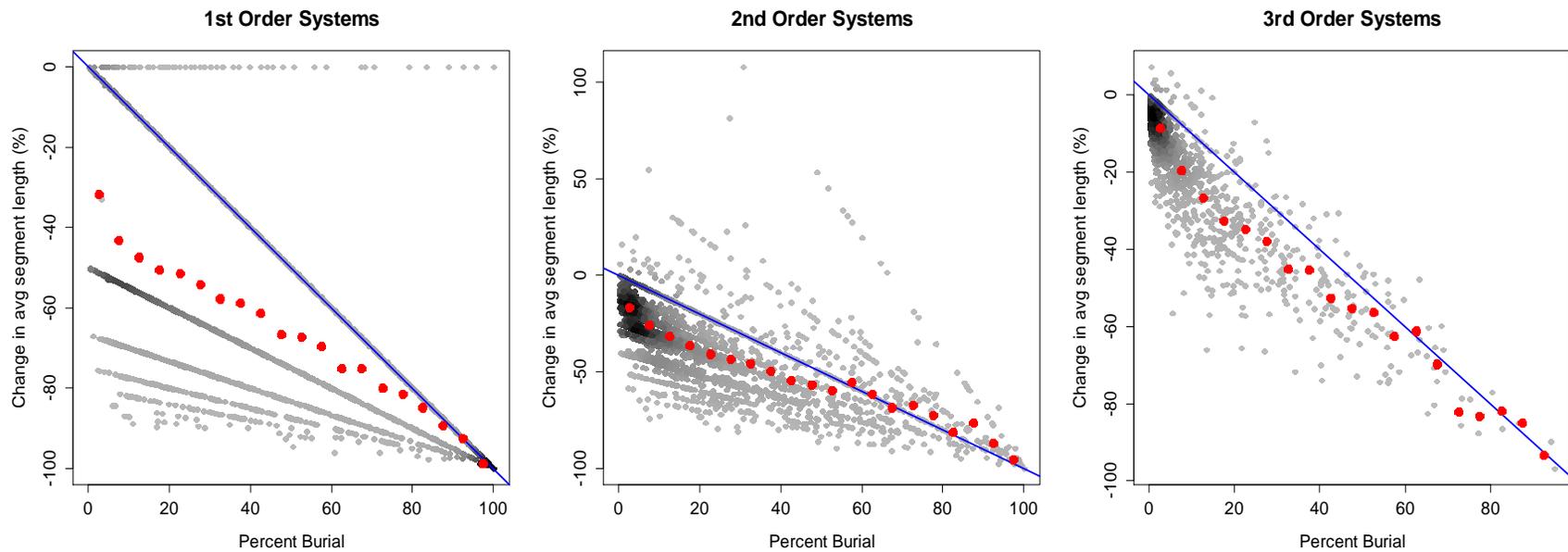


Figure 21 Percent change in the average segment length of stream segments with increasing percent burial within systems. Points represent individual systems, with the degree of gray shading representing the density of systems with a particular change value along the gradient in percent burial. Red dots represent the mean value for all systems within each 5% burial bin. The blue line is the 1:1 line for percent change by percent burial.

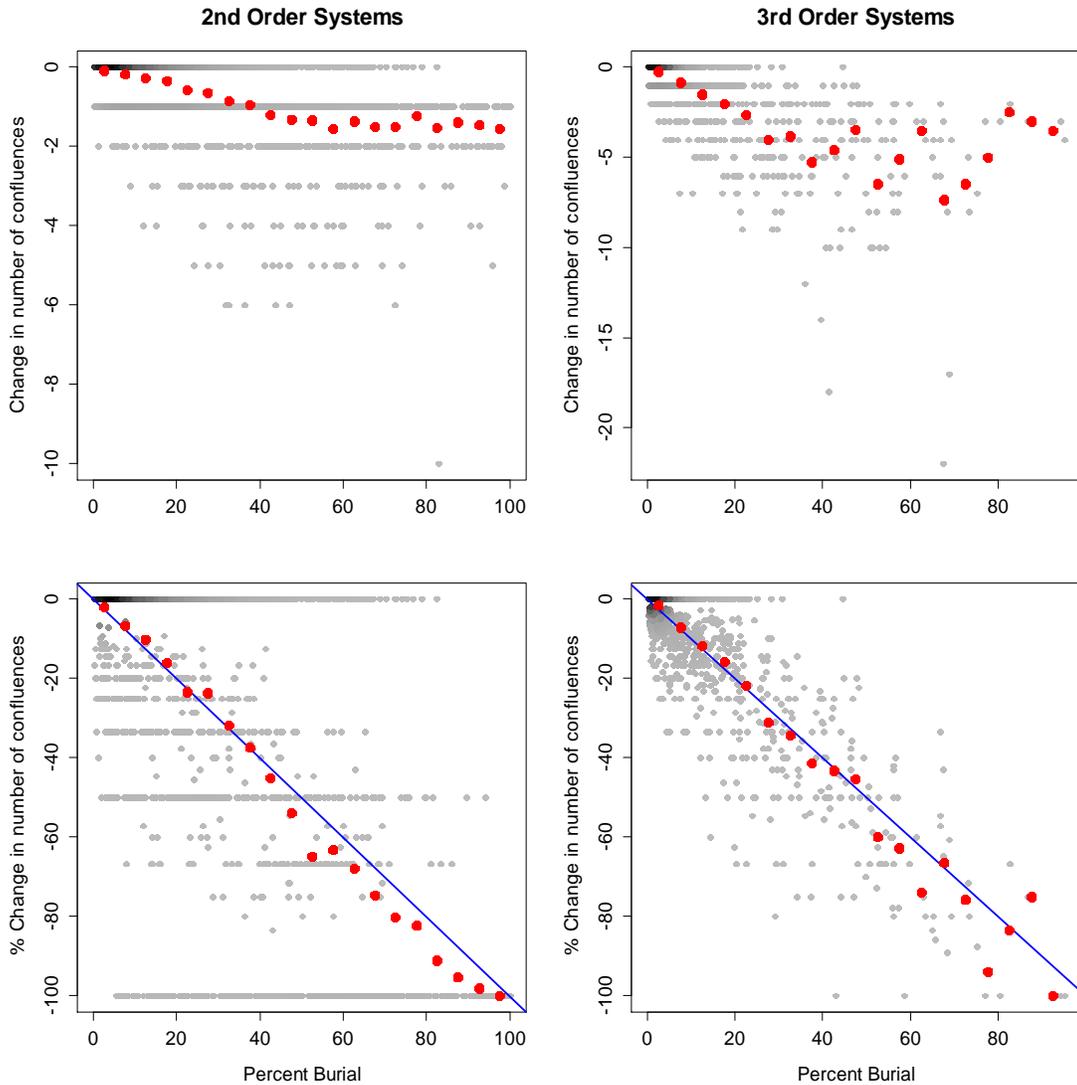


Figure 22 Change and percent change in the number of confluences with increasing percent burial within systems. Points represent individual systems, with the degree of gray shading representing the density of systems with a particular change value along the gradient in percent burial. Red dots represent the mean value for all systems within each 5% burial bin. The blue line is the 1:1 line for percent change by percent burial.

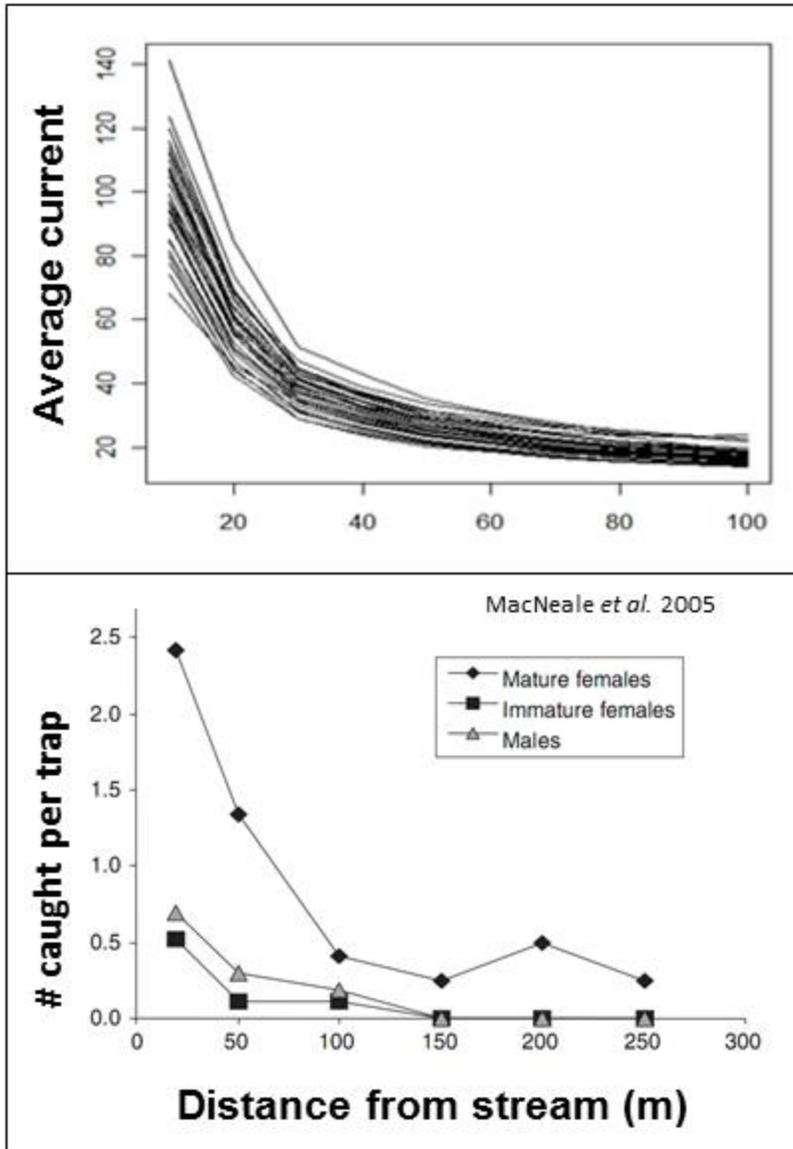


Figure 23 Decay curve for current flow with distance from the stream segments (top panel) in the pilot landscape. This curve approximated empirical distance decay curves (bottom panel) for the distribution of adult aquatic insects captured at different distance from streams (e.g., MacNeale et al. 2005).

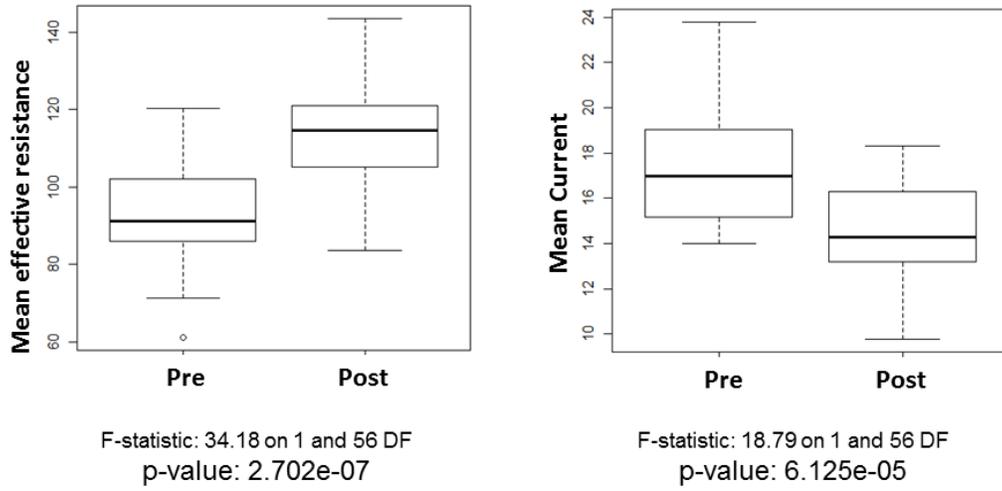


Figure 24 Pre- and post-burial mean effective resistance (left) and mean current values (right) for the pilot landscape.

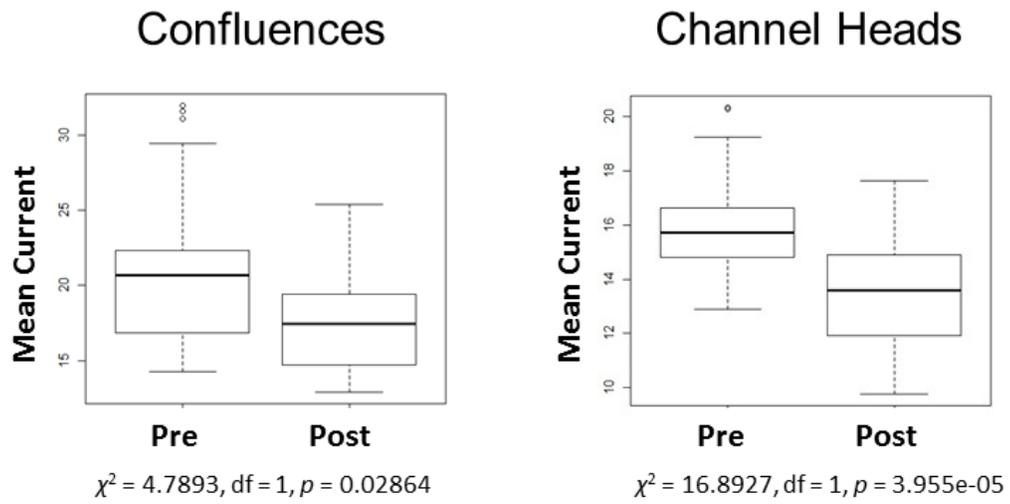


Figure 25 Pre- and post-burial mean current values for confluences and channel heads for the pilot landscape.

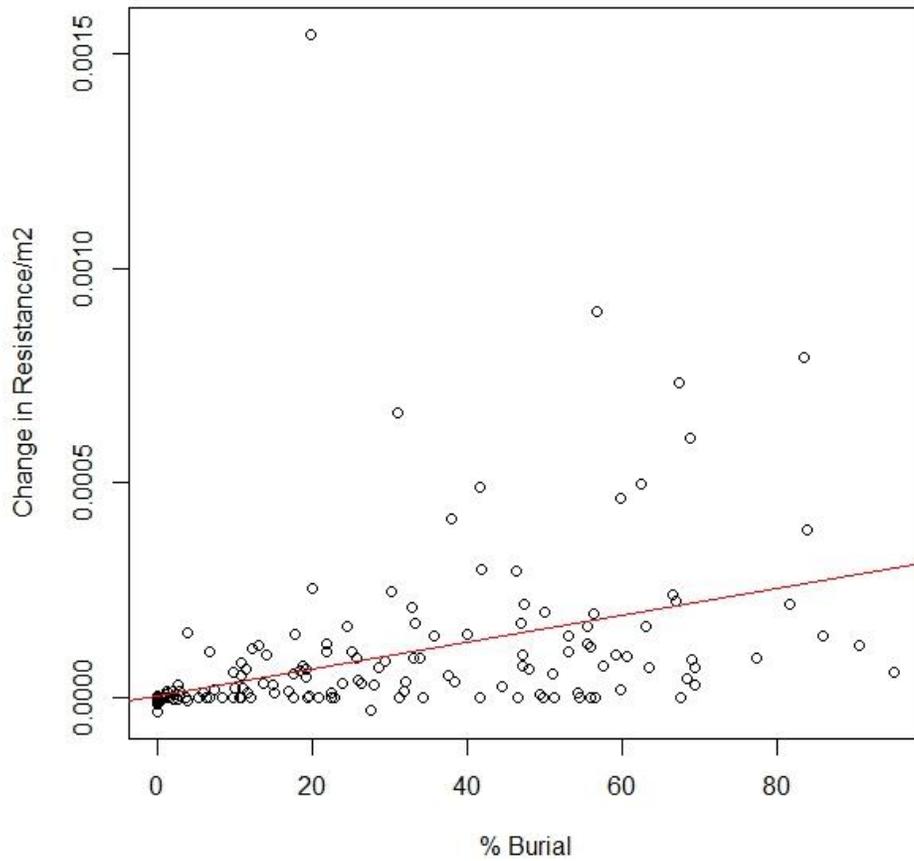


Figure 26 Change in landscape resistance (normalized by system area) as a function of percent burial for 301 headwater systems within the Middle Potomac-Anacostia-Occoquan Watershed (HUC 02070010) within the larger Potomac River Basin.

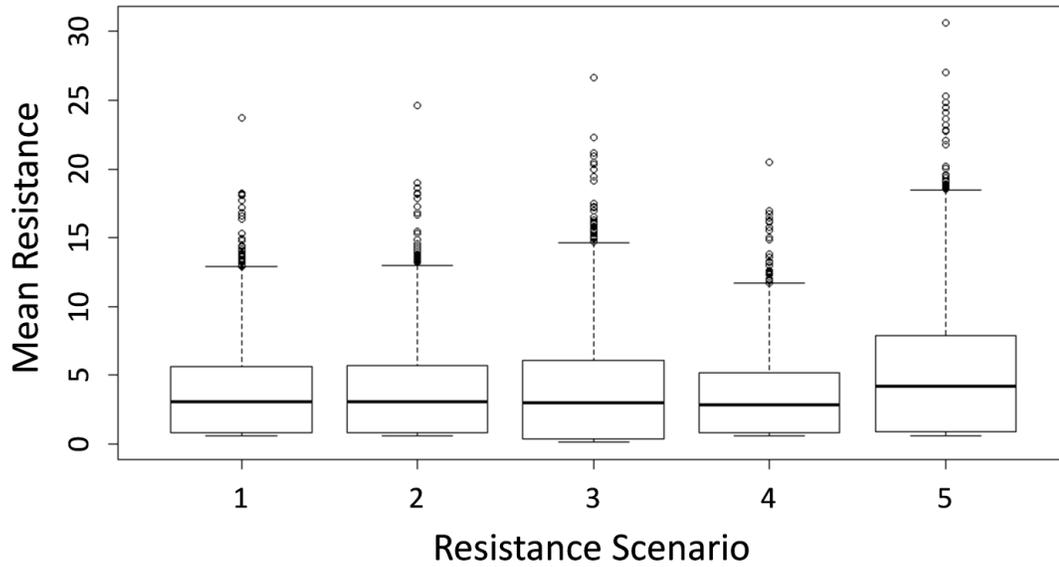


Figure 27 Variability in output resistance values for headwater systems utilizing 5 different landscape resistance classification scenarios. Scenario numbers refer to those scenarios outlined in Table X, and in the discussion section for the chapter. No significant differences in group means between any two scenarios were observed.

Chapter 4: The relative roles of environment and distance in structuring aquatic communities in headwater stream systems

4.1 Abstract

Though often species-poor as compared to larger, downstream reaches, headwater streams are critical reservoirs of biodiversity, with high rates of species turnover between systems contributing disproportionately to regional species pools. Proper management of headwater systems, and the ecosystem services they provide, requires a clear understanding of the environmental and spatial controls governing the structure of headwater communities, and the scales at which these processes operate. Leveraging recent advancements in biodiversity modeling and the generation of estimates of landscape resistance to movement by aquatic organisms, we used an extensive stream biological survey to compare environmental and spatial controls on species turnover of fish and aquatic insect communities across headwater stream systems in Maryland. Biotic communities were analyzed using (1) generalized dissimilarity modeling, a novel approach that accommodates variation in the rates of species turnover along and between gradients, and (2) two novel measures of resistance distance, which combine aspects of space and environment, specifically the spatial extent, orientation, and relative favorability of habitat across the landscape, and along the stream network. We predict that diversity in headwaters is highly sensitive to environmental parameters, and that less mobile species (e.g., fish compared with insects) are more sensitive to habitat fragmentation and required dispersal distances (i.e., space). Results generally support these hypotheses, but show

a weaker effect of landscape and network resistance distance than expected in controlling patterns of species turnover in both communities. Environmental variables consistently account for the majority of deviance in community structure in headwater systems, across both taxonomic groups and physiographic regions. Distance measures explained a higher proportion of deviance in fish assemblages as compared to insects, across most regions. Of the distance measures, landscape resistance distance generally explained more deviance in insect community structure, while differences in fish communities could not reliably be explained by any one distance measure. In virtually all cases, one of the resistance distance measures accounted for a higher proportion of deviance explained in headwater communities than did Euclidean distance. Finally, the most rapid compositional turnover in both communities occurred within a short distance from the sampled reaches, suggesting that headwater taxa disperse only short distances, and that to capture this process biotic surveys must include closely spaced sample sites. From a management perspective, this result also suggests that even small obstructions or removal of habitat have the potential to impact biological turnover within headwater systems.

4.2 Introduction

Headwater streams are important for maintaining aquatic biodiversity (Meyer and Wallace 2001, Gomi et al. 2002, Meyer et al. 2007), yet species richness (α -diversity) in individual headwaters is highly variable (Feminella 1996, Haggerty et al. 2004, Frady et al. 2007, Meyer et al. 2007). While typically not as species rich as larger, downstream reaches (Vannote et al. 1980, Malmqvist and Maki 1994, Heino et

al. 2004), the contribution of headwater taxa to regional species pools (γ -diversity) is often substantial, due to a high degree of species turnover (β -diversity) between headwaters systems (Nekola and White 1999, Clarke et al. 2008). In other words, headwater streams often support communities with similar numbers of species, but differ in species composition, and therefore contribute disproportionately to regional patterns of biodiversity than local measures of species richness might imply. Therefore, changes in patterns of species turnover between streams may be essential information for efforts to quantify the effects of urban development on headwater stream ecosystems.

Rates of species turnover can vary across both natural and anthropogenic gradients, and are generally considered to be either niche- (e.g., Leibold et al. 2004) or dispersal-limited (Hubbell 2001, Heino and Mykka 2008). Recent beta-diversity meta-analyses across taxa and ecosystems show rates of turnover (i.e., variability in species composition) are driven by multiple factors related to species functional traits, geographical gradients and ecosystem properties (Soininen et al. 2007a, Soininen et al. 2007b). The environment and geographic constraints on species turnover of insects and fish species in headwater systems, while not extensively studied, suggest similar relationships (e.g., Poff 1997, Heino et al. 2003, Buisson et al. 2008, Costa and Melo 2008).

Focusing specifically on relatively undisturbed, headwater systems on the Appalachian Plateau of Western Maryland, Brown and Swan (2010) found a positive relationship between community similarity and environmental similarity, suggesting turnover rates in headwater communities are controlled by local environmental

factors. Several additional studies confirm the importance of environmental variables in structuring headwater communities, citing factors such as substrate type (Ligeiro et al. 2010), water quality parameters (Patrick and Swan 2011), stream size and pH (Al-Shami et al. 2013), habitat heterogeneity and the presence of landscape barriers that limit dispersal (Múrria et al. 2013). The distance between adjacent habitats, both within and between headwater systems, has also been recognized as an important determinant of community structure in headwater systems. In their study of an urban stream system, Rouquette et al. (2013) found that invertebrate community structure was most strongly associated with geographic distance measures, and in particular, the distance along the stream network between sampling localities. More recent work suggests that diversity patterns of aquatic insects are related to local environmental factors, but interact with network properties and the connectivity of sites along and between stream paths (Altermatt et al. 2013, Cañedo-Argüelles et al. 2015). Whether similar mechanisms govern turnover across larger regions spanning strong physiographic and land-use gradients (e.g., rural to urban) remains unknown, but is critical information for decision making at management scales confronting state conservation agencies.

Changes to stream network and upland landscape properties through urbanization may affect both the environmental and spatial controls on species turnover in headwater systems. Urban phenomena such as stream burial eliminate in-stream habitat (Elmore and Kaushal 2008), and the introduction of man-made structures such as culverts inhibits the dispersal of both larval and adult aquatic insects (Meyer et al. 2005b, Blakely et al. 2006), as well as fish (Warren Jr and

Pardew 1998, Boubée et al. 1999). Increased surface runoff from impervious cover alters the flow of water and materials to streams, disrupting natural environmental conditions and cues necessary for the successful completion of invertebrate life-cycles (Vinson and Hawkins 1998, Allan 2004, Walsh et al. 2005). Urban-related degradation of riparian and upland matrix habitats may be particularly detrimental to adult aquatic insect populations reliant on terrestrial pathways for dispersal, with changes in microclimatic factors (Oke et al. 1989) and the creation of “ecological traps” (Kristan 2003) affecting adult fitness, survival, and mating potential (Smith et al. 2009).

Urbanization of stream catchments also affects spatial network properties such as drainage density and the arrangement of stream segments across the landscape, which, in turn may influence diversity patterns in headwater communities (Meyer and Wallace 2001, Grant et al. 2007, Smith and Lamp 2008). Community similarity generally decreases with increased distance between sites (Nekola and White 1999, Tuomisto et al. 2003, Soininen et al. 2007b), and urbanization events, such as stream burial and the degradation of the terrestrial matrix, further isolate relatively remote headwater habitats and populations (Lowe 2002, Smith et al. 2009), limiting the chances of successful dispersal within and among headwater systems. Cumulative losses to headwater stream connectivity are likely to affect regional patterns of biodiversity in streams, with serious implications to proper ecosystem function (Chapin et al. 1997, Vinson and Hawkins 1998, Loreau et al. 2003, Freeman et al. 2007).

Investigations into the effects of land use change on habitat connectivity and species turnover in aquatic ecosystems must consider both the distance between habitat, and the environmental context of dispersal pathways through the landscape. To address these considerations, we developed two novel ‘resistance distance’ measures that explicitly incorporate information on the relative proportion and spatial location of land cover types, and what we hypothesize are more ecologically-realistic measures of distance, and therefore, connectivity between headwater stream habitats. To address the effects of distance on turnover of headwater insects, which utilize terrestrial habitats as adults, we calculated a “landscape resistance distance” measure, which considers both stream network characteristics, as well as those of the upland landscape. We also calculated “network resistance distance”, which considers only the landscape context within the stream network and surrounding riparian area, and expected this measure to represent fish dispersal pathways more effectively than landscape resistance distance.

We tested the relative ability of these three distance measures to explain patterns in headwater species turnover in relation to the environment, using a suite of environmental variables previously shown to affect community composition across our study region (M. Johnston *unpublished thesis*). To understand the utility of resistance distance measures, we compared their effect against that of Euclidean distance, or straight-line distance between sites, a measure often employed in aquatic connectivity analyses, with equivocal results (Finn et al. 2006, Brown and Swan 2010, Altermatt et al. 2013). Based on current knowledge of the ecology of headwater

communities, and the environmental and spatial controls affecting species turnover across these systems, we developed and tested the following hypotheses:

- (H1) Environment is more important in structuring headwater insect and fish communities than is distance.
- (H2) Distance is more important in structuring headwater fish communities than it is in structuring insect communities.
- (H3a) Landscape resistance distance, relative to network resistance distance, is more important in structuring headwater insect communities.
- (H3b) Network resistance distance, relative to landscape resistance distance, is more important in structuring headwater fish communities.
- (H4) Resistance distance is more important than Euclidean distance in structuring headwater insect and fish communities.

Insights gained through these investigations will create a better understanding of the dynamic of headwater biotic communities in relation to both space, and environment. Such knowledge is vital for effective management and conservation of critical headwater stream ecosystems in light of continued urbanization across the mid-Atlantic region.

4.3 Methods

4.3.1 Study region

The study region encompasses headwater stream sites from across Maryland, USA, selected from a larger database of biological monitoring sites and associated data developed by the Maryland Biological Stream Survey (MBSS) over the course of nearly 20 years (Stranko et al. 2007). Candidate localities were identified from the MBSS based on their spatial overlap with 1st – 3rd order reaches contained in ‘potential’ stream maps recently developed for the Potomac River Basin and adjacent watersheds across Maryland, east of the Chesapeake Bay (Elmore et al. 2013). The final selection consists of 1167 “site years”, or individual sampling events, spanning the years from 1995-2011, and the full range in physiography and land use across the study region (Figure 1A; see Chapter 2 for more detailed discussion of the regional setting).

4.3.2 Species occurrence data

Biological records for fish and aquatic insects associated with the selected headwater sites were extracted from the MBSS database, and include species occurrence data for 116 fish and 486 aquatic insect taxa. The majority of MBSS sampling localities are selected using a random, probability based design, and standardized sampling protocols are employed (Stranko et al. 2007) to ensure comparability of biological data across sites and years. Fish taxa are identified to species, and aquatic insects to the level of family or genus. Non-native fish species

were excluded from the analysis, as their presence in the region is largely due to human introduction, and their current distributions likely governed by factors other than simply environmental conditions (Christmas et al. 2001, Leprieur et al. 2009).

4.3.3 Environmental predictor variables

To compare the effects of environment and distance on headwater communities, we required a set of environmental predictors that could adequately represent the full suite of possible environment-species interactions occurring in these systems. However, because our objective was to compare against measures of distance, the relative importance of environmental predictors was of lower priority. Nevertheless, we took great care in ensuring we were using an appropriate set of environmental predictors, and for this we extensively leveraged recent work. Selection of environmental predictors was aided by previous and ongoing projects at the UMCES Appalachian Laboratory having compiled and calculated a large suite of field-measured and GIS-derived variables relevant to the physical, chemical, and biological regimes governing mid-Atlantic stream ecosystems (e.g., Julian et al. 2012, M. Johnston *unpublished thesis*). Predictor datasets include both “proximal” variables, those with direct, physiological influence on stream biota (e.g., pH and temperature), and “distal” variables, those with no direct physiological influence, but that indirectly influence faunal distributions through a correlative relationship with one or more functionally relevant, proximal variables (Guisan and Zimmermann 2000, Austin 2002, Elith and Leathwick 2009). The assembled suite of environmental predictors also include measures at different scales relevant to survey sites, either “local” (measured in-stream or at the site, or derived for the area

immediately adjacent and surrounding the site) or “accumulated” (derived measures pertaining to the upstream contributing area for a site); discussed in more detail, below.

Field-measured variables include select observations from the MBSS database, collected at survey locations coincident with the biological samples described above (Stranko et al. 2007), and include measures related to water chemistry, hydrologic flow, stream gradient, and the quality and amount of various in-stream habitat features. The measures represent conditions at the time of faunal sampling, and may vary between the seasons. Candidate field variables (n=24) included only those that were measured at all headwater sites, and were either continuous measures, or ordered, categorical variables with a sufficient number of categories to accommodate GDM use of environmental distances in model fitting (Ferrier et al. 2007, M. Johnston *unpublished thesis*).

The available set of derived variables (n=44) include a range of measures known to influence the distribution of aquatic organisms, including aspects of topography, hydrography, land use/land cover, soils, and climate (Jackson et al. 2001, Heino et al. 2003, Allan 2004, Walsh et al. 2005). These measures were calculated using GIS and remote sensing data, or downloaded from online databases (e.g., Worldclim, Hijmans et al. 2005), and either calculated or resampled at a scale of 10m, corresponding with the resolution of the ‘potential’ stream maps, mentioned above (Elmore et al. 2013). Most derived variables are available at both local and upstream scales. Local, derived values measure conditions within or immediately adjacent to the sampling site, and consist of average values for each variable within a 3 x 3 pixel

(900m²) ‘window’ surrounding the site (e.g., land cover, soils, topography), or in the case of hydrographic variables (e.g., stream length), a 1 x 3 pixel window encompassing the site pixel, and the immediate upstream and downstream pixels in the stream layer (see Julian et al. 2012 for details).

Accumulated derived variables consider conditions upstream of each site, and consist of the average value of each variable across all pixels flowing into the site (i.e., the site’s contributing area, or watershed). An additional class of “spatially-accumulated” land cover variables was recently generated (M. Johnston *unpublished thesis*), reflecting the spatially-explicit effects of upstream conditions (Peterson et al. 2011) by weighting the value of each land use by (1) its proximity to the nearest stream channel (flow path length), and (2) the number of pixels flowing into that pixel (flow accumulation weight). Accordingly, land pixels closer to a site (along the flow path) are more heavily weighted, as are pixels through which more water flows (see M. Johnston *unpublished thesis* for more detail).

The total suite of available environmental predictors was subjected to correlation analysis (R Core Development Team 2013), and the degree of correlation visualized both in matrix form, and as a dendrogram, with the terminal branches representing groups of variables with the highest degree of correlation (Figure 2). The tree was dissected at a branch height of approximately 0.85, resulting in 20 sub-groups of highly correlated variables. A single variable from each group was then selected, informed in part by the recent work of Miriam Johnston (*unpublished thesis*) investigating the role of proximal and distal environmental variables in structuring aquatic communities across physiographic regions in Maryland. Decisions were

based primarily on (1) the relative importance of each variable in her models, and (2) the relative frequency of models for which each variable explained a significant proportion of the variation in species turnover between site pairs (see her thesis for details). Extra weight was assigned to variables that were important for both fish and invertebrate models. The final selection of variables (Table 1) includes 16, relatively uncorrelated variables (≤ 0.6 , Figure 2) spanning all predictor categories (e.g., land use, hydrography, etc.) and spatial extents (e.g., local, accumulated, and spatially-accumulated).

4.3.4 Distance measures

“Landscape” and “network” resistance distances for site pairs were calculated using Circuitscape (McRae et al. 2008), a circuit-theoretical model that treats the landscape as an electrical circuit, passing ecological “current” through a series of landscape “resistors” between focal habitats units. In the model, landscapes are represented as conductive surfaces, with habitat more permeable to individual movement assigned low resistance, and less-permeable habitat types and barriers to movement assigned high resistance. Total (effective) resistance of the landscape, the “resistance distance,” is modeled between any two headwater stream sampling sites and represents a measure of connectivity between those two locations (McRae et al. 2008). Our overall strategy was to generate two representations of the aquatic network, one with finite resistance applied to the entire watershed area and a second, within-network layer, in which finite resistance values were only applied to the stream channel and adjacent riparian zones. In each case the resistance distance from Circuitscape was used to arrive at a measure of distance.

A Circuitscape model requires two raster inputs to calculate resistance distance; a “focal node” file, representing the habitats between which to calculate resistance distance, and a “habitat raster”, representing the landscape matrix, with habitat types classified by their relative resistance to movement for the focal taxon. For this analysis, focal nodes consist of point localities for MBSS monitoring sites. To establish the extent of the analysis landscape, a spatial file representing the Maryland state boundary, within which all the MBSS sites reside, was imported into ArcGIS (ESRI 2012). The state boundary was clipped along the western shore of the Chesapeake Bay (representing the easternmost extent of sampling sites within the state, and the easternmost extent of the improved, headwater stream maps used throughout this dissertation). The resulting polygon was then buffered by 5 km, creating a relatively even landscape extent surrounding the distribution of MBSS sites, in an attempt to minimize any effects of the map boundary on calculations of landscape resistance to organism movement (Koen et al. 2010). The southern portion of the landscape boundary (largely consisting of the portion of the Potomac River Basin in Virginia) was then expanded outward to allow for the possibility of straight-line movement between any two site pairs across the landscape resulting in a final analysis landscape roughly trapezoidal in shape (Figure 1).

The habitat layer for the resistance analyses consisted of the 2001 version of the National Land Cover Dataset (30m NLCD, resampled to 10m resolution; Homer et al. 2007), overlaid with the 2001 buried stream maps (10m resolution, described in Chapter 2) to create a seamless habitat raster. Once combined, each habitat pixel was assigned a resistance value (0% - 100%) based on its relative favorability to

movement of fish (in-stream) and adult aquatic insects (upland habitats) through the landscape, as identified from the literature. Due to the lack of empirical data on movement/dispersal for most species across most habitats, additional expert input/review was solicited to assure the most accurate assignment of resistance values across aquatic insect taxa. Experts were identified from the literature, and as recommended by their peers, and approached with a simple survey containing brief background information on the classification process, and asking for comments on the provisional resistance classification. They were asked to rank land cover classes in order, based on their knowledge of favorability to aquatic insects, and, where possible, to assign a relative resistance value (0%-100%) to each land cover class, including the ability to lump land cover types into similar resistance classes where applicable. A complete description of the survey method, the materials forwarded to potential reviewers, and a summary table of results from those who responded can be found in Appendix A.

Survey responses from the subject area experts were compared with the provisional classification, and a “consensus” classification was finalized (Table 2), consisting of 8 terrestrial resistance classes. Headwater streams were assigned low resistance (2%) relative to terrestrial classes, to favor movement in the model along and within streams and their near riparian areas. Larger rivers and open water habitats (lakes, ponds, estuaries) were assigned higher values (5% and 10%, respectively), to reflect their status as less-favorable habitat for headwater stream organisms.

To create the final habitat resistance rasters for input into the Circuitscape model, the reclassified NLCD was first clipped to the boundary of the analyses extent discussed above. Due to computational issues involved with running such a large landscape at 10m resolution, we resampled the resistance network to the 90m pixel scale, assigning each cell a resistance value based on the average of the 81, 10m pixels located within its extent. The final “landscape” resistance layer consisted of a seamless habitat raster for the entire analysis extent, containing over 4.5 million 90m cells. The “network” resistance layer was created by extracting all 90m cells within the “landscape” resistance layer that intersected the hydrologic network (including riverine, lacustrine and estuarine habitats) (Figure 3). The final resistance layers were entered into individual circuit models, along with the sample points, resulting in pairwise value matrices for both landscape and network resistance distance.

4.3.5 Generalized dissimilarity modeling (GDM)

To assess the relative effects of environmental versus spatial controls on the structure of headwater fish and insect communities across the study area, we used Generalized Dissimilarity Modeling (GDM), a novel statistical method for analyzing and predicting spatial patterns of turnover in community composition (beta-diversity) across large regions (Ferrier et al. 2002, Ferrier et al. 2004, Ferrier et al. 2007). Measures of compositional dissimilarity are based on presence or abundance of species, and can accommodate special types of environmental data, including information on barriers to dispersal (e.g. stream burial, measures of spatial separation) between geographic locations (Ferrier et al. 2007). Of particular interest to this study, GDM can also incorporate information on the relative impedance (cost) to biological

dispersal, such as the landscape resistance values generated by the circuit-theoretical landscape connectivity analysis described above.

An extension of matrix regression, GDM uses a “distance” approach to relate dissimilarities in predictor variables (e.g. environmental or geographic variables) to dissimilarities in response variables (e.g. Bray-Curtis dissimilarity in biological composition between pairs of survey sites) along and between gradients (Thomassen et al. 2010, Fitzpatrick et al. 2013). Inherent in the GDM approach are a number of strengths for analyzing beta-diversity patterns. Foremost among these is the use of Generalized Linear Models (GLMs) and non-linear I-spline functions to account for common, but often ignored, nonlinearities in the relationships between biological data and the environmental gradients across which they are sampled: variation in the rate of compositional turnover along environmental gradients, and the curvilinear relationship between compositional dissimilarity and environmental/geographic distance (Ferrier et al. 2007, Dodds et al. 2010). The shape of the I-spline indicates the rate of biological turnover at each position along the gradient, while its amplitude, quantified by the sum of its coefficients, corresponds to the relative importance of the predictor variable in contributing to biological turnover between pairs of sites, holding all other variables constant (Ferrier et al. 2007).

GDM requires two corresponding input tables to fit models: a site *by* taxa table, and a site *by* environment table. GDM converts the former into pairwise site biological distances using the Bray-Curtis measure of dissimilarity, for use as the response variable in the models. We chose to base our models on presence/absence of species at a site, based on the “un-censused” nature of the benthic invertebrate data

included in the MBSS dataset (Boward and Friedman 2011, M. Johnston *unpublished thesis*). Data from the site *by* environment table are converted to environmental and geographic (Euclidean) distances by GDM, and comprise the predictor variables for the models. Additional spatial predictors were introduced as pairwise distance matrices to GDM, and included measures of landscape and network resistance between all site pairs, as described above. All pairwise comparisons between sites sampled in different years were eliminated from the input tables, to minimize the effects of inter-annual variation in species composition due to unmeasured environmental stochasticity. GDM analyses were performed using the “gdm” package (<http://CRAN.R-project.org/package=gdm>, Manion et al. 2014) in R (R Core Development Team 2013).

A total of 56 GDMs were fit, including the majority of occurrence data for headwater streams from the MBSS (N=1167 sites). Ten (10) MBSS sampling sites were excluded due to missing environmental or species data, or if the site location could not be precisely mapped. Separate sets of models were run for each taxon (insects and fish), with each set (7 per taxon) including models consisting of each unique combination of a distance measure and the environmental predictors, as well as separate models each using the distance measure or environmental predictors, alone. Models were further stratified by physiographic province, acknowledging the role of their unique geologic characteristics and geomorphic history in structuring biotic communities and critical abiotic variables (Melles et al. 2004). For this study, sampling sites were grouped by the physiographic regions used by Johnston (*unpublished thesis*), as adapted from those frequently used by the Maryland

Department of Natural Resources : the Coastal Plain (C), Piedmont (P), Highlands (H), and Youghiogheny (Y) (Figure 1B).

Comparison of deviance explained for the seven models in each set allowed for determination of the proportion of deviance uniquely explained by the variables (Jones et al. 2013), distance versus environment, for each taxon, in each region. For example, in a model set using environmental predictors (ENV) and the landscape resistance (LR) distance predictor, the proportion of deviance explained (DE) attributable to LR alone is:

$$DE_{LR} = \frac{(DE_{ENV+LR} - DE_{ENV})}{DE_{ENV+LR}} * 100$$

The same suite of environmental predictors was applied across equivalent sets of site pairs for all models, thereby ensuring the direct comparability of resulting values for explained deviance in community composition across the study area.

4.4 Results

4.4.1 Contribution of environment and distance to beta diversity in headwater communities

GDMs explained between 0.25 and 42.23% of the deviance in compositional turnover across the study region, depending on the variable set and taxon (Table 3). The least explanatory model was built with only network resistance distance for aquatic insects in the Piedmont ecoregion. The most explanatory model was also for insects, and included both the suite of environmental variables and landscape

resistance distance in the Highlands ecoregion. The best, and worst, models for compositional turnover in fish were for the Youghiogheny ecoregion, and were those including environmental variables + network resistance (28.35%) and landscape resistance distance only (0.30%), respectively. GDMs including both environmental variables and a distance variable always outperformed models with these predictors in isolation, though never explained more than 2.06% (0.01 – 2.06%) additional deviance than companion models built with environment only.

When the deviance explained from GDM was partitioned into unique and shared components of environment and space, environment always accounted for the majority of deviance explained, ranging from 66.47 – 99.15% across all model sets (Table 4). As hypothesized (H1), environmental variables provided higher explanatory power than the distance measures, across both headwater taxon groups.

Across the majority of models, distance measures accounted for a higher proportion of deviance explained for fish (0.37-13.54%), as compared to insect communities (0.02-11.07%), generally supporting our second hypothesis (H2) that distance is more important for structuring headwater fish communities than for structuring insect communities. The relationship does not hold, however, for the Youghiogheny and Coastal Plain regions, where landscape resistance distance (LR) and Euclidean distance (ED), respectively, explain a higher proportion of deviance in species turnover for aquatic insects than for fish. However, the difference in deviance explained by landscape resistance distance for insect communities in the Youghiogheny region is marginal (0.79%).

The remaining hypotheses (H3a, H3b, and H4) were also only partially supported by the model results, in that landscape resistance distance accounted for a higher proportion of deviance explained in insect communities across all regions (H3a) except the Youghiogheny, where network resistance distance explained a higher proportion of deviance. For fish, network resistance distance explained a higher proportion of deviance than did landscape resistance (H3b) in the Youghiogheny and Highlands regions, but was outperformed by the landscape resistance measure in the Coastal Plain and Piedmont. In virtually all cases, across both taxa, one of the resistance distance measures accounted for a higher proportion of deviance explained than did Euclidean distance (H4), the single exception being for fish in the Piedmont region, where Euclidean distance outperformed both resistance measures.

Shared deviance for models including both environment and distance variables ranges from 0.3-22.46% of the total deviance explained (Table 4). In general, models with a higher total deviance explained exhibit lower proportions of shared variance. Likewise, models with a lower proportion of total deviance explained by environment, and a correspondingly higher proportion explained by the distance measure, exhibit a higher proportion of shared deviance (Table 4).

4.5 Discussion

4.5.1 Relative performance of environment and distance measures

Consistent with our first hypothesis (H1), of the two variable groups, environment accounted for the majority of explained deviance in composition (66.47 – 99.15%) for both insect and fish communities in headwater systems. These finding

agree with previous studies suggesting that community structure in headwater communities is governed mainly by environment (e.g., Heino et al. 2003, Clarke et al. 2008, Costa and Melo 2008, Brown and Swan 2010, Ligeiro et al. 2010, Al-Shami et al. 2013, Múrria et al. 2013). Maryland spans 5 very different physiographic regions, “from the mountains, to the sea”, creating very strong longitudinal and elevational gradients in habitat and environmental regimes across the study area. The fact that we see a strong effect of environment on these two headwater taxa suggests that species across the region are essentially at equilibrium with their environment, at least at the scale of the sample data we analyzed, discussed below. That is, on average, the sampling sites represent different environments, and with sites distributed widely (average distance to nearest neighbor ~ 1.7km) across such diverse physiographic settings, there are not very many points with the same environment. These strong natural gradients have been exacerbated by novel drivers of environmental change, e.g., urbanization and other anthropogenic land use change, further increasing variation in environment across the state. Aquatic insects are widely known to respond to these landscape-scale phenomena, as supported by their widespread use as indicators of environmental health (e.g., Resh 2008).

In most models, distance explained a higher percentage of deviance in composition for fish communities than for insects, largely confirming our second hypothesis. Fish are less mobile than most insect taxa, because they are confined to the channel, and therefore unable to disperse across land to reach adjacent habitats and populations. In the case of naturally isolated headwater habitats, the channel network from one headwater stream to another represents a long path through largely

inhospitable habitat (Fagan 2002, Gomi et al. 2002). As such, fish are subject to any manner of in-stream obstructions, including dams and reservoirs, exacerbating the effects of spatial separation. Even for fish widely distributed within a single headwater system, the effects of limited distance between stream reaches may be enough to prohibit movement between populations. For example, “cryptic” populations of brook trout in the Appalachian region of western Maryland, though distributed in two adjacent, and connected stream reaches, have maintained their spatial separation long enough to become genetically distinct subpopulations, despite the lack of physical obstruction between the two (Aunins et al. 2014) .

For the two regions where distance models explained a higher proportion of deviance in species turnover for insects than for fish, physiographic characteristics of those regions may be interacting with species traits to constrain dispersal. The Youghiogheny, while largely forested, is a highly dissected landscape with steep hills typically dividing headwater drainages. While individual stream sites may be relatively close to each other, the rugged topography presents a strong elevation gradient that adult insects must overcome to successfully disperse between sites and populations, which may explain the relatively poor performance of Euclidean distance in the Youghiogheny, as compared to other regions. In the Coastal Plain, Euclidean distance performs significantly better (+7.81) for the insect model than for fish, which may indicate decreased dispersal due to increased distances between potential habitats associated with lower drainage densities in this region (Elmore et al. 2013).

Our third hypotheses (H3a & H3b) explored the relative importance of the two measures of resistance distance we modeled: landscape resistance distance and within network resistance distance. For aquatic insects, H3a was largely upheld by the data, with landscape resistance explaining significantly more deviance in community composition compared to network resistance distance. Aquatic insects, which are able to leave the stream channel and fly across the landscape during the adult portion of their life-cycle, are more directly exposed to conditions within the landscape, and are therefore more responsive to the distance measure that integrates this landscape perspective. In the Youghiogheny, however, network resistance distance marginally outperformed landscape resistance distance for insect communities. As with the discrepancy between landscape resistance and Euclidean distance, discussed above, this may be due to the heavily dissected drainages characteristic of the region, with high drainage divides posing a formidable obstacle to dispersal, constraining the movement of adult insects to the stream corridor, thereby increasing the importance of distance between sites along the stream network. For fish communities, H3b was supported in two of four regions, with network resistance distance outperforming resistance distance for the Youghiogheny and Highlands, only. The landscape in both the Piedmont and Coastal Plain regions are heavily impacted, with land cover largely consisting of agriculture and urban development. While network resistance distance should still be important in governing the dispersal of fish within stream systems, it is possible that the cumulative impact on habitat and water quality of the activities occurring in the upland landscape is swamping the more local, network-related effects in these regions.

Finally, our final hypothesis (H4) was largely supported, as one of the two resistance distance measures outperformed both Euclidean distance in explaining turnover for both insect and fish communities. The only exception was for fish communities in the Piedmont, where Euclidean distance outperformed both resistance distance measures. In only two regions did both resistance distance measures outperform Euclidean distance (for insects in the Youghiogheny, and fish in the Highlands), and there, only marginal differences between Euclidean distance and the next best resistance distance measure were observed (0.79% and 0.14%, respectively).

4.5.2 Shared deviance between environment and distance measures

Overall, the shared deviance (the proportion of explained deviance attributable to environment and distance) is relatively low (<4% for most models), though there are a number of models that have shared deviance between environment and distance variables that are much higher (up to 22.46%). Models with the highest shared deviance tend to be those where the proportion of total deviance explained by environment are lowest, with an increased proportion explained the distance measures (Table 4). This is especially evident for models including environment and landscape resistance distance, as the latter was specifically designed to incorporate a combination of distance and environment in a single measure. Total deviance explained by each model tends to be highest for those with the lowest proportion of shared deviance.

Moving from west to east across the 4 regions studied, shared deviance in the models tends to increase for both taxa groups (Table 4), indicating a greater degree of correlation between environment and distance measures. This trend is likely attributable to changes in physiography and land use, which both vary significantly from the mountains to the sea, and interact with species dispersal traits to alter the relative importance of environment and distance in structuring headwater communities along these gradients. For example, shared deviance for both fish and insect models is lowest in the Youghiogheny region, with the explained deviance almost entirely attributable to environment (~96-99%), while distance measures account for almost nothing. Unexplained deviance in these models is most likely attributable to some aspect of the environment not adequately captured by the model variables, either through omission or mismeasurement of critical variables (discussed below). At the other extreme, models in the Coastal Plain region of the study area exhibit the highest amount of shared deviance. The proportion of deviance explained by environment tends to be lowest for these models, with correspondingly higher proportions of deviance explained by the various distance measures. These altered proportions, and increased shared deviance, indicate a greater correlation between distance and environment in these models, and result in a lower total deviance explained. Land cover has been heavily altered in the Coastal Plain, both by urban and agricultural development, and stream drainage density (and, therefore the distance between potential habitats) is naturally lower as compared to the other regions (Elmore et al. 2013), perhaps explaining the greater degree of correlation between environment and distance in this region.

4.5.2 Unexplained deviance in aquatic community composition

While environment is the overwhelming explanatory variable across all models, accounting for up to 99.15% of the proportion of deviance explained, a large proportion (57.77-88.08%) of the total deviance in community composition remains unexplained. There are obviously either factors that the included variables attempt to measure and fail to do so, or just as likely, critical factors that structure ecological communities that are simply not included, either as a result of the variable selection process, or because measures for these factors do not exist. For instance, while we have included measures of instream habitat structure (INSTRHAB) and riffle quality (RIFFQUAL), which have been shown to be important predictor variables for fish and invertebrate communities (Johnston *unpublished thesis*), these simple ranking variables fail to capture finer, yet perhaps critical information on the type of substrates present or their relative amounts within a site. Additionally, simply by the nature of our variable selection process (detailed, above), we eliminated from our models numerous variables that had been previously shown to have at least some importance in structuring fish and insect communities across the study region (Johnston *unpublished thesis*).

Similarly, neither environment, nor distance variables, alone, can adequately explain the varying degrees of turnover observed between sites that have the same, or very similar, environments, as indicated by positive (non-zero) intercept values for most models (Table 3). Intercepts for models including only environment, or only distance measures, are comparable, though in all cases, environment-only models

explain a significantly higher proportion (~2.6 – 117.8% as much) of the total deviance in headwater communities. Non-zero intercepts in Euclidean distance models indicate that even sites that are very close in proximity, can have significantly different community composition, suggesting dispersal limitation may prevent taxa from moving between nearby sites. Intercept values for Euclidean distance models are generally higher for insect communities, as compared to fish, suggesting that insects are more susceptible to such limitations. In all but one case, intercept values for models incorporating only Euclidean distance are higher than those for resistance distance-only models, presumably because, in addition to simple distance between sites, both landscape and network resistance incorporate some aspect of the environment governing turnover between adjacent sites. Models that combine environment and some measure of distance always explain a higher percentage of the deviance in aquatic communities than do models with either of the components in isolation. Total deviance explained by these combination models, however, is only marginally better than values for the corresponding environment model, again suggesting that environmental characteristics are the primary forces governing structure of aquatic communities. For fish, however, there are several combination models with intercepts equal to 0, suggesting that for this taxon, at least, differences in composition of species assemblages between nearby sites is governed, at least in part, by the distance between sites.

4.5.3 Potential issues of scale

Overall, our resistance measures performed poorer than expected, considering they were developed to incorporate various factors important to structuring aquatic communities that simple measures such as Euclidean distance do not, specifically the spatial organization, proportion, and relative favorability of various land cover classes in relation to the stream channel. Nor does Euclidean distance address connectivity between sites, such as in-stream obstructions, including dams, reservoirs, and stream burial. Perhaps at the spatial scale studied here, the environmental context of space is not important to organisms moving through and among headwater systems.

Considering the premise we outlined in the introduction that distance between sites does matter to the structure of headwater communities, we must look critically at the data in an attempt to explain why these effects were not more evident. One plausible explanation is that the greater explanatory power of environment relative to distance has more to do with the nature of the biological sampling data, than with the effectiveness of the measure themselves. MBSS sampling protocols are designed to bring out the “environmental signal” describing biological communities. Selection of sites follows a stratified-random design, using stream size, land use, and physiographic variables within basins as a strategy for capturing the variability of stream community types across the various environmental settings in Maryland. This design has its practical side, in that it effectively captures the variability in the biological communities and the environment needed to accomplish their goal of monitoring the general biological health of the state’s waters. Compared to other

states, the quality and coverage of the dataset is quite remarkable, and useful in answering many important ecological questions in stream ecosystems.

For the purposes of this paper, however, the distribution of biological sampling points may be too far apart to realize the full effects of resistance distance in our models, especially for headwater systems. The fitted spline functions from GDM describe the relationship between biologic turnover and landscape resistance (Figure 4.), and show that for both fish and insect communities, there is an initial interval of rapid turnover at very short distances from each sampled reach. This was true for all three distance-measures (all splines not shown). The amount of turnover occurring within this short area is similar for both fish and insects, after which, further increases in turnover approximate a linear trend. This supports the idea that these taxa disperse only short distances and even small obstructions or removal of small portions of habitat have the potential to impact biologic turnover (Fagan 2002).

As stated previously, the average separation between headwater sampling sites and their nearest neighbor is approximately 1.7 km. Considering the high degree of inherent isolation within and between headwater systems, the MBSS samples may be positioned too far apart to capture the primary effects of space on these communities. Furthermore, the MBSS does not include samples in the smallest of headwater streams because many aren't included in the National Hydrography Data used to select streams for sampling (Elmore et al. 2013). Two solutions to this problem come to mind: (1) sampling density could be increased in select areas, with the goal of capturing the fine scale processes we expect are important to biodiversity; and (2) consider novel ways of modeling connectivity of sampled streams to adjacent stream

segments that do not have samples. Replicates of such a sampling regime across physiographic regions, and in varying land use scenarios, would better inform future analyses of the relative effect of distance and environment on headwater species turnover across these gradients.

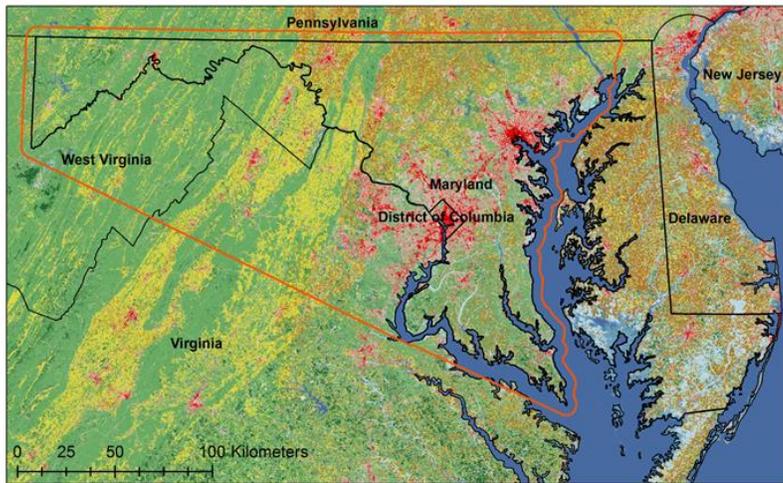
4.6 Conclusions

Environmental characteristics, rather than spatial factors (distance), appear to be the dominant force controlling species turnover among headwater stream systems in Maryland, with strong gradients in physiography and land cover exacerbated by novel drivers of environmental change, namely urbanization. Distance has a larger effect on the structure of headwater fish assemblages, as reflected by a higher proportion of deviance in community composition explained by distance measures for fish, as compared to insects. While not accounting for a large proportion of the total deviance explained for this dataset, Euclidean (straight-line) distance can act as a suitable surrogate to measures of resistance distance developed specifically to account for the spatial organization, proportion, and relative favorability of various land cover classes in relation to the stream channel. Of the two resistance distance measures, landscape resistance better integrates the effects of distance and environment on species turnover in insect communities, while none of the three distance measures consistently explains patterns for fish.

The overall effect of both resistance distance measures was relatively weak, calling into question their ability to adequately integrate the spatial constraints experienced by organisms moving across the landscape and through stream networks. However, the poor performance of these measures may be due to incompatibilities in

scale between the ecological and spatial processes governing turnover headwater communities, and the sampling regime employed to monitor the ecological health of stream ecosystems in Maryland. Although it is always easy to say that we need more data, our results justify this statement in the context of the smaller spatial scales of the ecological processes operating in headwater ecosystems.

A)



B)

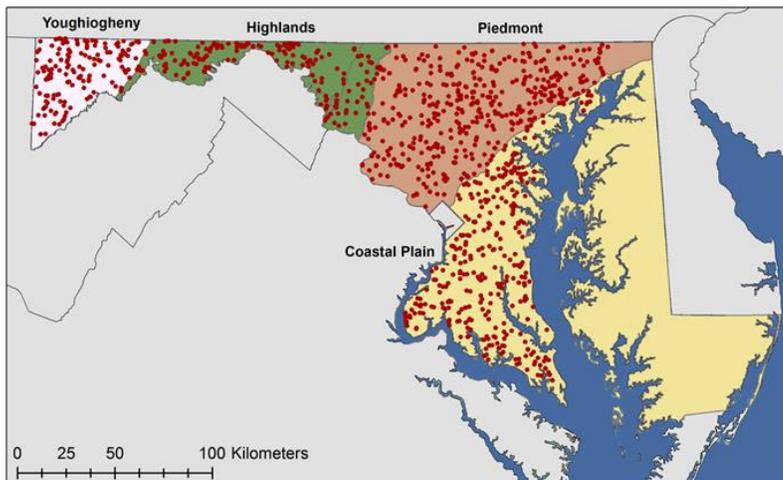


Figure 28 Maps of the study region showing (A) land cover from the 2001 National Land Cover Database (Homer et al. 2007), and (B), the distribution of headwater stream survey locations sampled by the Maryland Biological Stream Survey (MBSS). In (A), land cover classes consist of: urban development (reds and pinks), forest (greens), wetlands and open water (blues), and agriculture (yellow and brown). The orange bounded polygon represents the analysis extent for the landscape and network resistance analyses. In (B), red dots are survey sites for biological data used in GDM. Colored polygons represent the boundaries of Maryland physiographic regions.

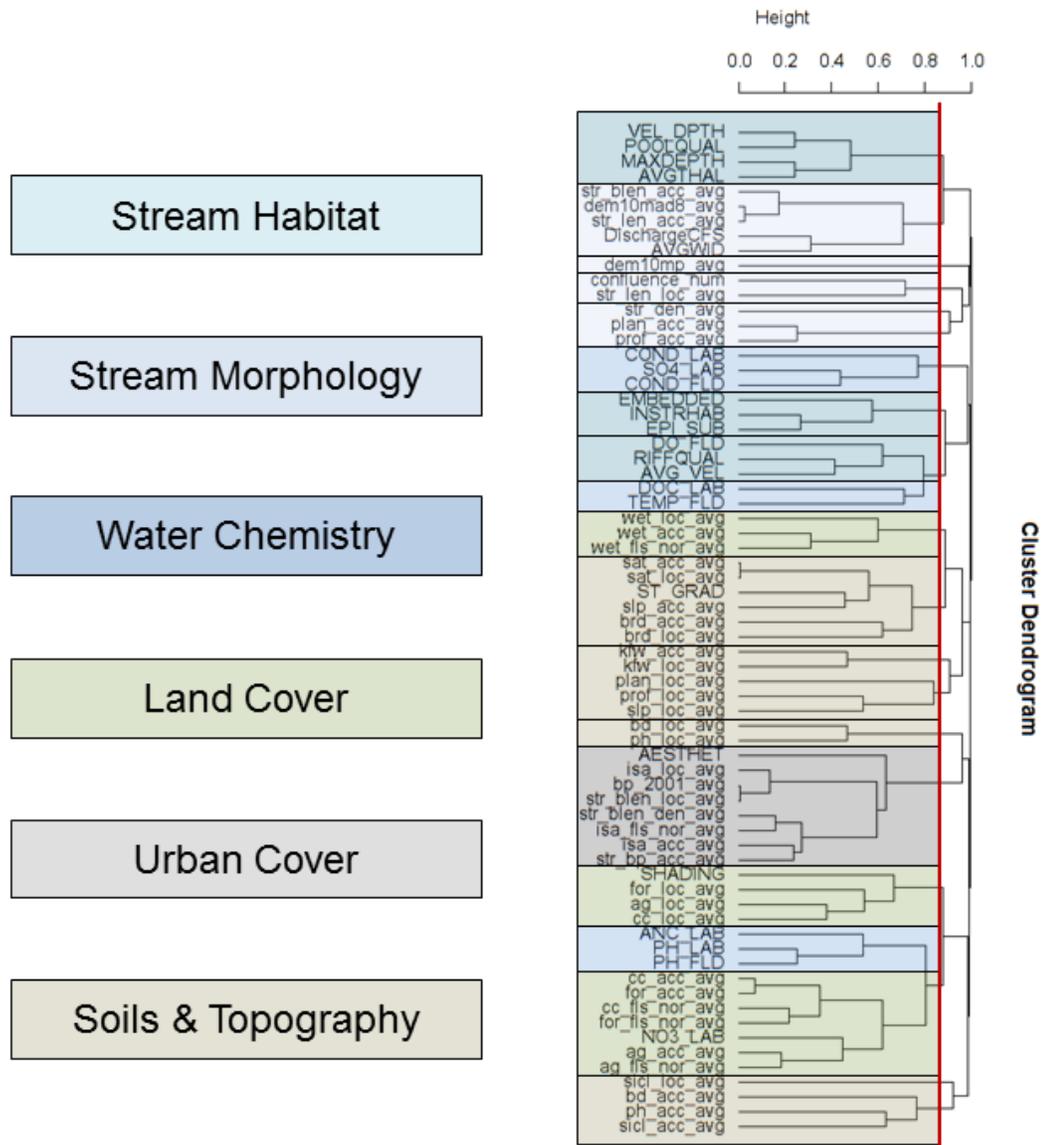


Figure 29 Dendrogram (right) showing correlation structure between all potential environmental predictors. Clusters contain variables that are most correlated with each other within the dataset. The red line represents the level chosen to split the tree into “correlation groups”, and one variable was selected from each group to form a final selection of 20 environmental predictors. Colored boxes represent different predictor classes, as indicated on the left.

Table 4.1 Final set of environmental predictors included in GDMs

Variable code	Description/units	Source/resolution
Field-measured		
NO3_LAB	Nitrate nitrogen (mg/L), lab	MBSS
TEMP_FLD	Summer in-situ water temperature (°C)	MBSS
PH_FLD	In-situ summer pH (pH units)	MBSS
COND_FLD	In-situ summer conductance (µmho/cm)	MBSS
ST_GRAD	Stream gradient (%)	MBSS
DischargeCFS	Summer stream flow (cfs)	MBSS
INSTRHAB	In-stream fish habitat structure rating (0-20)	MBSS
RIFFQUAL	Riffle/run quality rating (0-20)	MBSS
MAXDEPTH	Maximum depth in sample reach (cm)	MBSS
Local-derived		
for_loc	Proportion forest presence (0-1)	NLCD 2001 forest data, 30m, forest = [41,42,43]
ph_loc	Relative acidity or alkalinity of the soil (pH units)	SSURGO, 0.6ha
str_len_loc	Length of stream (km)	Elmore et al. (2013) map
Accumulated-derived		
bd_acc	Bulk density indicator of soil compaction (g/cm ³)	SSURGO, 0.6ha
kfw_acc	Soil erodibility (K value)	SSURGO, 0.6ha
prof_acc	Longitudinal curvature at cell, parallel to flow direction (1/100 elevation units)	NED DEM
wet_acc	Proportion wetland presence (0-1)	NLCD 2001 LULC data, 30m, wetland = [90,95]

Data citations: MBSS (Stranko et al. 2007)
 NLCD (Homer et al. 2007)
 SSURGO (Natural Resources Conservation Service, USDA. Web Soil Survey. Available online at <http://websoilsurvey.nrcs.usda.gov/>)
 NED (Gesch et al. 2002)

Table 4.2 Final resistance classification for streams and land cover classes (2001NLCD) used in calculating landscape and network resistance distance values between sampling sites for GDM. Individual results from expert surveys used to formulate this final classification can be found in Table 2 of Appendix A.

Stream Size		Resistance (%)
Headwater stream (1 st – 3 rd order)		2
Mainstem stream (>3 rd order)		5
NLCD Land Cover Class	NLCD Code	
Open water	11	10
Emergent herbaceous wetland	95	10
Woody wetlands	90	10
Deciduous forest	41	25
Evergreen forest	42	25
Mixed forest	43	25
Grassland/Herbaceous	71	30
Shrub/Scrub	52	30
Barren land	31	40
Pasture/hay	81	40
Cultivated crops	82	50
Developed/open space	21	50
Developed/low intensity	22	65
Developed/medium intensity	23	75
Developed/high intensity	24	90

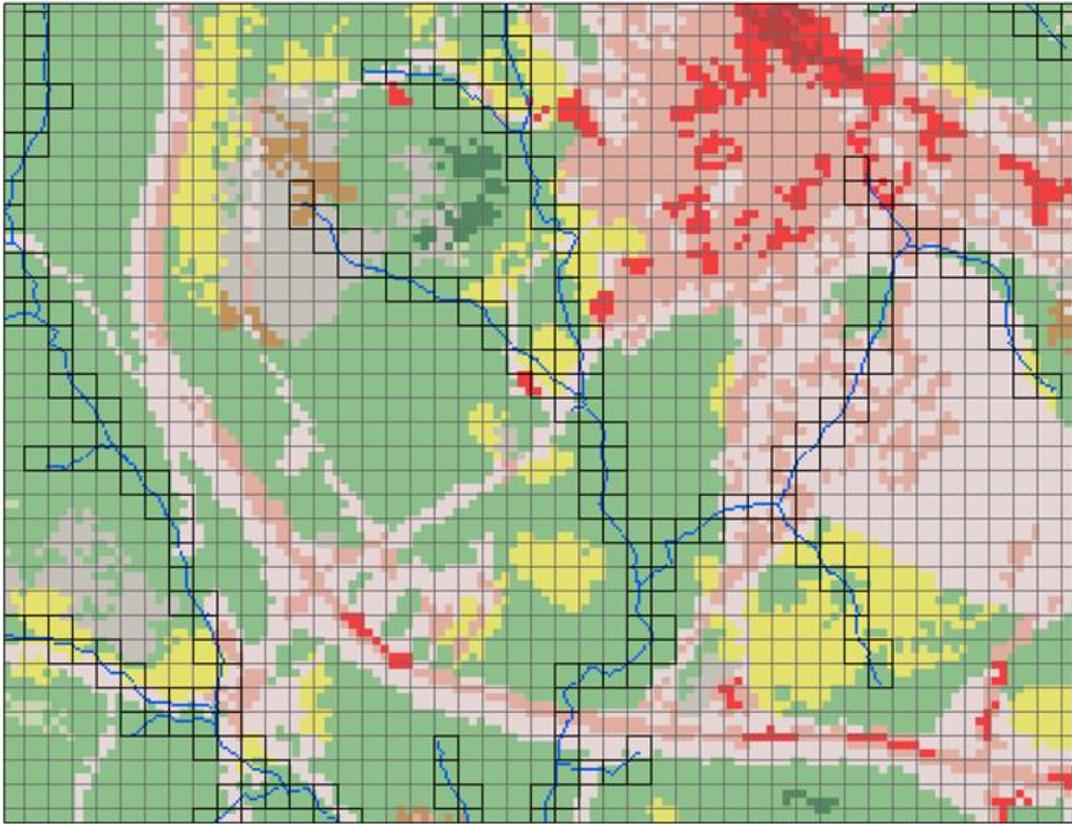


Figure 30 Representation of 90 meter grid cells across an example landscape, used to create resistance grids for calculations of pairwise landscape (grey outlines) and network (black outlines) resistance distance. Blue lines (10m raster) represent streams, with the other colored areas corresponding to land use/land cover classes from the 2001 National Land Cover Dataset (NLCD; Homer et al. 2007).

Table 4.3 Percent deviance explained for individual GDMs.

Model Set	Community	Individual Models	Model Intercept	Total Deviance Explained (%)
Youghiogheny	Insects	ENV	0.79	34.17
		LR	0.81	0.38
		NR	1.14	0.89
		ED	1.18	0.29
		ENV + LR	0.71	34.45
		ENV + NR	0.75	34.49
		ENV + ED	0.78	34.18
	Fish	ENV	1.15	27.90
		LR	1.12	0.30
		NR	1.06	1.23
		ED	0.81	0.63
		ENV + LR	0.00	28.00
		ENV + NR	0.10	28.35
		ENV + ED	0.03	28.02
Highlands	Insects	ENV	0.73	41.44
		LR	0.74	8.62
		NR	0.77	0.67
		ED	1.16	1.57
		ENV + LR	0.63	42.23
		ENV + NR	0.66	41.82
		ENV + ED	0.68	41.88
	Fish	ENV	0.21	10.23
		LR	0.13	1.22
		NR	0.13	1.20
		ED	0.98	0.72
		ENV + LR	0.00	10.48
		ENV + NR	0.00	10.59
		ENV + ED	0.07	10.46
Piedmont	Insects	ENV	0.93	17.24
		LR	0.84	2.99
		NR	0.84	0.25
		ED	1.31	0.95
		ENV + LR	0.73	17.84
		ENV + NR	0.73	17.27
		ENV + ED	0.86	17.55
	Fish	ENV	0.22	21.63
		LR	0.19	1.59
		NR	0.19	1.33
		ED	0.68	1.58
		ENV + LR	0.00	22.36
		ENV + NR	0.00	22.18
		ENV + ED	0.03	22.45
Coastal Plain	Insects	ENV	1.34	10.94
		LR	1.05	4.13
		NR	1.05	0.35
		ED	1.73	3.64
		ENV + LR	0.85	12.30
		ENV + NR	0.91	11.02
		ENV + ED	1.27	12.26
	Fish	ENV	0.48	13.13
		LR	0.37	4.22
		NR	0.37	0.83
		ED	1.04	1.50
		ENV + LR	0.10	15.19
		ENV + NR	0.10	13.55
		ENV + ED	0.37	13.64

Table 4.4 Proportion of unique deviance explained for environmental and distance components of GDMs.

Model Set	Community	Individual Models	Model Components	Proportion Deviance Explained (%)	Shared Deviance (%)	Model Intercept	Total Deviance Explained (%)
Youghiogheny	Insects	ENV + LR	ENV	98.89	0.30	0.71	34.45
			LR	0.81			
		ENV + NR	ENV	97.42	1.65	0.75	
			NR	0.93			
		ENV + ED	ENV	99.15	0.83	0.78	
			ED	0.02			
	Fish	ENV + LR	ENV	98.94	0.69	0.00	28.00
			LR	0.37			
		ENV + NR	ENV	95.66	2.73	0.10	
			NR	1.61			
		ENV + ED	ENV	97.75	1.82	0.03	
			ED	0.43			
Highlands	Insects	ENV + LR	ENV	79.59	18.56	0.63	42.23
			LR	1.85			
		ENV + NR	ENV	98.39	0.74	0.66	
			NR	0.90			
		ENV + ED	ENV	96.24	2.72	0.68	
			ED	1.04			
	Fish	ENV + LR	ENV	88.34	9.32	0.00	10.48
			LR	2.34			
		ENV + NR	ENV	88.63	8.00	0.00	
			NR	3.37			
		ENV + ED	ENV	93.09	4.71	0.07	
			ED	2.20			
Piedmont	Insects	ENV + LR	ENV	83.23	13.39	0.73	17.84
			LR	3.38			
		ENV + NR	ENV	98.57	1.26	0.73	
			NR	0.17			
		ENV + ED	ENV	94.56	3.64	0.86	
			ED	1.80			
	Fish	ENV + LR	ENV	92.89	3.88	0.00	22.36
			LR	3.23			
		ENV + NR	ENV	94.01	3.53	0.00	
			NR	2.46			
		ENV + ED	ENV	92.97	3.40	0.03	
			ED	3.63			
Coastal Plain	Insects	ENV + LR	ENV	66.47	22.46	0.85	12.30
			LR	11.07			
		ENV + NR	ENV	96.83	2.46	0.91	
			NR	0.71			
		ENV + ED	ENV	70.19	19.31	1.27	
			ED	10.50			
	Fish	ENV + LR	ENV	72.22	14.24	0.10	15.19
			LR	13.54			
		ENV + NR	ENV	93.84	3.11	0.10	
			NR	3.05			
		ENV + ED	ENV	88.97	7.34	0.37	
			ED	3.69			

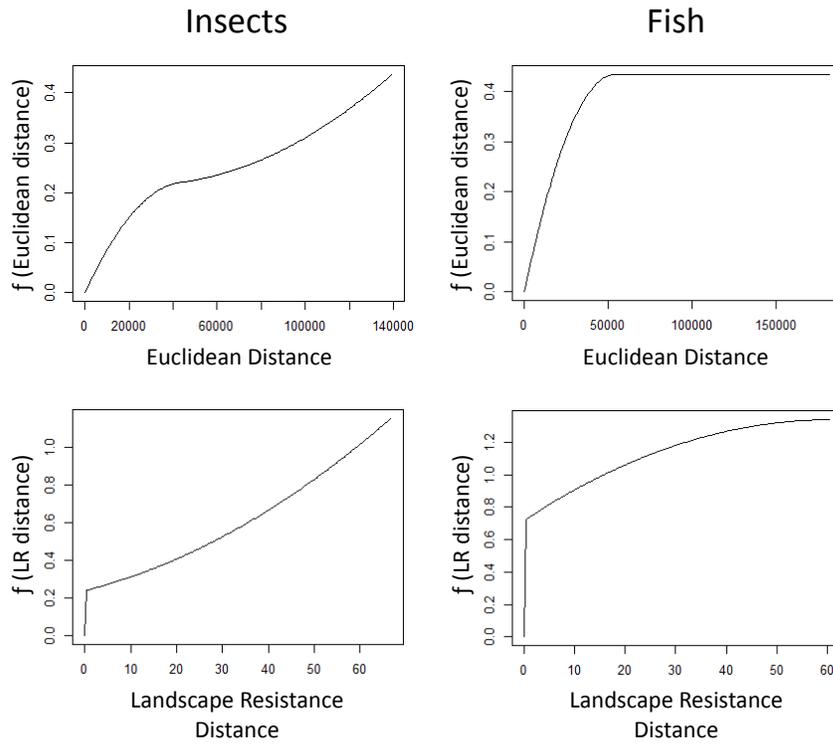


Figure 31 Fitted splines from generalized dissimilarity modelling for Euclidean distance and landscape resistance distance variables for each biotic group. The splines depict the non-linear relationship between the environmental variables and biotic assemblage structure.

Chapter 5: Conclusions

Stream burial is common during the process of urbanization. Headwater streams are particularly vulnerable, due to their small size, and ubiquity on the landscape, and continue to be buried at disproportionate rates as compared to larger streams. Stream burial affects critical aspects of the geometry of headwater networks, and thus the flow of organisms and materials within and between headwater systems, and to downstream waters, with potentially severe ramifications for water quality and biodiversity loss at regional scales (Meyer et al 2007). In an effort to better understand the cumulative effects of stream burial on headwater ecosystem function, I have: (1) modeled and mapped the distribution of buried streams across the urbanizing Potomac River Basin (PRB), and evaluated its relationship to select physiographic variables across the a gradient in urbanization (Chapter II); (2) evaluated burial related impacts to stream network structure and connectivity within PRB headwater systems (Chapter III); and, (3) assessed the relative roles of space and environment on species turnover in headwater stream communities across the state of Maryland.

Mapping the distribution of stream burial was accomplished by combining training observations made with high-resolution aerial photography, to classify PRB stream reaches as buried or intact, with spatial analyses of impervious cover data and decision-tree classification, to generate burial probabilities for every stream reach in the basin. I then spatially-related the burial maps to similar data for stream catchment area and topographic slope, to examine how these physiographic variables might

influence rates of stream burial across urbanizing counties within the basin. I learned that headwater stream burial is an ongoing phenomenon, with burial increasing linearly with total impervious cover across all levels of development, bringing into question the effectiveness of existing stream protections. Furthermore, as urbanization proceeds across counties, consistent patterns in burial rates emerge in relation to both slope and stream size, indicating that these factors function, in part, to constrain the distribution of burial to certain ranges for both variables. As counties continue to urbanize, the need for developable land appears to override these initial constraints, with burial proceeding on steeper slopes and larger stream sizes, until the only headwaters left are those afforded some protection by established parks and other designated natural areas. The stream burial data could be used by managers to identify and prioritize opportunities for stream and riparian restoration, address issues with burial-related losses to connectivity in stream networks, and to manage the effects of urbanization-induced changes to hydrologic regimes and water quality in downstream waters such as the Chesapeake Bay.

Once I identified the spatial extent and severity of stream burial across the PRB, I could determine how stream burial has affected the network geometry and habitat connectivity of headwater systems. This was accomplished through spatial comparisons of buried and intact stream networks, to quantify burial related habitat loss and fragmentation within headwater systems. I also developed a novel application of circuit theoretical modeling to quantify changes to habitat connectivity within headwater systems, with particular attention to confluences and channel head areas critical for supporting headwater biodiversity. I learned that stream burial has

caused significant changes to network geometry in headwater systems, eliminating critical habitats, and severely fragmenting remaining stream reaches. First order systems are disproportionately affected as compared to larger systems, across all levels of burial. In-stream burial, and associated increases in impervious cover in upland areas, conspire to increase landscape resistance movement by aquatic organisms, including through stream confluences, known to be hotspots for aquatic biodiversity within headwater systems. Burial-related changes to headwater networks have the potential to severely disrupt species' dispersal, and other ecological processes vital to the persistence of headwater populations, and human provision of ecological services.

The final stage of my research investigated the relative role of space versus environment in structuring headwater communities. This was accomplished by coupling extensive biological monitoring datasets for headwater fish and insects, with generalized dissimilarity modeling, to quantify the degree of compositional turnover in headwater communities in relation to environmental and spatial gradients across the state of Maryland. As part of this research, I developed two, novel measures of resistance distance that, unlike Euclidean distance, incorporate information on the spatial extent, orientation, and relative favorability of habitat between sampling sites. I learned that abiotic characteristics of headwater environments, rather than the distance between sites, is the major structuring force in headwater communities. Furthermore, it appears that urbanization has exacerbated the naturally strong environmental gradients across the study area, further emphasizing the importance of environment over geography.

I learned that resistance distance measures may not be the appropriate method for evaluating the effects of distance on headwater communities, as Euclidean distance, despite not accounting for the spatial components of differing habitat types, outperformed both the landscape and network resistance measures developed for this project. Of the two resistance measures, however, landscape resistance better integrates the effects of space and environment on species turnover in both communities. Finally, I suggest that the poor performance of these measures may be due to incompatibilities in scale between the ecological and spatial processes governing turnover in headwater communities, and the sampling regime employed to monitor the ecological health of stream ecosystems in Maryland.

5.1 Opportunities for future research

Although this study examines the phenomenon of stream burial to a greater extent than previous efforts, there remain plenty of open questions in regards to the extent and severity of stream burial across the landscape, and its effects on ecosystem function. There are several topics that could be expanded, and gaps in our knowledge about aspects of stream burial that warrant further investigation, including:

- Examination of trends in burial distribution and the rate of stream burial across time, to better discern how burial has proceeded in relation to physiographic constraints, and related effects to ecosystem structure and function across developing watersheds

- Critical analyses of development policies across urbanizing counties, to identify and develop more effective protection policies for headwater streams
- Further research investigating the relationships between landscape resistance and the total amount and spatial distribution of land cover/resistance classes both in-stream, and across upland landscapes
- Additional research on dispersal processes in headwater communities across various land cover types, to better understand spatial and environmental processes for development of better measures of resistance distance
- Develop modified sampling regimes to match the scale of biological monitoring to that of potentially critical spatial processes in headwater systems

In order to maintain a balance between future urban growth and ecosystem health, it is critical for managers to have access to and understand the cumulative effects of stream burial,

Collectively, these findings lay the groundwork for a more complete understanding of the consequences of stream burial on the structural aspects of stream networks, and the potential ramifications for biodiversity and ecosystem function within headwater systems and downstream waters.

Appendices

A.1 Expert review materials and summary of landscape resistance classification by stream order and land cover type for the Potomac River Basin study area

The following pages contain the outreach document forwarded to subject area experts to obtain review of an initial landscape resistance classification by stream order and land cover class (NLCD 2006, Table 1) the Potomac River Basin. Experts were identified through similar work in the literature, and by subsequent recommendation by those approached for review. A total of 10 potential reviewers were contacted, with 5 reviewers (50%) providing responses (Table 2). Reviewers were provided basic background information on circuit theory and the Circuitscape model (McRae et al. 2008), including the theory of ‘isolation by resistance (McRae 2006), and asked to rank and value stream orders and landcover classes by their relative resistance to the movement of winged-adult aquatic insects across the landscape.

A preliminary resistance classification (see RED values in the ‘Worksheet’ included below) was provided, based on my review of the existing literature on movement of aquatic insects through various land cover types, including natural, agricultural, and urban settings. Potential reviewers were asked to react to this initial classification by altering the numbers to match their understanding of the relative favorability of different habitat types, including justification of their decisions where possible.

Three reviewers did not feel confident providing a resistance ranking by stream order, two of which also declined to provide resistance values for stream order. One reviewer failed to provide resistance ranks or values for the Grassland/Herbaceous and Shrub/Scrub land cover classes, therefore, average values for these cover classes are based on the values provided by the other 4 reviewers. Final value assignments were based on these rankings, with consideration of additional comments provided by reviewers, and the best professional judgement of the author.

A1.1 Classifying the resistance of streams and land cover to movement by adult aquatic insects

Traditional network models that treat streams as simple, linear networks are insufficient to represent key ecological features of headwater stream systems, where energy and organisms flow not only within and along the stream channel, but laterally across the terrestrial landscape to adjacent streams and watersheds. I am working to develop an aquatic connectivity model, from the perspective of adult aquatic insects, that considers both movement components, using a circuit-theoretical model (Circuitscape; McRae et al. 2008) that treats the landscape as an electrical circuit, passing ecological ‘current’ through a series of landscape ‘resistors’ between focal habitat patches.

Borrowing algorithms from engineering models that predict electricity flow through circuits, circuit theory utilizes the principle of ‘isolation by resistance’ (McRae 2006) to quantify how habitat connectivity is affected by environmental

characteristics of the landscape. In the model, landscapes are represented as conductive surfaces (Figure 1, left panel) with ‘habitat’ more permeable to individual movement assigned low resistance, and less-permeable habitat types and barriers to movement assigned high resistance. Total (effective) resistance of the landscape (the “resistance distance”) between any two headwater stream reaches represents a measure of connectivity for those two reaches (McRae et al. 2008). In addition to numerical measures of effective resistance between individual stream reaches and/or systems, resulting “cumulative current” maps can be visualized in GIS (Figure 1, right panel), allowing users to effectively “see” the landscape through the eyes of a dispersing organism.

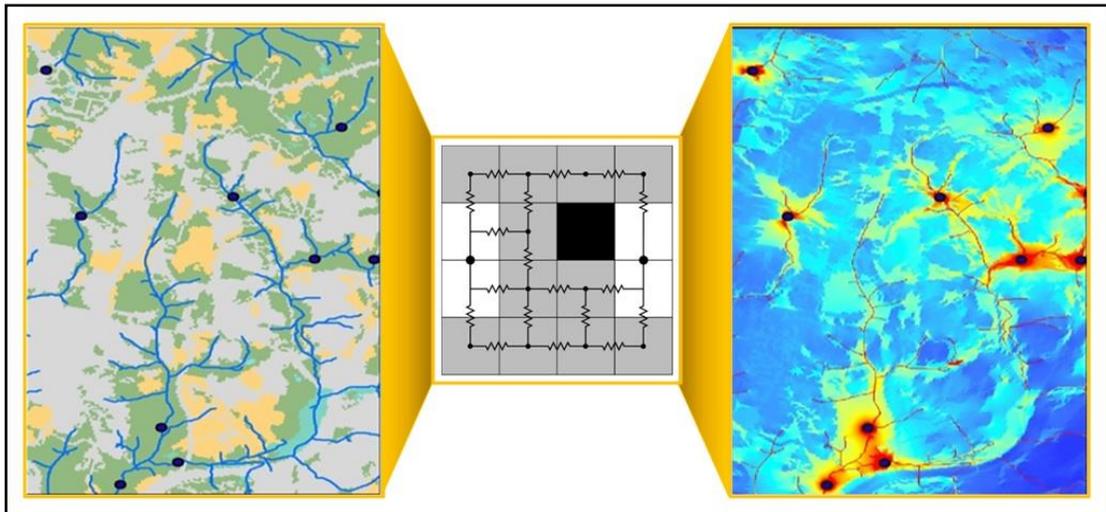


Figure 1: Land cover and streams (left panel) are assigned resistance values based on their relative permeability to organism movement. Circuitscape treats the landscape like an electrical circuit (center panel, adapted from McRae *et al.* 2008), passing current through a series of variable resistors (land cover pixels) between two or more focal habitat patches (black circles). Cumulative current flow through the landscape can be mapped (right panel), with current densities through cells indicating the probability of an organism passing each cell

Key to a successful model is the accurate assignment of resistance values to the various ‘habitat’ types within the study area. For this exercise, the habitat layer

will consist of the 2006 National Land Cover Dataset (30m res, resampled to 10m; Fry et al. 2011), overlaid with improved headwater stream maps (10m res; Elmore et al. 2013) to create a seamless habitat raster. Once combined, each habitat pixel will be assigned a resistance value (0% - 100%) based on its relative favorability to movement of adult aquatic insects, identified from the literature to the extent possible. Due to a lack of empirical data on movement/dispersal for most species, across most habitat types, additional expert input/review is essential to achieve the appropriate assignment of resistance values. This is where you come in.

Attached, you will find a list of the NLCD classes and the range of stream sizes (Strahler order) found within the study area (Worksheet 1). Written descriptions of each land cover class can be found in Table 1. I am interested in obtaining input, based on your knowledge and experience, as to the resistance (both rank and a relative value) to aquatic insect movement for each stream size and habitat type. While diversity and dispersal mechanisms/abilities are highly variable in the study communities, we plan to use the resistance output in community-level modeling exercises. With this in mind, for the purposes of this study, the resistance classification should be developed with a ‘generalized’ aquatic insect species in mind.

I have developed a preliminary classification based on the very limited empirical data available, and in consultation with a couple of other colleagues. My rankings and resistance classification are indicated in **RED** on the attached worksheet. I ask that you consider my preliminary classification with the two tasks and associated questions in mind, listed below. Once adequate feedback is obtained, I

will create a final classification based on the general consensus of the expert review of my initial classification.

Please feel free to contact with questions or additional discussion points, and thank you very much for your input. Any assistance provided will be duly acknowledged in my dissertation and all resulting publications.

A1.2 Reviewer tasks/questions

- 1) Rank streams as to their relative resistance to movement of adult insects, by stream size (order).
 - a. Should all streams be ranked with the same resistance, or should certain sized streams have less/more resistance?
 - b. How should resistance values for stream habitats compare with open water habitats (e.g., lakes, large rivers) and wetlands (e.g., emergent and woody wetland categories) that appear in the NLCD?
- 2) Rank NLCD land cover classes by relative resistance to movement (use attached worksheet).
 - a. Should similar cover types (e.g., forest categories) be assigned the same resistance value? Are there other categories (e.g., agricultural land cover types) that can be collapsed into a single resistance class, based on similar favorability for insect movement?
 - b. Please provide a 'rank' value to each class or category, from least to most resistant, as well as an 'absolute' resistance value for each, with values between 0 and 100%.

- 3) Recommend additional reviewers and/or resources that may be helpful with these questions

A1.3 References

Fry, J, Xian, G, Jin, S, Dewitz, J, Homer, C., Yang, L, Barnes, C, Herold, N, and Wickham, J, 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States. *PE&RS* 77(9):858-864.

McRae, BH. 2006. Isolation by resistance. *Evolution* 60(8):1551-1561

McRae, BH, BG Dickson, TH Keitt, and VB Shah. 2008. Using circuit theory to model connectivity in ecology and conservation. *Ecology* 10: 2712-2724

A1.4 Worksheet: Land cover classification by resistance

Stream order

	<u>Rank</u> (low-high)	<u>Value</u> (0% - 100%)
1	1	2
2	2	2
3	3	2
4	4	5
5	5	5
6	6	5
7	7	5
8	8	5

NLCD Class (descriptions in Table 1)

(0% - 100%)	<u>Rank</u> (low-high)	<u>Value</u>
Open water	1	5
Emergent herbaceous wetland	2	10
Woody wetlands	3	10
Deciduous forest	4	25
Evergreen forest	5	25
Mixed forest	6	25
Grassland/Herbaceous	7	30
Shrub/Scrub	8	30
Barren land	9	40
Pasture/hay	10	40
Cultivated crops	11	50
Developed/open space	12	50
Developed/low intensity	13	70
Developed/medium intensity	14	80
Developed/high intensity	15	90

A1.5 Category descriptions for the 2006 National Land Cover Database (Fry et al. 2011)

Class \ Value	Classification Description
Water	
11	Open Water - areas of open water, generally with less than 25% cover of vegetation or soil.
12	Perennial Ice/Snow - areas characterized by a perennial cover of ice and/or snow, generally greater than 25% of total cover.
Developed	
21	Developed, Open Space - areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20% of total cover. These areas most commonly include large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.
22	Developed, Low Intensity - areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20% to 49% percent of total cover. These areas most commonly include single-family housing units.
23	Developed, Medium Intensity - areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50% to 79% of the total cover. These areas most commonly include single-family housing units.
24	Developed High Intensity -highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses and commercial/industrial. Impervious surfaces account for 80% to 100% of the total cover.
Barren	
31	Barren Land (Rock/Sand/Clay) - areas of bedrock, desert pavement, scarps, talus, slides, volcanic material, glacial debris, sand dunes, strip mines, gravel pits and other accumulations of earthen material. Generally, vegetation accounts for less than 15% of total cover.
Forest	
41	Deciduous Forest - areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change.
42	Evergreen Forest - areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.
43	Mixed Forest - areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of total tree cover.
Shrubland	
51	Dwarf Scrub - Alaska only areas dominated by shrubs less than 20 centimeters tall with shrub canopy typically greater than 20% of total vegetation. This type is often co-associated with grasses, sedges, herbs, and non-vascular vegetation.
52	Shrub/Scrub - areas dominated by shrubs; less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation. This class includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions.
Herbaceous	
71	Grassland/Herbaceous - areas dominated by graminoid or herbaceous vegetation, generally greater than 80% of total vegetation. These areas are not subject to intensive management such as tilling, but can be utilized for grazing.
72	Sedge/Herbaceous - Alaska only areas dominated by sedges and forbs, generally greater than 80% of total vegetation. This type can occur with significant other grasses or other grass like plants, and includes sedge tundra, and sedge tussock tundra.
73	Lichens - Alaska only areas dominated by fruticose or foliose lichens generally greater than 80% of total vegetation.
74	Moss - Alaska only areas dominated by mosses, generally greater than 80% of total vegetation.
Planted/Cultivated	
81	Pasture/Hay - areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle. Pasture/hay vegetation accounts for greater than 20% of total vegetation.
82	Cultivated Crops - areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20% of total vegetation. This class also includes all land being actively tilled.
Wetlands	
90	Woody Wetlands - areas where forest or shrubland vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.
95	Emergent Herbaceous Wetlands - Areas where perennial herbaceous vegetation accounts for greater than 80% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.

A1.6 Rank and resistance values provided by reviewers for stream and land cover classification units

Classification Unit	Reviewer 1		Reviewer 2		Reviewer 3		Reviewer 4		Reviewer 5		Average Value	Final Value
	Rank	Value										
Stream Order												
1	1	-	3	30	1	2	-	-	-	-	-	2
2	1	-	2	15	2	2	-	-	-	-	-	2
3	2	-	1	10	3	2	-	-	-	-	-	2
4	2	-	4	50	4	5	-	-	-	-	-	5
5	3	-	5	60	5	5	-	-	-	-	-	5
6	3	-	6	65	6	5	-	-	-	-	-	5
7	4	-	7	70	7	5	-	-	-	-	-	5
8	4	-	8	80	8	5	-	-	-	-	-	5
NLCD Class												
Open water	1	10	1	5	1	5	2	29	1	5	11	10
Emergent herbaceous wetland	2	10	3	15	2	10	2	29	2	10	15	10
Woody wetlands	3	10	2	12	3	10	1	14	3	10	11	10
Deciduous forest	8	40	5	20	4	25	3	43	4	25	31	25
Evergreen forest	9	40	6	25	5	25	3	43	5	25	32	25
Mixed forest	10	40	4	17	6	25	3	43	6	25	30	25
Grassland/Herbaceous	4	20	-	-	7	30	4	57	7	30	34	30
Shrub/Scrub	5	20	-	-	8	30	4	57	8	30	34	30
Barren land	6	20	9	51	9	40	4	57	11	50	44	40
Pasture/hay	7	20	7	40	10	40	5	71	9	40	42	40
Cultivated crops	11	50	8	50	11	50	5	71	10	40	52	50
Developed/open space	12	60	10	52	12	50	6	86	12	50	60	50
Developed/low intensity	13	60	11	58	13	70	7	100	13	70	72	65
Developed/medium intensity	14	70	12	60	14	80	7	100	14	80	78	75
Developed/high intensity	15	80	13	65	15	90	7	100	15	90	85	90

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