Piedmont Alluvial Vegetation:
Classification, Geographic Variation, and Restoration

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Abstract

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(Under the direction of Robert K. Peet)

Riparian ecosystems are home to diverse and highly productive plant communities, long known to be among the more species-rich terrestrial communities. However, few pristine riparian systems remain, particularly in North America. Due to their ecological significance and their current imperiled status, there is substantial interest in conservation and restoration of riparian habitat in the Southeastern United States. Successful conservation and restoration require detailed information regarding the composition and structure of natural floodplain plant communities, in addition to an understanding of the environmental drivers associated with compositional variation. While southeastern alluvial vegetation has been well-studied, most studies have focused on the larger rivers of the Coastal Plain region, rather than the relatively smaller streams of the topographically more complex inland Piedmont. In fact, there is relatively little documentation or understanding of Piedmont bottomland vegetation in North Carolina or elsewhere on the Southeastern Piedmont.

This dissertation advances our understanding of Piedmont alluvial vegetation by documenting and describing vegetation patterns and environmental drivers in this system. This work provides the vital information that is necessary both for successful management of alluvial habitat and for restoration of degraded alluvial vegetation. As part of this work, I sampled high-quality alluvial vegetation in five North Carolina river basins: the Catawba,

Yadkin-Pee Dee, Cape Fear, Neuse, and Tar-Pamlico. As a first step towards advancing our understanding of these systems, I developed a vegetation classification of the Piedmont alluvial plant communities in North Carolina. I expect this classification will provide guidance for revising Piedmont alluvial plant community concepts currently recognized in the U.S. National Vegetation Classification. I also explored the spatial distribution of plant species richness across the Piedmont riparian landscape and examined compositional variation in a metacommunity context, quantifying the relative influence of niche-processes and dispersal-processes in shaping riparian plant community composition. I found that niche-processes are dominant in this system, with environmental variables explaining more variation in community composition than spatial structure. Finally, I developed an approach for using quantitative vegetation descriptions to develop reference information for riparian restoration efforts. Because these communities are strongly structured by environmental variables, I was able to develop a matching tool to link restoration sites to described vegetation types based on environmental similarity. In all, I expect the work described in this dissertation to improve management and restoration outcomes for alluvial plant communities in the North Carolina Piedmont.

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CHAPTER 1
Introduction: Piedmont brown-water alluvial vegetation

Introduction

Riparian areas are known to be diverse and highly productive systems, functioning as both boundaries between terrestrial and aquatic ecosystems and corridors for the movement of nutrients and biota across the natural landscape (Gregory et al. 1991; Naiman et al. 1993; Johansson et al. 1996). Floodplain plant communities, in particular, have been shown to be among the more species-rich terrestrial habitats (Nilsson et al. 1989; Naiman et al. 1993; Brown and Peet 2003). In addition to the ecological value of these communities, riparian areas also provide many ecosystem services to the human population, including filtration of pollutants, flood and erosion control, carbon storage, fish and wildlife habitat, and a wide variety of recreational opportunities. However, few pristine riparian ecosystems remain in the Southeastern United States (Sharitz and Mitsch 1993; Sudduth et al. 2007). Many riparian landscapes have been converted to agriculture, damaged by impoundments and hydrologic alterations, or degraded by non-native invasion, eutrophication, and urban development (Sharitz and Mitsch 1993; Graf 1999; Brinson and Malvarez 2002; Tockner and Stanford 2002; King et al. 2009). In fact, only 2% of river kilometers in the United States remain relatively unimpacted (Abell et al. 2000), and floodplain ecosystems are considered to be among the most threatened ecosystems globally (Tockner and Stanford 2002).

North Carolina's rivers have not escaped these trends. As residential and commercial development keep pace with the growing North Carolina population, waterways continue to

face new threats, particularly in the rapidly developing Piedmont region. According to the U.S. Census Bureau, four North Carolina Piedmont cities are among the 25 fastest growing U.S. cities: Cary, Raleigh, Charlotte, and Durham (U.S. Census Bureau 2008), and the effects of this growth on our water resources are already evident. The American Rivers organization has identified two North Carolina rivers as being among America's most endangered rivers: the Catawba (#1 most endangered; 2008) and the Neuse (#8 most endangered; 2007). The Rivers of Life publication, produced by The Nature Conservancy and various non-profit and state agency partners, also listed two North Carolina rivers, the Neuse and the Tar, as hot-spots for at-risk freshwater species (Masters et al. 1998).

As a result of the growing threats to riparian systems and the increasing recognition of the ecological importance and imperiled status of these systems, there is significant interest among the scientific community, government agencies, and the general public in the management and restoration of floodplain ecosystems (Wohl et al. 2008; King et al. 2009). River restoration has become an increasingly common approach to management (Bernhardt et al. 2005; Bernhardt et al. 2007), and North Carolina is a hotspot for stream restoration in the Southeastern U.S. (Sudduth et al. 2007). However, informed management decisions, restoration project design, and restoration evaluation all require detailed information regarding the composition and structure of natural floodplain communities, in addition to an understanding of the environmental drivers associated with compositional variation.

Although riparian ecosystems of the Southeastern United States have been the focus of many past studies (e.g., Wharton et al. 1982; Hupp and Osterkamp 1985; Hodges 1997; Kellison et al. 1998; Hupp 2000; Townsend 2001), few authors have addressed the floodplain plant communities of the inland physiographic regions Piedmont (except see Hupp and

Osterkamp 1985; Hupp 1986), and relatively little is known about these plant communities. The alluvial vegetation of the North Carolina Piedmont region, in particular, has not previously been well-documented nor described, and the relationship between alluvial vegetation and the Piedmont riparian landscape remains poorly understood. The current understanding of these floodplain plant communities is based primarily on qualitative vegetation descriptions, with little or no quantitative data supporting the descriptions (e.g., Classification of the Natural Communities of North Carolina, Third Approximation; Schafale and Weakley 1990).

Data-based, quantitative community classifications are a critical tool for the conservation, management, and restoration of natural communities, providing the detailed floristic and environmental information necessary for successful management action. Standardized classifications, based on uniform criteria for distinguishing units, facilitate communication among conservation and land management agencies, advance basic scientific understanding of vegetation patterns, and provide reference information for restoration (Faber-Langendoen et al. 2007; Lane and Texler 2009; Jennings et al. 2009). The collection of quantitative vegetation plot data is a crucial step in the process of developing vegetation descriptions; the U.S. National Vegetation Classification (NVC), in fact, requires vegetation associations and alliances be documented by field plot data, ideally "collected across the range of a vegetation type and closely related types, irrespective of political borders" (Jennings et al. 2009).

In the research program summarized in this dissertation, my initial goal was to document the remaining high-quality floodplain vegetation of the North Carolina Piedmont and to collect the quantitative vegetation data necessary to characterize vegetation patterns of

this region. To this end, I sampled vegetation in five North Carolina river basins: the

Catawba, Yadkin-Pee Dee, Cape Fear, Neuse, and Tar-Pamlico. In Chapter 2, I use these data

to develop a classification and description of the alluvial plant communities of the North

Carolina Piedmont as a first step towards advancing our understanding of these systems.

Each subsequent chapter is intended to further expand our understanding of Piedmont

riparian plant communities and inform future conservation and restoration efforts. In addition

to the classification presented in Chapter 2, I explore the spatial distribution of plant species

richness across the Piedmont riparian landscape and examine the relative influence of niche

and dispersal processes in shaping riparian plant community composition. Finally, I develop

an approach for applying quantitative vegetation descriptions to riparian restoration

activities. It is my hope and expectation that the chapters of this dissertation will provide

critical information necessary for effective conservation and restoration of North Carolina

Piedmont alluvial vegetation.

Chapter Summaries

In Chapter 2, I present a classification and description of the North Carolina Piedmont

alluvial plant communities. I develop a hierarchical classification, with five higher-level

groups representing broad geomorphic-floristic conditions across the Piedmont and fourteen

lower-level groups characterizing finer-scale floristic variation. I use constrained ordination

to illustrate the environmental setting of the higher-level forested vegetation groups. For each

of the finer-scale groups, I present a summary of floristic composition, structure,

environmental setting, and geographic distribution. I also present a comparison of the

vegetation types developed in this chapter with the currently recognized NVC communities,

a comparison that suggests a need for revision and reworking of the currently recognized NVC alluvial type concepts.

In Chapter 3, I examine the distribution of plant species richness across the Piedmont riparian landscape. Although riparian systems are known to be species-rich, there is substantial debate in the literature about the spatial distribution of this diversity. The unique habitat arrangement of riparian systems is a crucial factor to consider when exploring richness patterns, as riparian habitat is not a simple linear system, but instead is composed of different sized channels that coalesce to create a dendritic landscape structure. In this chapter, I examine richness across rivers of various sizes in the dendritic riparian landscape, and explore how different species groups contribute to these patterns.

In Chapter 4, I examine compositional variation of alluvial plant communities in a metacommunity framework. I explore how riparian connectivity influences the relative role of niche processes and dispersal processes in shaping community composition. I explore riparian connectivity by examining metacommunity structure at two landscape scales and in four species groups based on dispersal mode, each spatial scale and dispersal mode representing different levels of connectivity. I also investigate the importance of the spatial model in analyzing riparian metacommunity structure, using both Euclidean distance based spatial models, representing overland dispersal, and network distance based spatial models, representing dispersal through the riparian corridor.

Finally, in Chapter 5, I develop an approach for utilizing quantitative vegetation descriptions, such as those presented in Chapter 2 and currently being developed in the U.S. National Vegetation Classification, in the design of reference conditions for riparian restoration projects. I first outline a methodology for matching new restoration sites to

quantitative plant community descriptions based upon their environmental setting and then present a matching tool developed using the Piedmont alluvial vegetation classification and North Carolina-Ecosystem Enhancement Program (EEP) restoration sites as a case study.

I conclude by synthesizing results presented in this dissertation and discussing how this work has advanced our understanding of Piedmont brown-water vegetation. Additionally, I suggest places where gaps in our knowledge remain, important future research areas to achieve successful management of riparian systems.

References

Abell, R.A., Olson, D.M., Dinerstein, E., Hurley, P.T., Diggs, J.T., Eichbaum, W., Walters, S., Wettengel, W., Allnutt, T., Loucks, C.J., and P. Hedao. 2000. Freshwater ecoregions of North America: a conservation assessment. Island Press, Washington D.C.

Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B., and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636- 637.

Bernhardt, E.S., Sudduth, E.B., Palmer, M.A., Allan, J.D., Meyer, J.L., Alexander, G., Follastad-Shah, J., Hassett, B., Jenkinson, R., Lave, R., Rumps, J., and L. Pagano. 2007. Restoring rivers one reach at a time: results from a survey of U.S. river restoration practitioners. Restoration Ecology 15: 482-493.

Brinson, M.M, and A.I. Malvarez. 2002. Temperate freshwater wetlands: types, status, and threats. Environmental Conservation 29: 115-133.

Brown, R. L. and R.K. Peet. 2003. Diversity and invasibility of Southern Appalachian plant communities. Ecology 84: 32-39.

Faber-Langendoen, D., Aaseng, N., Hop, K., Lew-Smith, M., and J. Drake. 2007. Vegetation classification, mapping, and monitoring at Voyageurs National Park, Minnesota: An application of the U.S. National Vegetation Classification. Applied Vegetation Science 10: 361-374.

Graf, W.L. 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research 35: 1305-1311.

Gregory, S.V., Swanson, F.J., McKee, S.W., and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41: 540-551.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest ecology and management 90:117-125.

Hupp, C.R. and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.

Hupp, C.R. 1986. Upstream variation in bottomland vegetation patterns, Northwestern Virginia. *Bulletin of the Torrey Botanical Club* 113: 421-430.

Hupp, C.R. 2000. Hydrology, geomorphology and vegetation of Coastal Plain rivers in the south-eastern USA. Hydrological Processes 14, 2991-3010.

Jennings, M.D., Faber-Langendoen, D., Loucks, O.L., Peet, R.K. and D. Roberts. 2009. Standards for associations and alliances of the U.S. National Vegetation Classification. *Ecological Monographs* 79: 173-199.

Johansson, M.E., Nilsson, C., and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? Journal of Vegetation Science 7: 593-598.

Lane, C.P. and Texler, H.D. 2009. Generating quantitative regional plant community descriptions for restoration. *Restoration Ecology* 17: 42-50.

Kellison, R.C., Young, M.J., Braham, R.R., and E.J. Jones. 1998. Major alluvial floodplains. In: Messina, M.G., and Conner, W.H. (eds.) *Southern Forested Wetlands: Ecology and Management,* pp. 291-324. Lewis, Boca Raton, Florida, USA.

King, S.L., Sharitz, R.R., Groninger, J.W., and L.L. Battaglia. 2009. The ecology, restoration, and management of southeastern floodplain ecosystems: a synthesis. Wetlands 29: 624-634.

Masters, L. L., S.R. Flack and B.A. Stein, eds. 1998. *Rivers of Life: Critical Watersheds for Protecting Freshwater Biodiversity*. The Nature Conservancy, Arlington, Virginia.

Naiman, R.J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3: 209-212.

Nilsson, C., G. Grelsson, G. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. Ecology 70:77-84.

Schafale, M.P., and A.S. Weakley. 1990. Classification of the Natural Communities of North Carolina (Third Approximation). Natural Heritage Program, Raleigh, N.C. 325 pp. http://www.ncnhp.org/Images/Other%20Publications/class.pdf

Sharitz, R.R. and W.J. Mitsch. 1993. Southern floodplain forests. In: Martin, W.H., S.G. Boyce, and A.C. Echternacht, eds. *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities.* Wiley and Sons, New York, pp.311-372.

Sudduth, E.B., Meyer, J.L., and E.S. Bernhardt. 2007. Stream restoration practices in the Southeastern United States. Restoration Ecology 15: 573-583.

Tockner, K., and J.A. Stanford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation 29: 308-330.

Townsend, P.A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. Plant Ecology 156: 43-58.

U.S. Census Bureau. Fastest Growing Cities in 2008.
www.census.gov/newsroom/releases/xls/cb09-99_Table1.xls. Accessed on 19 October,
2010.

Wharton, C.H., Kitchens, W.M., Pendleton, E.C., and T.W. Sipe. 1982. The ecology of
bottomland hardwood swamps of the southeast: A community profile. U.S. Fish and
Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37.
133 pp.

Wohl, E., Palmer, M.A., and G.M. Kondolf. 2008. River Management in the United States.
In Brierley, G.J. and K.A. Fryirs, eds. *River Futures: An Integrative Scientific
Approach to River Restoration.* Island Press, Washington, D.C.

CHAPTER 2

Classification and description of alluvial plant communities of the Piedmont region, North Carolina, U.S.A.

Abstract

Floodplain ecosystems have long been known to be diverse and highly productive communities. Despite their ecological significance, there is relatively little documentation or understanding of bottomland vegetation types in North Carolina or elsewhere on the Southeastern Piedmont. As population growth and continued development disturb larger areas of the North Carolina Piedmont, ecosystem restoration activities are becoming more common, and the need for detailed knowledge of vegetation composition and structure is becoming more critical. However, our current understanding of these brownwater bottomlands is based primarily on qualitative data, and there has been no comprehensive, data-based classification and description of these community types. A detailed vegetation classification can provide the vital information needed for effective restoration and conservation of North Carolina bottomland plant communities.

In this chapter, I present a classification and description of the Piedmont alluvial vegetation communities found in North Carolina. I inventoried 194 alluvial vegetation plots in the Catawba, Yadkin-PeeDee, Cape Fear, Neuse, and Tar-Pamlico River Basins. Vegetation types were derived using flexible-β hierarchical cluster analysis and random

forests classifiers to reassign misclassified plots. I identified fourteen vegetation types, including twelve forested vegetation types and two herbaceous types, nested within a hierarchical classification structure with five higher-level groups. The five higher-level groups describe broad geomorphic-floristic conditions, whereas the narrower vegetation types characterize finer-scale floristic variation. I used Canonical Correspondence Analysis to differentiate and characterize the environmental setting of the vegetation groups, providing a useful framework within which to compare the environmental settings of the four forested higher-level groups. For each of the four upper-level forest groups and the fourteen association-level types, I present a summary of floristic composition, structure, environmental setting, and geographic distribution. I suggest recognition of fourteen alluvial vegetation types in the North Carolina Piedmont. The major patterns of alluvial vegetation in this region are driven by fluvial geomorphology and are strongly correlated with stream size, floodplain width, and soil texture and nutrients.

Introduction

     Riparian ecosystems are home to diverse plant communities, in part due to the diversity of habitats found in this landscape. Floodplain plant communities, in particular, have long been known to be among the more species-rich terrestrial habitats (Nilsson et al. 1989; Gregory et al. 1991; Naiman et al. 1993, Brown and Peet 2003). In addition to the ecological value of these communities, floodplain vegetation provides many "ecosystem services" to the human population including filtration of pollutants, flood and erosion control, fish and wildlife habitat, and a variety of recreational opportunities. However, few pristine riparian ecosystems remain, particularly in North America (Sharitz and Mitsch 1993). Many of these landscapes have been converted to agriculture, damaged by impoundments, or degraded by the invasion of non-native species.

     Due to the ecological significance of floodplain ecosystems and their current imperiled status, there is significant interest in conservation and restoration of these habitats, and North Carolina, in particular, is a hotspot for riparian restoration in the Southeastern United States (Sudduth et al. 2007). However, informed management decisions and restoration project design and evaluation require detailed information regarding the composition and structure of natural alluvial plant communities, in addition to an understanding of the environmental drivers associated with compositional variation. Plant community classifications and descriptions can provide the detailed vegetation information necessary for many applications including facilitation of communication between conservation and land management agencies, advancing basic scientific understanding of vegetation patterns, and providing reference information for planning and assessing the

success of restoration activities (Harris 1999; Faber-Langendoen et al. 2007; Lane and Texler 2009; Jennings et al. 2009).

Whereas vegetation classification has a long history in Europe (Rodwell 1991, Rodwell et al. 1995), a national-scale classification has been slower to develop in the United States (Jennings et al. 2009). Although the U.S. National Vegetation Classification (NVC) is currently in development in an effort to meet the needs of the conservation and restoration communities in the U.S., most of the vegetation types currently recognized by the NVC have not yet been evaluated using quantitative floristic data and lack accessible plot data and summary tables (Jennings et al. 2009). In particular, previous documentation of floodplain vegetation in North Carolina, and elsewhere on the Southeastern Piedmont, is extremely limited.

Alluvial vegetation patterns of the Southeastern United States have been studied by many plant ecologists (e.g., Wharton et al. 1982; Hupp and Osterkamp 1985; Hupp 1986; Hodges 1997; Kellison et al. 1998; Hupp 2000; Townsend 2001), but most of these studies have focused on the larger rivers of the Coastal Plain region, rather than the relatively smaller streams of the topographically more complex inland Piedmont (except see Hupp and Osterkamp 1985; Hupp 1986). These previous Coastal Plain studies of southeastern alluvial vegetation found a strong relationship between bottomland vegetation and fluvial geomorphic processes and landforms. Wharton et al. (1982) emphasized the anaerobic gradient generated by hydroperiod on floodplains as the dominant driver of vegetation patterns in bottomland hardwood swamps, with soil pH and nutrient availability as secondary drivers. Hodges (1997) presented hydrologic events and the resulting patterns of deposition across the floodplain as the primary drivers of floristic composition and successional patterns

in Coastal Plain bottomland hardwoods. He also noted that patterns of deposition across floodplains are closely related to topographic features and result in a predictable distribution of soil texture and nutrient content. Hupp (2000) also emphasized the importance of hydrologic events in controlling the development of fluvial landforms and sediment deposition, which then determine vegetation patterns. In contrast to Coastal Plain rivers, however, Piedmont rivers are restricted by resistant bedrock, constraining the width of the floodplain and the development of topographic features and fluvial landforms. This may result in less species sorting than has been found along the strong hydrogeomorphic gradient evident in many Coastal Plain systems. As Hodges (1997) points out, in the narrower floodplains of the upper Coastal Plain there is less variation in soil texture and drainage class than one finds in the larger-order rivers of the outer Coastal Plain.

Although alluvial vegetation patterns of Coastal Plain rivers have been well-studied, the relationship between alluvial vegetation and the Piedmont floodplain landscape remains poorly understood and described. My goal was to document the remaining high-quality floodplain vegetation of the North Carolina Piedmont and to collect the quantitative vegetation data necessary to define and characterize the patterns in alluvial vegetation of this region. Here I present a classification and description of the alluvial plant communities of the North Carolina Piedmont based on 194 vegetation plots sampled in the Catawba, Yadkin-PeeDee, Cape Fear, Neuse, and Tar-Pamlico River Basins (Figure 2.1). I also describe the geographic distribution, geomorphic and hydrologic setting, and edaphic characteristics associated with each vegetation type to clarify the relationship between the Piedmont floodplain landscape and alluvial vegetation. I expect these results will provide the

information necessary to inform revisions of the NVC, guide management decisions, and generate appropriate restoration targets in the NC Piedmont region.

Methods

Study area

The study area included five contiguous North Carolina river basins: the Catawba, Yadkin, Cape Fear, Neuse, and Tar-Pamlico. The study area also includes the northern section of the Catawba River basin in South Carolina (Figure 2.1). I restricted study sites to the Piedmont portion of each river basin, as defined by mapped geologic and soil units. The Piedmont is one of three physiographic regions in North Carolina. It is underlain by metamorphic and igneous bedrock and bounded on the northwest by the Southern Appalachian Mountains and on the southeast where crystalline Piedmont bedrock meets the softer sedimentary bedrock of the Southeastern Coastal Plain. Although Piedmont bedrock is largely composed of erosion-resistant metamorphic and intrusive igneous rocks, a large southwest-northeast trending rift basin composed of Triassic sedimentary rock is a prominent geologic feature of the lower Piedmont (Benedetti et al. 2006). Where Piedmont rivers cross the more resistant igneous and metamorphic bedrock, the resulting river valleys are relatively narrow and incised, whereas in the Triassic Basins Piedmont rivers are better able to erode the softer sedimentary rock, resulting in wider floodplains (though still somewhat more constrained than in the unconsolidated sediments of the Coastal Plain).

There has been a long history of human disturbance in the North Carolina Piedmont, with the most extensive alteration of native forest vegetation occurring after European colonization. Although fertile, arable lands were most affected, even vegetation on land

unfavorable for cultivation has been altered by selective tree harvesting (Peet and

Christensen 1980). Bottomland habitat in the Piedmont that was not converted to agriculture

during European settlement was subject to this selective harvesting.

Site selection

Because I anticipate this classification will be used in the development of restoration

targets, I aimed to sample high-quality alluvial vegetation, defined as stands with minimal

recent natural disturbance (e.g. treefall gaps), minimal anthropogenic disturbance (e.g. ≥ 50

years since harvest), and minimal cover contributed by exotic species. However riparian

areas are known to be highly invaded (Brown and Peet 2003), and many stands included in

the dataset had high exotic species cover. Since large extents of the natural riparian

vegetation in the Piedmont region have been subject to anthropogenic disturbances, one of

the most important steps in collecting data for this project was the identification of remaining

patches of high-quality floodplain vegetation. This was accomplished with assistance from

state agencies and non-profit, conservation organizations, which track natural areas of the

state.

After I identified areas of remaining high-quality natural vegetation, I selected

sample sites to ensure representation from a broad geographic area within each of five river

basins. I also selected sites to provide a broad representation of various geologic features,

stream order, watershed area, and geomorphic setting. However, because high-quality

alluvial vegetation is rare in the highly fragmented and disturbed North Carolina Piedmont, I

sampled the majority of high-quality sites that were identified. At sample sites, plots were

located haphazardly, in representative, homogenous vegetation, with the intent of capturing

high-quality vegetation and a single geomorphic setting. In total, I established and recorded 194 vegetation plots (Figure 2.1).

Field Methods

I surveyed vegetation in May-August, 2006-2008, following the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Six alluvial plots surveyed by CVS prior to the 2006-2008 field seasons were exported from the archived CVS database and included in this dataset. Forested plots ranged in size from $400m^2$ (typically 20m × 20m) to $1000m^2$ (typically 20m × 50m), depending upon the width of the floodplain. The fourteen strictly herbaceous vegetation plots were $100m^2$. Within each plot, cover was estimated for all vascular plant taxa in intensive subplots ($100m^2$) following the CVS cover class scale (1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, 10 = >95%); all forested plots included four $100m^2$ intensive subplots. Cover by strata was also estimated for each taxon at the scale of the whole plot; strata include tree (>5m to canopy height), shrub (0.5 to 5m), and herb (0 to 0.5m) strata, although the height ranges of strata could be adjusted in the field to reflect local vegetation structure. Cover by strata better reflects the size and structure of the vegetation than a single cover value. Woody species reaching breast height were tallied by CVS size classes.

Plots were oriented with the long axis parallel to the longitudinal axis of the river in an effort to maintain a constant geomorphic setting. Sample sites on 1st and 2nd order streams, where geomorphology is poorly developed and there are not clear distinctions between geomorphic positions, were identified as *small stream floodplains*. Sites on larger streams were identified to one of five geomorphic positions: *rocky bar and shore* (within the river channel inside any levee structure); *levee* (the area of the floodplain closest to the river,

running parallel to the flow direction, and often slightly raised); *backswamp* (farther from the river channel, beyond the levee, and flooded for longer periods of time when compared to other geomorphic settings); *flat* (typically parallel to a levee or the actual levee in smaller rivers in the place of a true raised levee, generally intermediate to or intergrading with the levee and backswamp where geomorphology is poorly developed); and *bottomland* (primarily restricted to the Triassic Basins, on very wide floodplains with poorly defined and generally low-lying geomorphic settings).

All plots were located within the 100-year floodplain of the nearest river (the area adjoining a river that has a 1% annual chance of flooding). In the field, alluvial species suggested an area inside the 100-year floodplain, and following field data collection, I excluded plots that were determined to be outside of the 100-year floodplain when mapped in a geographic information system (GIS). Additional environmental data recorded at each site includes slope, aspect, evidence of disturbance (e.g. stumps, deer browse, flood debris), and soil nutrient content and texture as determined from field samples. Soil samples included one from the top 10 cm of mineral soil in each of the four intensive subplots and one sub-surface sample from the center of each plot collected approximately 50 cm below the ground surface. Samples were analyzed by Brookside Laboratories, Inc., New Oxford, OH using the Mehlich 3 extraction method (Mehlich 1984). Exchangeable Ca, Mg, K, and Na, total cation exchange capacity, pH, percent base saturation, extractable micronutrients (B, Fe, Mn, Cu, Zn, and Al), soluble sulfur, bulk density, and percent organic matter were reported. Texture analyses included percent clay, silt, and sand. Samples from the four intensive subplots were averaged for analysis.

Plant taxa were identified to the finest taxonomic resolution possible. Taxonomy follows Weakley 2010. Taxa that were difficult to identify to species without fruit or flower due to the timing of field sampling were grouped into lower resolution complexes (examples: *Viola spp*., *Oxalis spp., Solidago spp., Carex grisea* group). All finer scale taxa were included in the lower resolution complexes. Additionally, taxonomy was reviewed and standardized prior to analysis to account for differences due to plant identifications by a variety of individuals, both in the field and in the lab. The final analysis dataset contained 606 consistently recorded taxonomic units.

Following field sampling, plots were mapped in a GIS and additional environmental variables were calculated for each sample. These included Strahler stream order (an indication of river size), upstream area drained (the land area drained by any point on the river), the width of the 100-year floodplain, and elevation. GIS analyses were based on digital elevation models from the USGS National Elevation Dataset (NED; http://ned.usgs.gov/) and surface water themes from the USGS National Hydrography Dataset (NHD; http://nhd.usgs.gov/). NED data was downloaded at a 30m resolution, and NHD data were downloaded at medium resolution (1:100,000-scale). Elevation was derived directly from the NED data. Upstream area drained and stream order were derived using the ArcHydro toolset. Width of the 100-year floodplain was determined using the North Carolina digital floodplain maps (DFIRM; http://www.ncfloodmaps.com/), and bedrock was determined using the North Carolina digital geologic map (North Carolina Geological Survey (NCGS); http://www.nconemap.com/).

Analytical methods

Vegetation data were analyzed using cluster techniques, indicator species analysis, discriminant analyses using random forests (Breiman 2001), and ordination techniques. Group selection was based on agglomerative, hierarchical clustering (PC-ORD version 5; MjM Software, Gleneden Beach, Oregon, USA). Preliminary clusters were produced using flexible beta group linkage ($\beta = 0.25$) and Sörensen distance. Hierarchical analyses aided in illustrating the relationships of vegetation types recognized. Species importance values used to calculate the dissimilarity matrix were the original cover class codes by stratum. The matrix of "pseudo-species" (species-stratum couplets) for forested stands (182 plots $\times$ 842 "species") reflects species cover in each stratum, treated independently. Indicator species analysis was used as an initial guide for pruning the resulting cluster analysis dendrogram, following the method described by Dufrêne and Legendre (1997). An optimum number of clusters was determined based upon maximization of significant indicator values and minimization of average p-values (Dufrêne and Legendre 1997; McCune and Grace 2002).

I adjusted the number and composition of vegetation types using discriminant analyses with the random forests method (as implemented in the 'randomForest' 4.5-35 package in R 2.11.1; R Development Core Team 2010). Random forest classifiers have many of the same benefits as classification and regression tree (CART) models, including the ability to account for interactions among predictor variables and no underlying assumptions of normally distributed data. Random forests, however, improve on traditional CART models by producing more robust results that do not over fit data, yet still have very high classification accuracy; this is accomplished by repeatedly creating individual trees using a random subset of the data and then combining the predictions from all trees (Breiman 2001; Liaw and Wiener 2002; Cutler et al. 2007). To identify misclassified plots, I classified

clusters with random forests, using the floristic matrix as predictor variables; this analysis identified plots that could not be assigned to the correct group based upon the floristic data and identified a more appropriate group assignment. Random forest classifiers also allow the researcher to identify predictors that were most important in driving the splits in the classification; I classified clusters using the environmental matrix to identify the most useful environmental variables in discriminating between vegetation types. Following random forest analyses, I used ordination analyses to clarify how variation in vegetation relates to key environmental variables identified in the second random forests analysis. For this purpose I used Canonical Correspondence Analysis (CCA; as implemented in the 'vegan' 1.17-3 package in R) to constrain the ordination to subset of environmental drivers of vegetation patterns. Vegetation plots used for this study have been archived in VegBank (http://vegbank.org) and are available to the public for reanalysis.

Indicator species analysis was used to identify indicator species in each forested vegetation type. Dufrêne and Legendre (DL) indicator species analysis was performed using PC-ORD; this statistic reflects relative abundance and relative frequency of species present in each group. I evaluated the significance of indicator values using Monte Carlo tests with 100 randomizations. Only species with significant indicator values ($P < 0.05$) are reported. In addition to the DL indicator values, I calculated a diagnostic value (DV) of individual species based on constancy and fidelity relative to the assigned vegetation type (DV = constancy x fidelity / 100). This statistic identifies the degree to which species are both frequent within a group (high constancy) and relatively restricted to a group (high fidelity) and is more likely to identify potential indicator species with low abundance than the DL values.

Finally, I developed a community characterization for each vegetation type. Vegetation type names are consistent with the naming system used in the U.S. National Vegetation Classification (U.S. FGDC 2008; Jennings et al. 2009). Names reflect species with high constancy, high cover, and/or higher indicator value. A "-" separates species within the same vertical strata, while a "/" separates strata. For each group, I determined average cover and constancy of each pseudo-species. Average cover class was calculated using only plots where the species was present. Constancy was calculated as the percent of plots within a group in which a given species occurred. Only prevalent species (*sensu* Curtis 1959) in each group are reported in the floristic tables, where prevalent species were identified by ranking species by constancy and selecting the most common species such that the total number of prevalent species equals average species richness per 400m^2 within the group. Prevalence was calculated separately for each stratum. Cover and constancy for woody vines were calculated separately with slightly altered methodology in the two synoptic tables. Since many woody vines cross stratum boundaries, I limited reported species to a single stratum. Vine cover and constancy in these tables were calculated based on the geometric mean cover in the four intensive subplots (cover in the subplots is not recorded in separate strata). Woody vine species summarized by these methods include *Bignonia capreolata, Campsis radicans, Lonicera japonica, Parthenocissus quinquefolia, Smilax spp., Toxicodendron radicans,* and *Vitis spp*. Homotoneity (Peet 1981), or mean constancy of the prevalent species, was calculated for each group. Homotoneity is an indicator of the degree of compositional variability among plots belonging to a described community type. Non-native species are identified in the floristic tables based on Weakley 2010. Appendices

include floristic tables for each group, including diagnostic and indicator values, in addition to summarized basal area and average values of soil variables (Appendices 1-7).

Results

Cluster analysis, indicator species analysis, and discriminant analysis together suggested recognition of twelve forested vegetation types and two herbaceous types, nested within five broad vegetation groups (Figure 2.2). Cluster analyses consistently indicated that herbaceous vegetation plots formed a unique cluster, and these plots were removed and analyzed separately from further analyses of forested communities. Indicator species analyses suggested recognition of 14 forested types, based on a dip in average p-value and peak in the total number of significant p-values. The random forests analysis indicated four problematic groups in the classification because no plots in these groups were classified correctly by the random forests algorithm. Two of these groups were small and incohesive; plots in these groups were reassigned based on random forests output. I recognize the additional two problematic groups as separate vegetation types here, despite the random forests output, based on high cover of species not normally present in the Piedmont of North Carolina. Random forests indicated that both the *Quercus lyrata - Fraxinus pennsylvanica / Saururus cernuus* and the *Carya aquatica - Nyssa aquatica* swamp types (IVd and IVe in the notation below) should be relocated into the *Fraxinus pennsylvanica - Acer rubrum - Ulmus americana / Ilex decidua / Saururus cernuus* (IVb) type, likely due to all three of these types having very high *Acer rubrum* and *Fraxinus pennsylvanica* cover. However, I elected to recognize these types as different due to the high cover of *Quercus lyrata* in the first type and *Carya aquatica* and *Nyssa aquatica* in the second (see further discussion below in the

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sections describing these vegetation types). Twenty-five additional plots were reassigned to different vegetation types based on the random forests output.

The twelve forested types are nested within four broader mega groups, where compositional variation among the groups is strongly related to geomorphology and edaphic variables. CCA ordination illustrates the relationship of floristic variation among the four mega groups to five key environmental variables identified in the second random forest analysis: % clay, % sand, pH, Ca-Mg ratio, and 100-year floodplain width (Figure 2.3). Stream order is a strong differentiating factor among the mega groups. Two mega groups are plotted on the upper left portion of the ordination diagram, associated with low to mid-order rivers, narrow floodplains, and sandy soils; these groups most commonly occur along small streams and alluvial flats. Alternatively, the large river levees are plotted on the right side of the ordination space and are related to higher pH, Ca-Mg ratio, and stream order. The second axis is mainly related to soil texture and floodplain width. The bottomland and swamp forests are plotted in the lower portion of the ordination diagram, associated with decreasing sand and increasing clay content and floodplain width.

Additional floristic differences within both the high stream order mega groups and the low stream order groups can be attributed primarily to soil chemistry and texture (Figure 2.3; Appendix 1). In the set of types associated with smaller floodplains, chemistry is the strongest gradient differentiating between the two mega groups, with *Quercus-Carya* dominated flats occurring in the more nutrient poor sites and small stream alluvial forests occurring in the sites where soils have a higher average pH and percent base saturation. In the larger floodplain forests, there is substantial variation in soil texture. The texture gradient is related to variation in flooding dynamics and hydroperiod. High sand content is associated

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with the levee landform and high clay content is associated with backswamps, where longer periods of standing water result in fine sediment deposition. I recognize two mega groups in the larger floodplain forests associated with each end of this geomorphic gradient: the drier levee sites and the wetter bottomland and swamps sites. Levee vegetation types are also differentiated from other larger floodplain forests by more nutrient-rich soils. The twelve forested vegetation types are presented below, nested in their mega groups reflecting four geomorphic settings: small streams and narrow floodplains (I), alluvial flats (II), large river levees (III), and wide-floodplain bottoms and swamps (IV). The two herbaceous vegetation types are presented in a fifth group (V).

I. Small streams and narrow floodplain forests

The two vegetation types of this group are associated with narrow floodplains. The narrow floodplains of the Piedmont occur for two reasons: low order rivers or geologic formations that restrict floodplain development, typically metamorphic and igneous bedrock. The narrow floodplain restricts geomorphic development and results in communities where species are not well sorted along a hydrologic gradient and are more strongly influenced by the surrounding upland flora than are the alluvial types found on larger rivers This group is associated with higher elevations of the North Carolina Piedmont, occurring in areas farther removed from the fall-line. The soils are very sandy (both types recognized having higher average percent sand in both the A and B horizons than any of the other 10 forested types recognized; Appendix 1) and are associated with high pH and base saturation when compared with other types occurring along low-order streams. The vegetation of these sites tends to be species-rich in comparison to the other mega groups (Table 2.1); I recognize two types in this group.

Ia. *Liriodendron tulipifera - Liquidambar styraciflua / Lindera benzoin / Amphicarpaea bracteata* **Forest (18 plots):**

This small stream, narrow floodplain community type occurs on sandy soils, with high cation exchange capacity, high Ca and Mg content, and high pH (Appendix 1) and is distributed across all five river basins (Figure 2.1). It is found across a variety of stream orders, but all occurrences are associated with narrow floodplains (x̄= 171.5m, s.e.= 26.1).

The type is typically species rich, with an average of 79 species / 400m^2 and includes plots having some of the highest richness values observed in this study (Table 2.2). The tree stratum is dominated by the nominal species (*Liriodendron* and *Liquidambar*) in addition to *Betula nigra, Fagus grandifolia,* and *Acer rubrum*, with substantial sub-canopy cover contributed by *Cornus florida* and *Carpinus caroliniana* (Appendix 2, 3). Both nominals are common successional species in Piedmont forests and may be somewhat transient dominants in this type; *Quercus* and *Carya* species, presently found at low constancy and cover, may become more dominant with succession. The shrub stratum is dense with smaller individuals from the sub-canopy in addition to abundant *Lindera benzoin* and frequent *Viburnum prunifolium. Corylus americana* has a high diagnostic value for this group and may also contribute substantial shrub cover. The diverse herb stratum is dominated by a mix of alluvial and mesic slope species and frequently includes *Botrypus virginianus, Galium triflorum,* and *Phryma leptostachya* (which is also an indicator for this type). The exotic grass *Microstegium vimineum* often has high cover.

 Ib. *Liriodendron tulipifera - Betula nigra / Cornus florida / Sanicula canadensis var. canadensis* **Forest (6 plots):**

This type is found on first and second order streams in three river basins: the Catawba, Cape Fear, and Neuse (Figure 2.1). This type is floristically similar to group Ia, but it is associated with lower cation exchange capacity and extremely sandy soils in comparison to the other narrow-floodplain forest type (Appendix 1).

These sites are infrequently flooded, resulting in the presence of more species commonly associated with both mesic slopes and upland forests. The canopy is dominated by the nominal species, in addition to species more typical of well-drained upland forests, such as *Oxydendrum arboreum* and *Quercus alba* (Table 2.2; Appendix 3)*. Ilex opaca* and the indicator species *Ostrya virginiana* are also frequent subcanopy species. The shrub layer is relatively open and primarily composed of small individuals of the tree stratum. In contrast to Ia, where *Lindera benzoin* contributes a large percentage of shrub cover, *Lindera benzoin* was not observed in any plots assigned to this group.

II. Oak-hickory flats

The vegetation types in this group occur on levees and flats along mid-sized rivers, primarily 3rd to 5th order, although IIb occurs on larger order rivers (IIb was treated in this section due to its floristic affinity with the other *Quercus-Carya* dominated vegetation types of group II). In general, the soils of oak-hickory flats are relatively infertile with low base saturation, Ca/Mg ratios, and cation exchange capacities (Appendix 1). The three vegetation types recognized are dominated by a mix of *Quercus* species and other common bottomland tree species, in addition to high *Carya* cover in some types (Table 1). Within this group, there is a strong gradient of floodplain width, with IIb occurring on the widest floodplains and consequently the finest textured soils and IIc on the narrowest floodplains (Table 2.2). IIa is associated with intermediate-width floodplains, but with the sandiest soils (Appendix 1).

IIa. *Liquidambar styraciflua - Quercus nigra / Carpinus caroliniana / Mitchella repens*
Forest (32 plots):

These forests are found on levees and flats along 3rd to 5th order streams in all five river basins (Figure 2.1). The geomorphic position of this type intergrades between the levee concept of larger order rivers and alluvial flats of smaller order rivers; these sites are often located directly adjacent to the river channel, yet may not be identifiable as a classic levee where floodplain geomorphology is not well developed. In contrast to IVa, which may also have high *Quercus* cover and is associated with wet areas of wide floodplains, this type is associated with relatively dry, flat landscape positions. The soils tend to be sandy, approaching the percent sand that characterized the low order, narrow floodplain forests mega group (Appendix 1).

This community is dominated by the nominal tree species, especially *Quercus* species and including *Q. nigra, Q. phellos, and Q. pagoda*, in addition to *Fagus grandifolia* (in contrast to all other oak-dominated groups) and a mix of *Carya* species, including *C. ovata* and *C. alba* (Table 2.2; Appendix 2)*.* The high sand content and abundance of *Fagus* suggests affinities with type Ia, but IIa has less affinity with the upland sites and is characteristic of higher order streams. *Fagus grandifolia* and *Ilex opaca* are known to be intolerant to extended flooding, further suggesting a drier setting with a short hydroperiod (Townsend 2001). In contrast to IVa, *Quercus nigra* more consistently contributes a large percentage of the tree cover in this type (Table 2.2). The dense shrub/understory stratum is dominated by *Carpinus caroliniana,* while a diverse set of grass species contribute significant cover to the herb stratum, including especially *Chasmanthium latifolium, Elymus virgincus s.l., Poa autumnalis*, and *Melica mutica* (Appendix 4).

IIb. *Liquidambar styraciflua - Quercus pagoda - Carya cordiformis / Asimina triloba / Arundinaria tecta* **Forest (3 plots):**

In contrast to the other oak-hickory flats, this type is found on wide flats along high-order rivers (all $\geq 4^{th}$ order). The soils are characterized by a high clay content and are associated with very high Ca content and cation exchange capacity (Appendix 1). The three plots documenting this vegetation type occur in the Yadkin River Basin in the Triassic Basins close to the fall line (Figure 2.1). As a result of its location in the Triassic Basins, this type is associated with very wide floodplains and has the widest average floodplain width of any group recognized here (> 1 km). In the CCA ordination, these three plots appear in the cloud of bottomland and swamp forest plots, reflecting the wide floodplains of this group (Figure 2.3). However, the abundance of species rarely present in the wetter types, including *Arundinaria tecta* and *Asimina triloba,* floristically distinguishes this type from the bottomland and swamp forests of group IV (Table 2.2).

The dominant trees of this type include the nominal species as well as *Quercus michauxii, Q. nigra*, and *Nyssa sylvatica,* and high sub-canopy cover of *Carpinus caroliniana* (Table 2.2; Appendix 2). The shrub stratum is sparse and frequently dominated by *Asimina triloba*, whereas the herb layer is dominated by *Arundinaria tecta*, which floristically distinguishes this type from IIa (Appendix 4). IIIa occasionally includes significant *Asimina* and *Arundinaria* cover, but lacks the frequent and abundant *Quercus* cover observed in this type.

IIc. *Carya carolinae-septentrionalis - Acer floridanum / Aesculus sylvatica / Zizia aurea* **Forest (8 plots):**

This community is found across a variety of stream orders, but primarily mid-sized, 2nd to 4th order streams. Even when found on higher-order rivers, it is always associated with narrow floodplains, similar to the forested vegetation group presented above (I). However, it is grouped with the oak-hickory flats because of its floristic affinity with these types. This type is also associated with higher percent slope values, suggesting sites influenced by the slope forests surrounding the floodplain. It is only found in the Cape Fear and Yadkin River Basins, on soils with high silt content (Figure 2.1; Appendix 1).

These forests are the most diverse among those documented here, with an average of 84.9 species observed in $400m^2$ (Table 2.2). The diverse tree stratum is dominated by the nominals, in addition to a mix of other *Quercus* and *Carya* species and a dense sub-canopy of *Carpinus caroliniana* (Table 2.2; Appendix 4). The sparse shrub stratum is primarily composed of smaller individuals of the tree stratum species. The herb stratum is dominated by grasses, many of which are significant indicators for this group, including *Elymus hystrix, Dichanthelium boscii,* and *Danthonia spicata* (Appendix 4)*.*

III. Large river levee forests

This group is associated with levees on mid to large-order rivers (3rd to 7th order streams). In contrast to other types associated with higher-order streams, the soils are sandy, with high pH and Ca/Mg ratios (Figure 2.3). Compositional variation within this group may reflect disturbance history. The canopy of IIIb is more frequently dominated by fast-growing, often early successional species, including *Platanus occidentalis, Fraxinus pennsylvanica,* and *Acer negundo,* which are typical dominants of young, newly accreted pointbar forests in southeastern riparian zones (Meitzen 2009; Romano2010). These dominants may also reflect a history of human disturbance as they are known to increase following tree harvesting.

Abundant species in IIIa, on the other hand, more frequently include long-lived successional species (*Liriodendron tulipifera* and *Liquidambar styraciflua*) and shade-tolerant species typically associated with older natural-levee forests (*Celtis laevigata* and *Ulmus americana*). Additional compositional variation within this group reflects geographic distribution of the types, as well as river size.

IIIa. ***Ulmus americana - Celtis laevigata / Lindera benzoin / Osmorhiza longistylis* Levee Forest (33 plots):**

This levee community occurs on large 4th to 7th order rivers in the Catawba, Yadkin, Cape Fear and Neuse River Basins (Figure 2.1). This type is associated with relatively wide floodplains of large watersheds (i.e. rivers that drain larger areas and more sub-watersheds) and tends to occur at lower elevation and further downstream than the other levee type, though the stream order range for the two types broadly overlaps. The soils associated with this type are some of the most fertile alluvial soils, with average pH, Mg content, and base saturation values higher than any other type described, although there is considerable overlap in the range of these measures with the other levee vegetation type (Appendix 1).

The dominant tree species include the nominals, with *Celtis* often contributing a large proportion of the cover (Table 2.2). Additional tree cover may be contributed by a variety of species commonly associated with nutrient-rich habitats, including *Carya cordiformis, Acer floridanum,* and *Juglans nigra* (Appendix 5)*. Acer negundo* is prominent in the sub-canopy. The shrub layer is relatively dense and diverse, with additional cover contributed by *Asimina triloba, Aesculus sylvatica,* and the exotic *Ligustrum sinense.* The herb stratum is composed of a mix of graminoid species, occasionally including substantial cover by *Arundinaria tecta,* and various forb species, commonly including *Laportea canadensis.* The exotic species

Microstegium vimineum, Glechoma hederacea, and *Lonicera japonica* may also contribute high cover in the herb stratum (Appendix 5).

IIIb. *Fraxinus pennsylvanica - Platanus occidentalis / Acer negundo / Chasmanthium latifolium* **Levee Forest (30 plots):**

This levee community primarily occurs on 3rd to 6th order rivers across all five river basins and is associated with slightly narrower floodplains than the other levee type. In comparison to IIIa, it is associated with higher elevations and longer river-course distances from the river mouth, reflecting locations more towards the interior Piedmont, although there is considerable spatial overlap (Figure 2.1). The soils are also fertile, with high pH and base saturation; in comparison to the other levee group, these soils have a higher percentage of sand, expected of interior types (Appendix 1).

The nominal species dominate the canopy of this levee type, in addition to *Ulmus americana, Betula nigra,* and *Liquidambar styraciflua. Acer negundo* consistently contributes very high cover in the subcanopy. In comparison to the other levee vegetation type, this type tends to have a less diverse tree stratum with higher cover and constancy of *Fraxinus pennsylvanica* and *Platanus occidentalis* (Table 2.2). The shrub layer is moderately diverse and primarily composed of smaller individuals from the tree stratum, in addition to *Lindera benzoin* and the exotic *Ligustrum sinense.* Graminoid species commonly dominate the herb stratum, particularly*, Chasmanthium latifolium, Elymus virginicus s.l.,* and *Carex grayi.* As with IIIa, exotic species may be prominent in this group; *Microstegium vimineum* often contributes substantial cover in the herb stratum (Appendix 5).

IV. Bottomland and swamp forests

The bottomland and swamp forest group occurs on the widest floodplains and mid- to high-order rivers (primarily 3rd order and higher). These types are found on low areas of the floodplain where standing water remains for a longer period of the year and growing season. The soils have a high concentration of silt, clay, and organic matter; they are relatively acidic and infertile, with low base saturation and Ca/Mg ratios. In ordination space, soil texture separates the drier oak-hickory flats (II) from the wetter, more commonly flooded oak bottomlands, which have much higher clay content (Figure 2.3). Soil variables suggest that floristic variation within this group is largely driven by hydroperiod, with types IVd and IVe occurring in the wettest sites, types IVa and IVb occurring in intermediate sites, and IVc occurring in the narrower floodplains of the inner Piedmont where the hydroperiod is shorter (Table 2.2). The two intermediate groups (IVa and IVb) are also separated by hydroperiod, with IVa being drier than IVb; the soils of IVa are characterized by high silt levels, while IVb is characterized by high clay content (Appendix 1).

IVa. *Quercus (phellos - pagoda - michauxii) - Ulmus americana / Ilex decidua / Arisaema triphyllum* **Bottomland Forest (17 plots):**

This bottomland forest community is found in wide floodplains on larger rivers in the Triassic Basins; six plots were classified to this group that do not map directly over Triassic Basin bedrock, but they were all located directly adjacent to this region. This type is associated with bottomland geomorphology, on low, broad Piedmont floodplains, often without obvious relief or geomorphologic development (in contrast to levees, which are often raised, or backswamps, which are often obvious depressions on the floodplain). This type is documented in every river basin except the Catawba, likely due to the North Carolina section of the Catawba basin lacking Triassic Basin bedrock (Figure 2.1). In addition, many of the

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larger-order rivers of the Catawba basin are heavily dammed, resulting in very little remaining bottomland forest habitat. The soils of this type have moderately high clay content, although not as high as the other swamp groups described below; this likely reflects the shorter flooding duration at these sites (Appendix 1).

The nominal *Quercus* spp. dominate the tree stratum, along with common canopy co-dominants of wet Piedmont forests, such as *Acer rubrum* and *Fraxinus pennsylvanica.* Climbing vines may also contribute substantial cover in the tree stratum, especially *Toxicodendron radicans* (Table 2.2). The considerable cover contributed by *A. rubrum* and *F. pennsylvanica* floristically differentiates this type from other vegetation types with high *Quercus* cover (IIa and IIb). Also in contrast to group II, *Quercus nigra* is much less common in the wetter vegetation types of group IV. As expected in these wetter sites, *Fagus grandifolia* is extremely rare, also differentiating this type from IIa. *Carpinus caroliniana* and *Ulmus alata* frequently contribute cover to the subcanopy and shrub strata. The herb stratum tends to be more open when compared to the other mega groups, with most cover contributed by patches of *Carex* species (Appendix 6).

IVb. *Fraxinus pennsylvanica - Acer rubrum - Ulmus americana / Ilex decidua / Saururus cernuus* **Swamp Forest (24 plots):**

This swamp forest type is associated with medium to large-sized rivers (all $\geq 3^{rd}$ order). Approximately a quarter of the plots in this group were located in the Triassic Basins, where Piedmont rivers have broader floodplains with better-developed geomorphology. Even where plots included in this type were found outside of the Triassic Basins, they were located on wider Piedmont floodplains. This type occurs in the backswamp geomorphic position,

with relatively acidic soils characterized by high clay content and frequent flooding (Appendix 1).

The dominant tree stratum species of this type include the nominal species in addition to *Liquidambar styraciflua* and *Quercus phellos.* There is some degree of overlap, both in floristics and environmental setting, of this type and the more oak-dominated types in this group, IVa and IVd. This type may be an earlier successional stage of the bottomland forests (IVa) and is found in slightly wetter sites with longer periods of flooding. Alternatively, in comparison to group IVd, this group represents slightly shorter hydroperiods, with *Quercus lyrata* occasionally present in small very wet inclusions (Appendix 6) .The shrub layer tends to be moderately open, while the herb stratum is heavily dominated by *Carex* species and wetland forbs.

IVc. *Fraxinus pennsylvanica - Betula nigra - Platanus occidentalis / Alnus serrulata / Boehmaria cylindrica* **Swamp Forest (6 plots):**

This forested type is found along the larger order rivers at high regional elevations in the river basin, farther from the fall line and mouth of the river (Figure 2.1). This type occurs on wet areas of the floodplain, but in contrast to the other bottomland and swamp forests, these floodplains are restricted by resistant granitic bedrock and tend to be narrower than those found closer to the fall line in the Triassic Basins. The wet areas of these narrower floodplains may be the result of ponding due to dams, natural or human, or seepage areas at the edge of the floodplain. Soils at these sites are sandier than the other swamp types, perhaps as a result of erratic, short-duration flooding events common in the narrow valleys of the upper Piedmont (Appendix 1).

The tree canopy of this type is more open than other swamp types and is dominated by the nominal species, with additional cover from *Ulmus americana, Liquidambar styraciflua,* and *Salix nigra.* The open canopy and dominance of many early successional species may be a result of flooding disturbance. The shrub stratum is composed of small individuals of the tree stratum, in addition to *Alnus serrulata, Carpinus caroliniana, Cornus amomum,* and *Viburnum dentatum.* The herb stratum is well developed and dominated by a mix of sedges and grasses (Appendix 6).

IVd. *Quercus lyrata - Fraxinus pennsylvanica / Saururus cernuus* **Swamp Forest (3 plots):**

This type is found in the wide floodplains of the Triassic Basins. While there is some floristic overlap with other swamp types, these forests dominate in sites where there is prolonged flooding over a larger area, and therefore they not included in other vegetation types (such as IVb, where *Quercus lyrata* is present in small-scale floodplain depressions). While random forests analysis indicated that these plots should be lumped with IVb, I chose to recognize this as a distinct type due to the high *Quercus lyrata* cover in these plots, which is not common in the Piedmont (Weakley 2010) and is generally associated with very wet conditions. The soils of this type are very acidic, with a very high clay content (Appendix 1).

This type is dominated by high *Quercus lyrata* cover, in addition to the other common swamp co-dominants. The shrub stratum is very sparse and mostly composed of young tree species. The herb layer is heavily dominated by *Saururus cernuus,* with additional herb cover contributed by common wetland species such as *Impatiens capensis, Bidens frondosa,* and *Carex* spp (Appendix 6).

IVe. *Carya aquatic - Nyssa aquatica* **Swamp Forest (2 plots):**

The two plots of this swamp forest type occur in very wide floodplains of the lower Triassic Basins, close to the fall line in the Yadkin River Basin. Soils at these sites are acidic, with very high clay content, indications of long flooding periods (Appendix 1).

The tree stratum is dominated by the two nominal species, both of which are more typical dominants of swamp vegetation on the Coastal Plain of North Carolina. *Carya aquatica* and *Nyssa aquatica* are rare in the Piedmont region of North Carolina (Weakley 2010). Random forests analysis also indicated that these plots should be lumped with IVb, but I chose to recognize this type due to the rarity of the dominant tree species. If the analysis had included Coastal Plain plots, this type would likely have been seen to have higher affinities to the Coastal Plain plots than to IVb. Other canopy trees include species commonly associated with the wettest sites in the floodplain, including *Quercus lyrata, Acer rubrum,* and *Fraxinus pennsylvanica.* The shrub and herb layer of this community type is very sparse as the plots are frequently inundated for extended periods (Appendix 6).

V. Riparian herbaceous vegetation

This group is comprised of two herbaceous vegetation types. It is found within the channels of rocky-bottomed Piedmont rivers. No soil data is presented for the types in this group, as there is little to no soil present in the rocky river channels where they are found. Cover data for these plots is presented in a single stratum.

Va. *Justicia americana* **herbaceous vegetation (10 plots):**

This type is found in rocky-bottomed rivers in all basins except the Catawba (Figure 2.1). The vegetation is heavily dominated by herbaceous cover from *Justicia americana* (Appendix 7). Other herbs that commonly contribute cover include *Boehmeria cylindrica* and the exotic *Murdannia keisak.* Occasional tree cover is contributed by overhanging

bottomland species that may include *Platanus occidentalis, Fraxinus pennslyvanica,* and *Betula nigra.*

Vb. *Hymenocallis coronaria - Justicia americana* **herbaceous vegetation (2 plots):**

The two plots documenting this type are located in the Catawba River in South Carolina, where *Hymenocallis coronaria* is a state-listed rare species (Figure 2.1; S.C. Department of Natural Resources). This vegetation type is heavily dominated by herbaceous cover of both nominal species (Appendix 7).

Discussion

Composition of alluvial plant communities varies continuously, as evidenced by plots reassigned to alternate vegetation types by different methodologies. This is particularly evident in the swamp group, where there is substantial floristic similarity in the vegetation types recognized here. However, it is possible to acknowledge the continuous nature of vegetation while recognizing that there are identifiable, repeated vegetation patterns across the landscape. This classification aims to clarify and document the recurrent patterns in Piedmont alluvial vegetation and their relationships to the alluvial landscape.

Piedmont alluvial vegetation is driven in large part by geomorphology, which is strongly related to stream order, floodplain width, and soil texture and chemistry. The floodplains of the lower-order Piedmont rivers are often narrow and the geomorphic landscape is poorly developed, primarily as a result of the prevalence of resistant metamorphic and granitic bedrock. Where distinct fluvial landforms are not easily identifiable in these narrow floodplain rivers, compositional variation is strongly correlated with soil texture and chemistry. Vegetation group I (small streams and narrow floodplain

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forests) and group II (oak hickory flats) generally occur in such settings: group I is associated with fertile, sandy soils and group II is associated with less fertile, loamy soils. In contrast, the higher-order rivers with wider floodplains have a better- developed geomorphic landscape, with distinct geomorphic settings and more variation in substrate. Vegetation group III (large river levee forests) and group IV (bottomland and swamp forests) are dominant in the higher-order rivers, where vegetation types are sorted along a hydrologic gradient and are associated with distinct fluvial landforms. The levee forests are associated with higher and drier regions of the floodplain, located close to the river channel, where flooding events are short in duration and soils are sandy and very fertile. The bottomland and swamp forests are often farther removed from the river channel, in the low topographic areas of floodplains where longer hydroperiods result in deposition of fine sediment and soils with high clay content. However, in contrast to the very wide floodplains of the Coastal Plain, where fluvial geomorphologic settings and their associated vegetation are distinct, the geomorphic features of the narrower Piedmont floodplains intergrade over smaller spatial distances. The results suggest less species-sorting in the narrower Piedmont floodplains and stronger species-sorting in the more Coastal Plain-like settings of group III and IV; however, I am unable to directly compare the degree of species sorting in the Piedmont versus the Coastal Plain because previous studies of Coastal Plain vegetation are primarily qualitative, descriptive studies, lacking plot data.

This classification describes remnant alluvial plant communities in a highly fragmented landscape, representing only a portion of the original diversity of these systems. The natural hydrologic regime of Piedmont rivers has been altered by anthropogenic activities since the beginning of European colonization. Although I attempted to locate and

sample the most natural, high-quality vegetation possible, it is important to realize the implications of the highly altered Piedmont landscape. A long history of selective tree harvesting may have resulted in certain species being under-represented in vegetation types where they historically may have been prominent. The presence of non-native invasive species in many samples suggests the structural and compositional differences between the pre-European native vegetation and the vegetation on the landscape today (7% of the riparian flora sampled was exotic; only 3 plots did not contain an exotic species). Additionally, extensive sediment deposition following European agriculture on the uplands during the period of 1700-1940 homogenized the hydrogeomorphic landscape of many Piedmont rivers, decreasing floodplain habitat complexity and likely resulting in floristic changes to pre-European riparian vegetation (Trimble 1974).

Vegetation sampling was restricted by common hurdles associated with working in the Southeastern U.S., including seasonal variation in the present and identifiable flora. Because each sample site was visited only once during the summer, there is likely a systematic under-sampling of spring ephemerals in this dataset, many of which are common in Piedmont bottomland habitats (e.g. *Erythronium* spp., *Dentaria* spp., *Claytonia virginica*). Additionally, many large tracts of alluvial forests in the North Carolina Piedmont are privately owned; while I was able to obtain permission from some landowners to access areas identified as potentially high-quality vegetation, there were sites that I was not able to access. Despite these obstacles, this classification provides the most comprehensive documentation and description of the remaining natural alluvial forests of the North Carolina Piedmont to date.

The classification presented here complements and can be expected to inform future revision of floodplain associations in the Southeastern United States recognized in the U.S. National Vegetation Classification (NVC; U.S. FGDC 2008; Jennings et al. 2009). The vegetation types I describe are comparable to NVC associations in terms of compositional variation and consistency, although NVC community concepts may reflect the broader geographic scope of the NVC. The current NVC floodplain associations of the Piedmont region are considered provisional and ranked as having low confidence, for although the current NVC floodplain associations are based on a synthesis of available literature and qualitative field surveys of variation across their range, plot data are usually lacking. The current NVC set of alluvial vegetation associations occurring in the Piedmont includes a mixture of broadly defined "placeholders" (provisional type concepts), types with uncertain conceptual boundaries, and types based on limited, unavailable or non-existent plot data. In contrast, the descriptions of most of these types are based upon a large number of plots distributed across a wide geographic area and capture compositional variation within the groups across this area. These plots are archived in VegBank and thus are available for reanalysis and integration into larger datasets that can better test the full range of variation expressed by current NVC types across their geographic extent.

Although some types recognized here fit well within currently recognized NVC community concepts, others deviate sharply from established types and may point to the need for reworking currently recognized NVC alluvial type concepts. To facilitate comparison of these types and existing NVC associations, I have matched each of the fourteen types to the closest recognized NVC association, as well as any other NVC associations that appear to overlap my own (Table 2.3). Table 2.3 illustrates the complexity of interrelationships

between the quantitatively derived types presented here and the current NVC associations, showing how future work in defining and characterizing NVC types might proceed. A more direct comparison between quantitative data-based classifications and the NVC will be available only when the established NVC types are documented with plot data as mandated for high confidence types in the FGDC. Standard procedures and requirements for establishing high confidence NVC types are provided in Jennings et al. (2009).

Quantitative vegetation classification and description are important for conservation and restoration activities. In particular, vegetation types provide a useful common language for the coordination of conservation activities across organizations. It is my intent that this classification promotes conservation of Piedmont alluvial systems by providing a comprehensive classification and description of the vegetation types found in this region and their associated environmental setting. In addition to furthering the documentation and understanding of these communities, I also expect that this classification will serve as reference material for restoration activities of alluvial forests in the North Carolina Piedmont and adjacent areas.

Table 2.1: Trees, vines and herbs with high constancy and high average cover where present in each of the four mega groups (see text for definition of each metric). Groups are identified by the roman numerals used in the text. Only prevalent species with constancy >25% and average cover >3 for trees and herbs and >2 for vines are shown. Species only appear in one stratum (i.e. the stratum where the adult life form is found). See text for description of prevalence and calculation of constancy and cover. Non-native species are identified with an asterisk.

Groups	I		II		III		IV	
Plot Count	24		43		63		52	
Avg Plot Spp Richness (400m^2)	77.1		72.6		55.2		52.6	
Avg Plot Spp Richness (100m^2)	42.8		42.8		32.6		31.4	
Avg Plot Spp Richness (10m^2)	23.8		23.2		17.1		15.6	
Avg Plot Spp Richness (1m^2)	10.4		10.0		8.0		6.6	
Homotoneity	58%		57%		57%		56%	
Tree taxon name	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Acer floridanum	29	7	33	7	41	7	13	6
Acer negundo var. negundo	8	5	2	2	79	7	4	4
Acer rubrum	88	6	72	6	19	6	96	7
Betula nigra	58	7	14	6	33	5	38	6
Carpinus caroliniana	75	7	86	7	48	6	44	6
Carya cordiformis	38	6	28	6	49	6	6	5
Carya ovata	25	6	40	6	10	6	21	5
Celtis laevigata	4	6	5	5	67	6	12	5
Cornus florida	92	6	42	5	29	4	4	3
Fagus grandifolia	50	6	40	6	5	6	4	3
Fraxinus pennsylvanica	42	4	56	5	73	6	87	7
Ilex opaca var. opaca	29	6	42	6	24	5	12	4
Juglans nigra	33	5	9	4	35	6	--	--
Liquidambar styraciflua	75	6	98	6	68	6	88	6
Liriodendron tulipifera	92	6	53	5	43	6	10	6
Nyssa sylvatica	17	5	58	5	8	4	27	4
Ostrya virginiana	33	6	23	6	11	5	--	--
Oxydendrum arboreum	42	5	14	4	--	--	--	--
Platanus occidentalis	29	6	14	6	73	6	31	5
Quercus alba	25	5	44	6	8	4	13	5
Quercus michauxii	8	6	26	6	21	7	29	6
Quercus nigra	13	6	58	6	11	7	19	5
Quercus pagoda	8	6	40	6	6	6	33	6
Quercus phellos	--	--	49	6	5	4	56	6
Quercus shumardii	33	6	26	6	10	5	12	5
Ulmus alata	29	5	63	6	29	6	48	6
Ulmus [americana + rubra]	42	5	42	5	79	6	87	6
Vine taxon name	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Bignonia capreolata	54	2	95	3	84	3	79	3
Campsis radicans	75	2	58	2	60	2	90	2
Lonicera japonica*	100	4	91	3	95	4	85	3
Parthenocissus quinquefolia	100	3	100	3	100	2	94	2
Smilax rotundifolia	63	2	93	2	73	3	98	3
Toxicodendron radicans	100	3	98	4	100	4	100	5
Vitis [cinerea + vulpina]	38	3	12	2	22	4	8	2
Vitis rotundifolia	100	3	95	3	67	3	67	2
Shrub taxon name	con.	cov.	con.	cov.	con.	cov.	con.	cov.

Ilex decidua	13	2	70	4	37	4	71	5
*Ligustrum sinense**	17	2	19	2	68	5	37	3
Lindera benzoin	42	7	14	3	56	6	12	5
Viburnum prunifolium	38	4	51	4	21	3	40	4
Herb taxon name	**con.**	**cov.**	**con.**	**cov.**	**con.**	**cov.**	**con.**	**cov.**
Boehmeria cylindrica	63	2	47	2	73	3	87	4
Carex [amphibola+grisea+corrugata]	58	3	65	4	73	4	42	4
Carex crinita	13	2	12	2	3	2	38	4
Carex grayi	4	1	16	2	51	4	23	5
Carex lupulina	4	1	--	--	10	2	46	4
Carex tribuloides	29	2	23	2	51	4	81	4
Carex typhina	8	2	16	2	16	3	63	4
Danthonia spicata	4	2	28	4	--	--	--	--
Elymus virginicus s.l.	38	2	42	4	65	6	44	2
Festuca subverticillata	71	2	40	2	49	4	21	3
Galium aparine	29	2	12	2	67	4	23	2
Laportea canadensis	4	1	--	--	54	5	10	2
Polystichum acrostichoides	100	4	65	3	44	2	19	2
Saururus cernuus	13	2	16	2	19	3	56	6
Verbesina occidentalis	46	4	30	2	68	2	8	2

Table 2.2: Prevalent species in each vegetation type (by stratum). Species shown are prevalent in at least one group and also have >50% constancy and average cover class of >2 (i.e. > 1% cover) in at least one group (see text for definition of each metric). Constancy and average cover are bolded in the group where a species is prevalent. Species are only listed in the stratum in which the adult life form is present (only one stratum per species). Non-native species are identified with an asterisk.

Groups	I. Small streams and narrow floodplain forests		II. Oak-hickory flats			III. Large river levees		IV. Swamps				
Types	Ia.	Ib.	IIa.	IIb.	IIc.	IIIa.	IIIb.	IVa.	IVb.	IVc.	IVd.	IVe.
Plot Count	18	6	32	3	8	33	30	17	24	6	3	2
Avg Plot Spp Richness (400m^2)	79.3	70.5	70.7	53.0	84.9	58.2	51.9	56.2	53.5	54.8	33.3	35.0
Avg Plot Spp Richness (100m^2)	43.0	42.5	42.3	33.9	48.2	36.3	28.5	36.1	31.8	27.6	18.7	16.6
Avg Plot Spp Richness (10m^2)	24.4	22.1	22.4	17.8	28.6	18.9	15.2	17.6	15,7	17.3	7.8	5.9
Avg Plot Spp Richness (1m^2)	10.6	9.6	9.6	8.1	12.7	8.7	7.1	7.4	6.6	7.4	3.5	2.1
Homotoneity	61%	60%	59%	78%	65%	61%	58%	58%	62%	59%	63%	62%
Average floodplain width (m)	172	119	420	1150	142	489	370	624	639	471	603	1100
Average pH	5.11	5.08	4.87	4.93	4.91	5.36	5.16	4.74	4.82	4.63	4.76	4.81
Average Ca Mg ratio (ppm)	5.54	5.34	3.91	2.77	3.39	6.15	6.11	3.83	4.52	4.38	4.03	3.95
Average % Ca	38.32	36.30	28.89	28.36	28.69	45.10	39.71	26.77	29.72	25.59	27.02	27.59
% Clay	14.55	11.40	18.40	43.82	17.49	20.37	21.94	27.45	35.58	30.91	35.65	44.25
% Sand	47.04	70.18	45.36	17.23	37.02	34.18	44.02	22.76	27.87	30.96	13.88	15.50

Trees	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Acer floridanum	33	8	17	2	19	7	--	--	100	7	55	7	27	6	35	6	4	5	--	--	--	--	--	--
Acer negundo var. negundo	11	5	--	--	--	--	33	2	--	--	64	6	97	7	6	5	--	--	17	3	--	--	--	--
Acer rubrum	83	6	100	7	78	7	100	6	38	5	18	5	20	6	88	6	100	8	100	7	100	7	100	6
Betula nigra	56	6	67	8	19	6	--	--	--	--	24	4	43	6	41	6	29	6	83	6	--	--	50	4
Carpinus caroliniana	78	7	67	7	88	7	100	7	75	7	52	6	43	6	71	6	33	7	17	6	33	3	50	6
Carya aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100	6
Carya carolinae-septentrionalis	--	--	--	--	--	--	--	--	100	7	3	6	--	--	6	5	--	--	--	--	--	--	--	--
Carya cordiformis	39	6	33	4	25	6	67	7	25	5	76	6	20	6	12	6	4	3	--	--	--	--	--	--
Carya ovata	33	6	--	--	38	6	67	5	38	4	18	6	--	--	41	6	17	5	--	--	--	--	--	--
Celtis laevigata	6	6	--	--	--	--	67	5	--	--	73	7	60	6	18	6	13	4	--	--	--	--	--	--
Cornus florida	89	6	100	6	44	5	--	--	50	4	42	5	13	4	6	3	4	3	--	--	--	--	--	--
Fagus grandifolia	56	6	33	3	50	6	--	--	13	3	9	6	--	--	6	3	4	2	--	--	--	--	--	--
Fraxinus pennsylvanica	44	5	33	3	53	5	67	3	63	6	58	6	90	7	71	6	96	7	100	8	100	6	50	4
Ilex opaca	17	6	67	6	53	6	--	--	13	4	36	5	10	4	29	4	4	4	--	--	--	--	--	--
Liquidambar styraciflua	78	6	67	6	97	6	100	5	100	6	94	6	40	6	100	7	88	6	67	6	67	5	100	5
Liriodendron tulipifera	100	6	67	6	66	5	--	--	25	6	58	6	27	6	24	6	--	--	17	6	--	--	--	--

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	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Nyssa aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100	8
Nyssa sylvatica	6	5	50	5	56	5	33	7	75	5	15	4	--	--	35	5	29	4	--	--	33	5	--	--
Ostrya virginiana	22	5	67	6	22	6	--	--	38	7	15	5	7	5	--	--	--	--	--	--	--	--	--	--
Platanus occidentalis	22	7	50	5	16	6	--	--	13	7	58	6	90	6	24	4	25	6	67	6	33	4	50	2
Quercus alba	22	5	33	5	41	6	33	6	63	5	12	4	3	3	41	5	--	--	--	--	--	--	--	--
Quercus lyrata	--	--	--	--	13	5	--	--	--	--	6	4	--	--	12	7	17	6	--	--	100	6	100	6
Quercus michauxii	6	4	17	7	28	6	67	6	--	--	36	7	3	6	41	6	33	6	--	--	--	--	--	--
Quercus nigra	6	7	33	5	69	6	67	6	13	5	15	7	7	6	35	5	8	4	33	6	--	--	--	--
Quercus pagoda	6	5	17	6	47	6	67	7	--	--	9	6	3	5	53	6	33	5	--	--	--	--	--	--
Quercus phellos	--	--	--	--	56	6	--	--	38	6	6	4	3	4	76	7	54	6	--	--	100	6	--	--
Ulmus alata	39	5	--	--	56	6	33	3	100	5	36	6	20	6	76	6	46	6	17	5	--	--	--	--
Ulmus [americana + rubra]	44	5	33	4	44	5	33	4	38	6	82	6	77	6	94	6	88	6	67	5	67	5	100	4
Vines	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Bignonia capreolata	56	2	50	2	94	3	100	5	100	2	97	3	70	2	100	3	79	3	67	2	--	--	50	2
*Lonicera japonica**	100	5	100	2	97	3	33	2	88	2	100	4	90	4	100	2	79	2	100	4	33	1	50	1
Parthenocissus quinquefolia	100	3	100	2	100	3	100	3	100	2	100	2	100	2	100	3	96	2	100	3	33	1	100	2
Smilax rotundifolia	67	2	50	2	94	2	100	2	88	2	76	2	70	4	94	4	100	3	100	3	100	2	100	2
Smilax walteri	6	2	33	2	13	2	--	--	25	5	12	3	--	--	18	3	21	2	17	2	--	--	50	3
Toxicodendron radicans	100	4	100	3	97	4	100	5	100	3	100	3	100	4	100	5	8	5	83	5	100	2	100	2
Vitis [cinerea + vulpina]	78	3	--	--	38	2	--	--	25	3	27	4	70	3	35	2	46	2	33	2	--	--	--	--
Vitis rotundifolia	100	3	100	4	100	4	100	2	75	2	85	3	47	3	88	2	58	2	67	3	--	--	100	2
Shrubs	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Aesculus sylvatica	11	4	--	--	9	2	--	--	63	4	42	4	17	4	24	4	4	3	--	--	33	2	--	--
Alnus serrulata	11	3	--	--	--	--	--	--	--	--	3	4	3	4	--	--	--	--	67	5	--	--	--	--
Asimina triloba	17	5	17	1	19	4	100	5	--	--	45	6	7	4	29	6	13	3	--	--	--	--	--	--
Carpinus caroliniana	78	6	67	4	91	6	67	4	75	6	64	5	37	4	88	5	71	4	50	6	67	4	--	--
Cornus florida	61	4	50	4	28	3	--	--	13	2	27	4	13	3	18	3	--	--	--	--	--	--	--	--
Ilex decidua	17	2	--	--	72	4	67	3	63	4	52	4	20	4	88	5	71	5	--	--	100	3	100	4
*Ligustrum sinense**	22	2	--	--	22	2	33	3	--	--	64	5	73	4	47	4	33	2	50	4	--	--	--	--
Lindera benzoin	56	7	--	--	19	3	--	--	--	--	67	6	43	6	18	4	8	4	17	7	--	--	--	--
Viburnum prunifolium	50	4	--	--	50	4	67	4	50	4	27	3	13	3	65	4	38	4	17	2	--	--	--	--
Herbs	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Amphicarpaea bracteata	89	3	50	2	44	2	--	--	63	2	39	2	27	2	6	1	8	2	17	3	--	--	--	--
Arisaema dracontium	11	2	--	--	3	1	67	2	13	1	42	2	17	2	24	2	4	1	17	1	--	--	--	--
Arisaema triphyllum	78	2	50	2	19	2	--	--	75	2	39	2	37	2	88	2	17	2	33	1	--	--	--	--
Arundinaria tecta	17	2	17	4	28	6	100	5	25	2	39	5	13	6	24	5	17	4	17	5	--	--	50	1
Asarum canadense	17	4	--	--	16	2	100	2	--	--	21	5	17	2	29	2	--	--	17	1	--	--	--	--
Bidens frondosa	11	1	17	2	13	2	33	1	25	1	6	3	27	2	24	2	29	2	50	3	67	2	100	2
Boehmeria cylindrica	67	2	50	2	47	2	100	2	25	2	64	2	83	3	76	2	92	3	100	6	100	2	50	1

Species																							
Botrypus virginianus	83	2	33	2	34	2	--	--	25	2	45	2	17	2	12	2	4	1	17	1	--	--	--	--
Bromus [nottowayanus + pubescens]	39	2	--	--	9	2	--	--	75	2	30	2	3	2	6	2	--	--	--	--	33	2	--	--
Carex [amphibola+grisea+corrugata]	72	3	17	2	66	5	100	3	50	3	73	4	73	4	59	4	38	4	33	1	--	--	50	3
Carex [radiata + rosea]	89	3	83	2	66	3	67	2	63	2	67	5	33	4	53	2	42	2	17	1	--	--	--	--
Carex blanda	61	3	50	2	41	3	--	--	63	3	67	3	33	3	35	2	29	2	--	--	--	--	50	1
Carex caroliniana	22	2	--	--	41	3	--	--	25	2	12	2	13	2	41	2	25	2	--	--	--	--	--	--
Carex crinita	11	2	17	3	16	2	--	--	--	--	3	2	3	2	29	2	33	3	83	6	67	2	--	--
Carex debilis	39	3	50	2	66	3	67	2	--	--	9	2	3	2	41	3	50	4	--	--	--	--	--	--
Carex grayi	6	1	--	--	13	2	--	--	38	2	61	3	40	5	12	3	33	5	17	3	--	--	50	2
Carex intumescens	6	2	33	1	41	2	100	2	--	--	3	2	10	2	47	3	29	5	--	--	67	2	--	--
Carex laxiculmis	17	3	33	2	9	2	--	--	63	3	6	2	--	--	--	--	--	--	--	--	--	--	--	--
Carex lupulina	6	1	--	--	--	--	--	--	--	--	3	1	17	2	29	2	58	4	67	4	33	5	--	--
Carex oxylepis	39	3	50	2	22	3	--	--	75	3	18	2	10	2	24	4	4	8	--	--	--	--	--	--
Carex tribuloides	33	2	17	1	25	2	33	1	13	1	42	2	60	4	76	3	88	4	100	4	33	2	50	2
Carex typhina	6	1	17	2	13	2	100	2	--	--	12	2	20	3	47	2	88	4	33	4	67	2	--	--
Chasmanthium latifolium	50	3	--	--	69	4	100	5	75	6	45	5	77	6	47	2	54	4	67	4	--	--	50	1
Commelina virginica	11	1	--	--	6	2	33	1	25	2	27	2	57	2	24	1	54	2	67	6	33	3	--	--
Danthonia spicata	--	--	17	2	22	3	--	--	63	5	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dichanthelium boscii	22	2	33	4	16	2	--	--	63	5	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dichanthelium commutatum	72	2	83	2	84	3	100	2	100	3	45	3	23	2	29	2	46	2	33	2	33	1	50	2
Dichanthelium laxiflorum	28	2	33	2	34	2	--	--	75	2	3	1	--	--	12	2	--	--	--	--	--	--	--	--
Dioscorea [quaternata + villosa]	28	2	--	--	56	2	33	2	63	2	27	2	13	2	6	2	8	2	17	2	--	--	--	--
Elephantopus carolinianus	--	--	--	--	6	2	67	2	--	--	--	--	--	--	--	--	4	2	--	--	--	--	--	--
Elymus virginicus s.l.	33	2	50	2	47	4	--	--	38	2	67	5	63	6	65	3	42	2	33	1	--	--	--	--
Elymus hystrix	33	4	33	3	9	2	--	--	100	3	15	3	23	4	--	--	--	--	--	--	--	--	--	--
Erechtites hieracifolia	22	2	33	1	16	1	100	2	13	1	30	2	37	2	59	2	63	1	17	1	33	1	100	1
Euonymus americanus	100	2	100	2	100	2	100	2	100	2	58	2	30	2	76	2	71	2	33	2	--	--	--	--
Festuca subverticillata	78	2	50	2	44	3	--	--	38	2	39	5	60	3	35	2	17	4	--	--	33	2	--	--
Galium aparine	39	2	--	--	3	1	--	--	50	2	64	2	70	4	18	2	17	2	67	2	33	1	--	--
Galium circaezans	78	2	17	1	50	2	--	--	63	2	6	1	3	1	--	--	4	1	--	--	--	--	--	--
Galium tinctorium	17	2	17	1	38	2	--	--	38	2	--	--	3	1	65	2	42	2	--	--	--	--	50	1
Galium triflorum	89	2	83	2	44	2	--	--	50	2	27	2	13	1	18	2	8	2	--	--	--	--	--	--
Gelsemium sempervirens	--	--	17	2	47	2	--	--	--	--	--	--	--	--	12	2	4	1	17	1	67	2	--	--
Geum canadense	84	2	50	2	34	2	--	--	50	1	48	2	43	2	29	2	50	2	50	2	--	--	--	--
Glyceria striata	39	2	50	2	16	2	--	--	13	1	15	2	37	2	65	2	50	4	83	4	67	2	--	--
[Gonolobus + Matelea]	33	2	33	1	34	2	67	2	25	2	73	2	60	2	18	2	8	2	--	--	--	--	--	--
Hexastylis arifolia	28	2	67	2	22	2	33	1	100	2	6	2	--	--	--	--	--	--	--	--	--	--	--	--
Hypericum hypericoides	6	1	33	2	59	2	--	--	88	2	--	--	--	--	6	1	8	1	--	--	--	--	--	--
Impatiens capensis	33	2	17	1	3	1	67	2	38	1	27	5	23	2	29	4	38	2	33	2	67	2	50	1
Juncus coriaceus	28	2	83	2	28	2	--	--	88	2	6	2	10	2	35	2	33	3	33	2	33	2	--	--

Species	%		%		%		%		%		%		%		%		%		%		%		%	
Juncus effusus	22	2	50	2	19	2	--	--	13	1	3	2	23	2	24	2	54	3	33	4	--	--	--	--
Laportea canadensis	6	1	--	--	--	--	--	--	--	--	52	5	57	4	24	2	4	1	--	--	--	--	--	--
Leersia virginica	17	2	33	2	31	2	--	--	63	4	9	3	53	2	18	2	50	3	50	3	--	--	--	--
Lobelia cardinalis	6	2	--	--	3	1	--	--	--	--	--	--	7	1	12	1	13	2	67	2	33	2	--	--
Lonicera japonica*	100	4	100	2	97	4	33	2	88	2	100	4	90	4	100	2	79	2	100	3	33	1	50	1
Ludwigia palustris	--	--	17	1	--	--	--	--	--	--	--	--	3	1	6	1	21	2	--	--	100	2	50	2
Lycopus virginicus	28	2	50	2	19	2	67	2	25	1	9	2	23	2	24	2	54	2	100	3	100	2	100	2
Melica mutica	22	3	--	--	56	2	--	--	25	2	12	3	--	--	18	1	8	2	--	--	--	--	--	--
Microstegium vimineum*	94	6	83	6	66	2	--	--	100	3	85	6	93	7	82	4	67	4	83	7	33	2	50	1
Mitchella repens	22	2	67	2	91	2	67	2	38	2	3	2	--	--	24	2	21	2	--	--	--	--	--	--
Oxalis sp	61	2	100	2	31	2	--	--	88	2	48	2	60	2	12	1	13	1	--	--	--	--	--	--
Parthenocissus quinquefolia	100	3	100	2	100	3	100	3	100	2	100	2	100	2	100	3	96	2	100	2	33	1	100	2
Passiflora lutea	39	2	67	2	38	2	67	1	50	2	39	2	27	2	6	1	4	1	--	--	--	--	--	--
Peltandra virginica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	29	2	83	4	--	--	--	--
Persicaria sp	11	1	17	2	--	--	33	1	--	--	6	2	40	2	12	2	46	3	83	3	33	1	50	2
Persicaria virginiana	50	2	50	2	19	2	33	2	25	1	76	2	87	2	53	2	42	2	67	2	33	2	--	--
Phryma leptostachya	72	2	--	--	6	1	--	--	--	--	6	2	3	1	--	--	4	2	--	--	--	--	--	--
Phytolacca americana	6	2	--	--	--	--	67	2	--	--	21	2	53	2	6	1	17	1	50	2	--	--	--	--
Pilea pumila	17	2	--	--	--	--	--	--	13	1	27	2	63	2	29	2	38	2	33	3	33	2	100	2
Poa [autumnalis + cuspidata]	50	5	50	2	78	4	--	--	63	3	45	3	27	2	82	3	42	3	50	2	--	--	50	2
Polygonatum biflorum	56	2	67	2	53	2	33	2	50	2	39	2	17	1	--	--	4	1	--	--	--	--	--	--
Polystichum acrostichoides	100	4	100	3	63	3	--	--	100	2	52	2	37	2	35	2	13	2	17	1	--	--	--	--
Potentilla [simplex + canadensis]	17	2	33	1	34	2	--	--	75	2	6	2	--	--	6	1	8	2	--	--	--	--	--	--
Ranunculus abortivus	44	2	17	1	6	1	100	2	50	1	39	2	33	2	41	2	17	2	50	1	--	--	50	2
Rosa sp	50	2	--	--	34	2	33	2	13	1	39	2	30	2	35	2	25	2	67	2	--	--	--	--
Rubus sp	94	2	50	2	94	2	100	2	38	1	55	2	40	2	71	3	79	2	100	2	67	2	50	2
Ruellia caroliniensis	33	2	17	1	31	2	--	--	75	2	3	2	--	--	18	1	21	2	--	--	--	--	--	--
Salvia lyrata	50	2	50	2	22	2	--	--	88	2	3	1	3	2	--	--	--	--	--	--	--	--	--	--
Sanicula canadensis	89	2	100	2	72	2	67	2	88	2	70	2	37	2	47	2	33	2	67	1	--	--	100	1
Saururus cernuus	6	2	33	2	19	2	--	--	13	2	15	2	23	3	29	2	71	6	33	6	100	7	100	2
Sceptridium [biternatum + dissectum]	67	2	50	2	78	2	33	1	50	2	39	2	17	2	53	2	54	2	17	2	--	--	50	1
Solidago sp	89	2	100	2	91	2	100	2	100	2	52	2	77	2	88	2	96	3	83	4	67	2	100	2
Symphoricarpos orbiculatus	17	2	--	--	13	2	--	--	63	2	36	3	10	2	--	--	--	--	--	--	--	--	--	--
Trachelospermum difforme	6	2	--	--	50	2	--	--	38	2	6	2	10	2	59	2	29	2	17	1	--	--	--	--
Verbesina alternifolia	39	2	33	2	38	2	--	--	100	2	70	3	80	3	12	1	8	1	17	2	--	--	--	--
Verbesina occidentalis	50	2	33	5	28	2	--	--	50	3	70	2	67	2	12	2	8	2	--	--	--	--	--	--
Viola sp	94	2	100	2	81	2	100	2	88	2	88	2	73	3	100	2	67	2	50	2	--	--	100	2
Zizia aurea	--	--	--	--	--	--	--	--	75	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Table 2.3: Relationship of the 14 recognized vegetation types to established NVC associations (http://www.natureserve.org/explorer/, September 1, 2010). Relationships are depicted in the table by five symbols: < indicating the type recognized here is included in the NVC concept, > indicating the type defined here includes the NVC concept, >< indicating that the two concepts overlap, ~ indicating the type recognized here is approximately equivalent to NVC concept, and = indicating the two concepts are equal to each other.

type	N	Alluvial vegetation type name	relationship		NVC community type (with CEGL code)
I. Small streams and narrow floodplain forests					
Ia.	18	*Liriodendron tulipifera – Liquidambar styraciflua / Lindera benzoin/ Amphicarpaea bracteata* Forest	><	4418	*Liquidambar styraciflua - Liriodendron tulipifera / Lindera benzoin / Arisaema triphyllum* Forest
			><	7329	*Liquidambar styraciflua - Liriodendron tulipifera / Onoclea sensibilis* Forest
			>	7321	*Fagus grandifolia - Acer barbatum / Asimina triloba / Toxicodendron radicans / Carex blanda* Forest
Ib.	6	*Liriodendron tulipifera - Betula nigra / Cornus florida / Sanicula canadensis var. canadensis* Forest	<	4418	*Liquidambar styraciflua - Liriodendron tulipifera / Lindera benzoin / Arisaema triphyllum* Forest
II. Oak-hickory flats					
IIa.	32	*Liquidambar styraciflua - Quercus nigra / Carpinus caroliniana / Mitchella repens* Forest	><	4419	*Liriodendron tulipifera / Asimina triloba / Arundinaria gigantea ssp. gigantea* Forest
			><	7329	*Liquidambar styraciflua - Liriodendron tulipifera / Onoclea sensibilis* Forest
IIb.	3	*Liquidambar styraciflua- Quercus pagoda- Carya cordiformis/ Asimina triloba/ Arundinaria tecta* Forest	><	4419	*Liriodendron tulipifera / Asimina triloba / Arundinaria gigantea ssp. gigantea* Forest
IIc.	8	*Carya carolinae-septentrionalis - Acer floridanum / Aesculus sylvatica/ Zizia aurea* Forest	>	8487	*Quercus shumardii - Quercus michauxii - Quercus nigra / Acer barbatum - Tilia americana var. heterophylla* Forest
			><	7356	*Quercus pagoda - Quercus phellos - Quercus lyrata - Quercus michauxii / Chasmanthium latifolium* Forest
III. Large river levee forests					
IIIa.	33	*Ulmus americana - Celtis laevigata/ Lindera benzoin / Osmorhiza longistylis* Levee Forest	>	7730	*Platanus occidentalis - Celtis laevigata - Fraxinus pennsylvanica / Lindera benzoin - Ilex decidua / Carex retroflexa* Forest
			><	7340	*Platanus occidentalis - Liquidambar styraciflua / Carpinus caroliniana - Asimina triloba* Forest
			><	4419	*Liriodendron tulipifera / Asimina triloba / Arundinaria gigantea ssp. gigantea* Forest
IIIb.	30	*Fraxinus pennsylvanica- Platanus occidentalis / Acer negundo/ Chasmanthium latifolium* Levee Forest	<	7340	*Platanus occidentalis - Liquidambar styraciflua / Carpinus caroliniana - Asimina triloba* Forest

type	N	Alluvial vegetation type name	relationship		NVC community type (with CEGL code)
		IV. Bottomland and swamp forests			
IVa.	17	*Quercus (phellos-pagoda-michauxii)- Ulmus americana / Ilex decidua / Arisaema triphyllum* Bottomland Forest	<	7356	*Quercus pagoda - Quercus phellos - Quercus lyrata - Quercus michauxii / Chasmanthium latifolium* Forest
IVb.	24	*Fraxinus pennsylvanica -Acer rubrum-Ulmus americana/ Ilex decidua / Saururus cernuus* Swamp Forest	~	6548	*Acer (rubrum, saccharinum) - Fraxinus pennsylvanica - Ulmus americana / Boehmeria cylindrica* Forest
IVc.	6	*Fraxinus pennsylvanica -Betula nigra-Platanus occidentalis/ Alnus serrulata / Boehmaria cylindrica* Swamp Forest	~	7312	*Betula nigra - Platanus occidentalis / Alnus serrulata / Boehmeria cylindrica* Forest
IVd.	3	*Quercus lyrata- Fraxinus pennsylvanica/ Saururus cernuus* Swamp Forest	<	7356	*Quercus pagoda - Quercus phellos - Quercus lyrata - Quercus michauxii / Chasmanthium latifolium* Forest
IVe.	2	*Carya aquatica- Nyssa aquatica* Swamp Forest	~	7397	*Quercus lyrata - Carya aquatica* Forest
		V. Riparian herbaceous vegetation			
Va.	10	*Justicia americana* herbaceous vegetation	=	4286	*Justicia americana* Herbaceous Vegetation
Vb.	2	*Hymenocallis coronaria - Justicia americana* herbaceous vegetation	=	4285	*Hymenocallis coronaria - Justicia americana* Herbaceous Vegetation
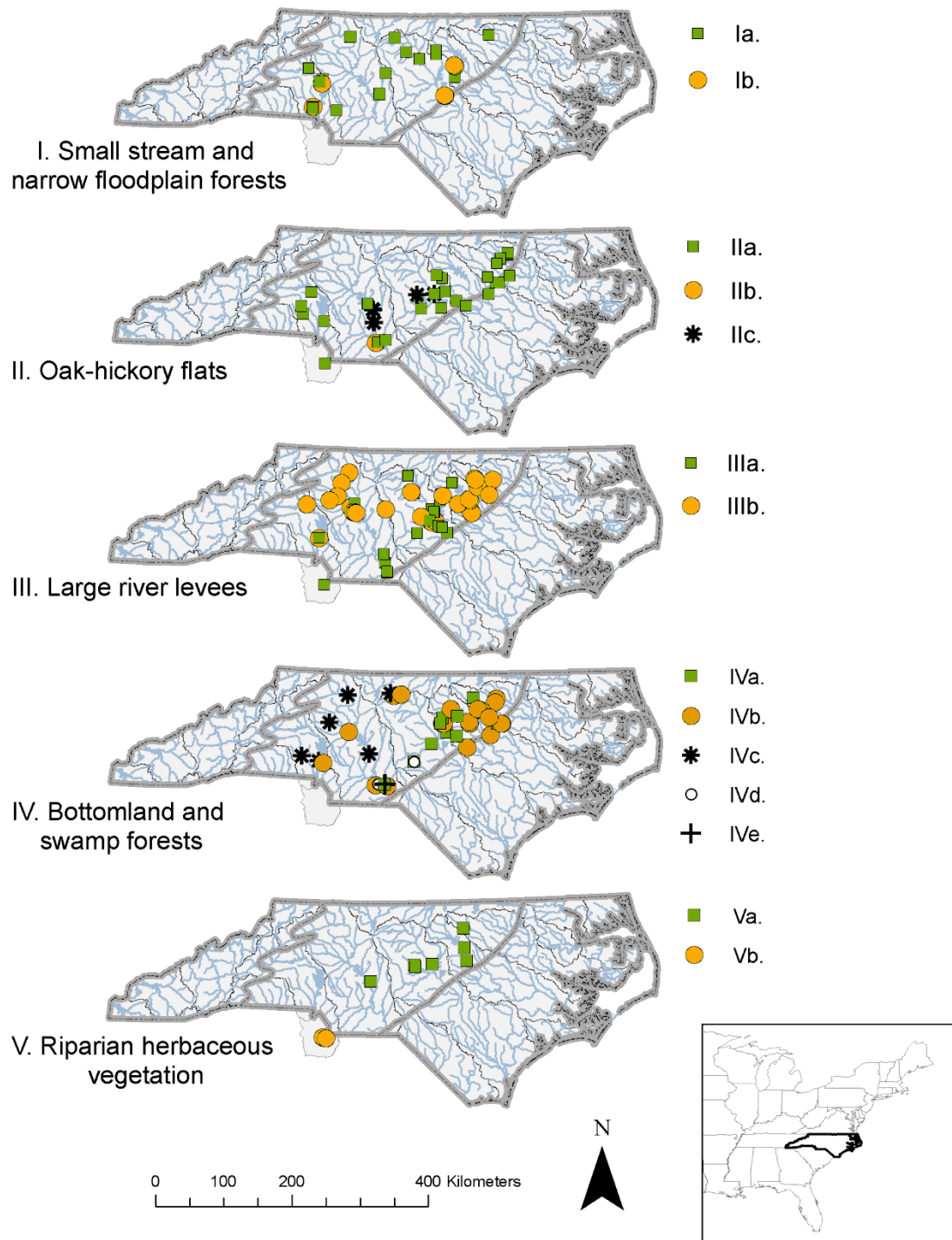
Figure 2.1: Distribution of 194 vegetation plots by the five mega vegetation groups. The inset map identifies the location of North Carolina in the U.S.A. In the North Carolina state maps, the wide grey lines delineate the three broad physiographic regions of North Carolina (left Mountains, center Piedmont, right Coastal Plain). The narrow grey lines delineate river basin boundaries; moving from West to East: Catawba, Yadkin- PeeDee, Cape Fear, Neuse, and Tar-Pamlico River Basins. The narrow blue lines indicate river courses.

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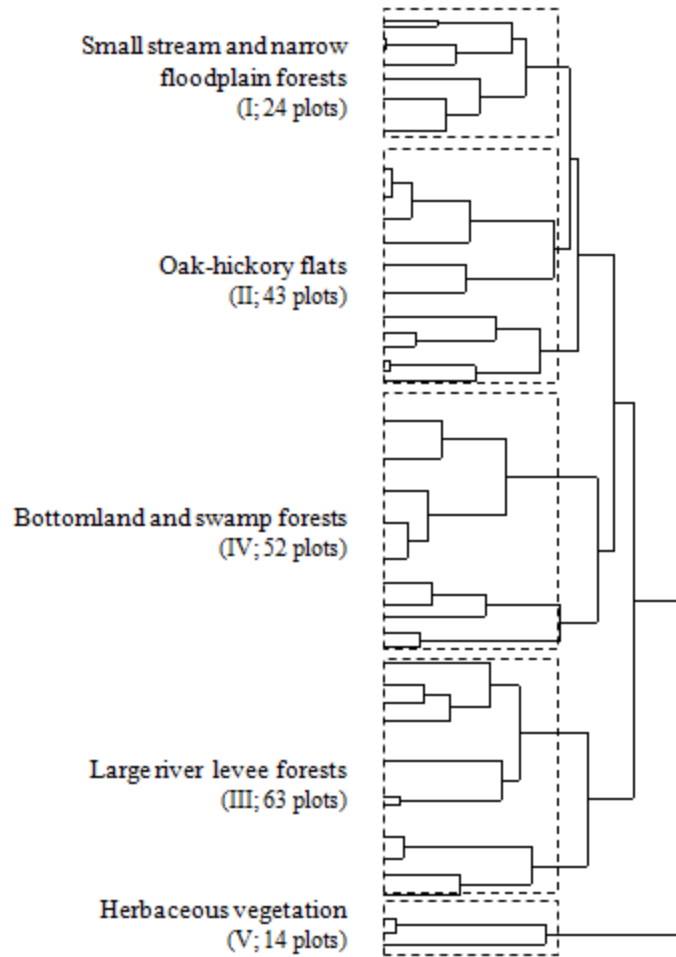
Figure 2.2: Dendrogram produced by flexible β cluster analysis (β = 0.25) of 194 vegetation plots. Five broader vegetation groups denoted by dashed boxes; roman numerals correspond with notation in the text.
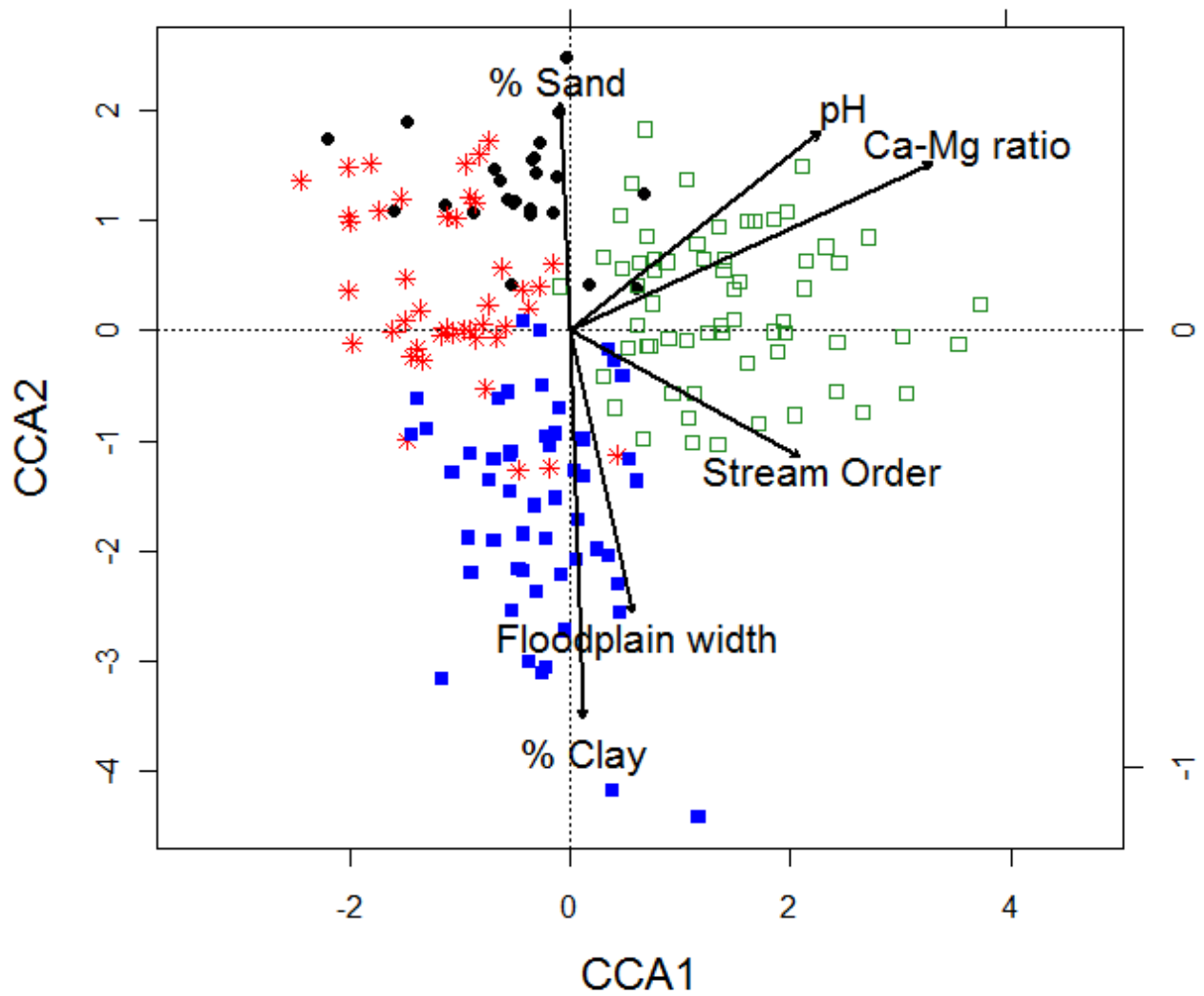
Figure 2.3: Canonical Correspondence Analysis (CCA) of 182 forest vegetation plots. The four broader geomorphic-floristic groups are indicated, where small stream and narrow floodplain forests (I) are indicated by filled circles, oak-hickory flats (II) are by asterisks, large river levees (III) by open squares, and bottomland and swamp forests (IV) by filled squares.

References

Benedetti, M.M., Raber, M.J., Smith, M.S., and Leonard, L.A. 2006. Mineralogical indicators of alluvial sediment sources in the Cape Fear River Basin, North Carolina. Physical Geography 27: 258-281.

Breiman, L. 2001. Random forests. Machine Learning 45: 5-32.

Brown, R. L. and R.K. Peet. 2003. Diversity and invasibility of Southern Appalachian plant communities. Ecology 84: 32-39.

Curtis, J.T. 1959. *The vegetation of Wisconsin: An ordination of plant communities.* The University of Wisconsin Press, Madison. 657p.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., and J.J. Lawler. 2007. Random forests for classification in ecology. Ecology 88: 2783-2792.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Faber-Langendoen, D., Aaseng, N., Hop, K., Lew-Smith, M., and J. Drake. 2007. Vegetation classification, mapping, and monitoring at Voyageurs National Park, Minnesota: An application of the U.S. National Vegetation Classification. Applied Vegetation Science 10: 361-374.

Gregory, S.V., Swanson, F.J., McKee, W.A. and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41: 540-551.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest ecology and management 90:117-125.

Hupp, C.R. 1986. Upstream variation in bottomland vegetation patterns, Northwestern Virginia. Bulletin of the Torrey Botanical Club 113: 421-430.

Hupp, C.R. and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.

Hupp, C.R. 2000. Hydrology, geomorphology and vegetation of Coastal Plain rivers in the south-eastern USA. Hydrological Processes 14, 2991-3010.

Jennings, M.D., Faber-Langendoen, D., Loucks, O.L., Peet, R.K. and D. Roberts. 2009. Standards for associations and alliances of the U.S. National Vegetation Classification. Ecological Monographs 79: 173-199.

Kellison, R.C., Young, M.J., Braham, R.R. and Jones, E.J. 1998. Major alluvial floodplains. In: Messina, M.G., and Conner, W.H. (eds.) *Southern Forested Wetlands: Ecology and Management,* pp. 291-324. Lewis, Boca Raton, Florida, USA.

Lane, C.P. and H.D. Texler. 2009. Generating quantitative regional plant community descriptions for restoration. Restoration Ecology 17: 42-50.

Liaw, A. and Wiener, M. 2002. Classification and Regression by randomForest. R News 2: 18-22.

McCune, B. and J.B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, USA.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis 15: 1409-1416.

Meitzen, K.M. 2009. Lateral channel migration effects on riparian forest structure and composition, Congaree River, South Carolina, USA. Wetlands 29: 465-475.

Nilsson, C., Grelsson, G., Johansson, M. and U. Sperens. 1989. Patterns of plant species richness along riverbanks. Ecology 70:77-84.

Naiman, R.J., Decamps, H. and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3: 209-213.

Peet, R.K. and N.L. Christensen. 1980. Hardwood forest vegetation of the North Carolina Piedmont. Veröffentlichungen Geobotanik Institut ETH. Stiftung Rübel 69: 14–39.

Peet, R. K., Wentworth, T. R. and P.S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262–274.

Rodwell, J.S. (ed.) 1991. *British plant communities.* Cambridge University Press, New York, NY, US.

Rodwell, J.S., Pignatti, S., Mucina, L. and J.H.J. Schaminée. 1995. European Vegetation Survey: update on progress. Journal of Vegetation Science 6: 759-762.

Romano, S.P. 2010. Our current understanding of the Upper Mississippi River System floodplain forest. Hydrobiologia 640: 115-124.

Schafale, M.P. and A.S. Weakley. 1990. *Classification of the Natural Communities of North Carolina: Third Approximation.* N.C. Natural Heritage Program, Raleigh, N.C. 325 pp.

Sharitz, R.R. and W.J. Mitsch. 1993. Southern floodplain forests. In: Martin, W.H., S.G.Boyce, and A.C. Echternacht, eds. *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities.* Wiley and Sons, New York, pp.311-372.

Sudduth, E.B., Meyer, J.L., and E.S. Bernhardt. 2007. Stream restoration practices in the Southeastern United States. Restoration Ecology 15: 573-583.

Trimble, S.W. 1974. *Man-induced soil erosion on the southern Piedmont, 1700-1970*. Soil Conservation Society of America, Ankeny, IA, U.S. A.

Townsend, P.A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. Plant Ecology 156: 43-58.

U.S. Federal Geographic Data Committee. 2008. National Vegetation Classification Standard, Version 2. FGDC Document number FGDC-STD-005-2008. Washington, D.C.

Weakley, A. S. 2010. *Flora of the Southern and Mid-Atlantic States.* University of North Carolina at Chapel Hill Herbarium, Chapel Hill, North Carolina, U.S.A.

Wharton, C.H., Kitchens, W.M., Pendleton, E.C., and T.W. Sipe. 1982. *The ecology of bottomland hardwood swamps of the southeast: A community profile.* U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37. 133 pp.

CHAPTER 3

High vascular plant richness in low order streams of the

Piedmont region, North Carolina, USA

Abstract

Riparian areas are known to be diverse and highly productive ecosystems. However, there is substantial debate over the spatial distribution of floodplain plant diversity across the riparian landscape. Few studies have explicitly examined the distribution of richness in this complex landscape, where small channels merge with larger channels producing a dendritic habitat-structure characterized by different sized rivers. This is particularly true in the Southeastern United States, where most riparian research has focused on larger-order Coastal Plain Rivers. In this chapter, I explore patterns of plant richness across rivers of different sizes in the Piedmont riparian landscape. I examine variation in total species richness and richness of species groups defined by nativity, growth habit, and habitat affinity across stream orders, in addition to testing for correlations between richness and environmental site descriptors.

Floodplain plant richness is highest in the smaller-order Piedmont rivers, whereas the proportion of exotic species and native species associated with bottomland-habitat increases with stream order. Total richness is also significantly related to floodplain width and soil texture variables, both of which reflect hydroperiod. Exotic richness is positively correlated

with soil fertility (pH). These results suggest that riparian richness is driven by local hydrologic and environmental settings, in addition to dispersal along the riparian corridor. Although native richness is negatively related to river size, the increasing proportion of exotic and native species associated with bottomland-habitat with increasing stream order suggests that these species accumulate in part as a consequence of the larger upstream propagule source. Significant correlations between richness and edaphic variables, however, suggest that local site conditions also influence riparian richness patterns.

Keywords: riparian vegetation, plant communities, spatial patterns, Southeastern United States, exotic plant species, stream order; dendritic landscape

Introduction

Riparian areas are known to be diverse and highly productive systems, functioning as both boundaries between terrestrial and aquatic ecosystems and corridors across the natural landscape, controlling the flux of energy, nutrients, and biota (Gregory et al. 1991; Naiman et al. 1993; Johansson et al. 1996; Naiman and Decamps 1997; Ward et al. 2002). The vascular plant communities of riparian corridors are unusually species rich, and riparian richness patterns have been the subject of many studies (Naiman et al. 1993; Nilsson et al. 1994; Brown and Peet 2003; Goebel et al. 2003; Mouw and Alaback 2003). However, there is still substantial debate over the spatial distribution of plant richness in these systems. Studies that have examined richness along the main channel of large rivers have found a variety of patterns, including a peak in native plant richness at the mid-reaches (Nilsson et al. 1989; Planty-Tabacchi et al. 1996), a monotonically increasing trend in native richness from the headwater regions to the river mouth (Gould and Walker 1997), and decreasing richness in downstream sections of the main stem (Renofalt et al. 2005). Contrary to the patterns exhibited by native taxa, some of the same studies that found decreasing native richness downstream found that exotic plant richness increases downstream (Planty-Tabacchi et al. 1996; Renofalt et al. 2005), suggesting that distinct plant groups may be distributed differently across the riparian landscape.

Many studies of riparian richness have focused on longitudinal patterns along the main river channel, and the diversity in the floodplain communities of these larger-order rivers is well documented (Nilsson et al. 1989; Tabacchi et al. 1996; Tabacchi and Planty-Tabacchi 2005; Mouw et al. 2009). However, real rivers are not simple linear

systems. Instead, they generally form a dendritic pattern, with small channels joining

larger channels to create a complex riparian landscape. Much less is known about the

biotic communities and processes associated with riparian zones bordering smaller

streams despite the fact that various authors have argued for the importance of unique

habitats in the headwater regions of the riparian landscape, which are home to rich and

distinctive biological communities (Richardson et al. 2005; Meyer et al. 2007).

Additionally, few studies have explicitly examined the distribution of richness in the

complex riparian landscape, spanning both smaller tributaries and larger channels (except

see Hupp 1986; Nilsson et al. 1994; Khomo and Rogers 2009). This is particularly true in

the Southeastern U.S., where studies of alluvial systems have primarily focused on the

larger coastal plain rivers, overlooking the smaller rivers of the inland physiographic

provinces (Wharton et al. 1982; Kellison et al. 1998; Townsend 2001).

In this paper, I explore spatial patterns of vascular plant richness and

environmental correlates in riparian landscapes of the Southeastern United States. I focus

on the distribution of richness across a range of river sizes in five Piedmont river basins.

In studies of large-order rivers, richness has been found to correlate with various

physiographic, hydrologic, and local environmental variables including elevation,

distance from river mouth, distance to channel, floodplain width, and soil texture and

nutrients (see Nilsson et al. 1989; Hupp and Osterkamp 1985; Tabacchi et al. 1996;

Turner et al. 2004; Renofalt et al. 2005; Mouw et al. 2009). I also explore how these

variables relate to plant richness and river size in Piedmont rivers. Additionally, since

species groups with different attributes may exhibit dissimilar spatial patterns and suggest

mechanisms driving these patterns, I also investigate richness patterns of species groups defined by nativity, growth habit, and habitat affinity.

Some studies of riparian plant richness have focused on the vegetation of the river margin (annual floodplain sensu Gould and Walker 1997; Nilsson et al. 1989; Nilsson et al. 1994; Renofalt et al. 2005), while others have expanded the focal spatial extent to include the whole floodplain (Gould and Walker 1997; Turner et al. 2004; Predick and Turner 2008; and others). This study examines vascular plant richness within the larger riparian corridor. I follow the definition of Naiman et al. 1993, where the riparian corridor "encompasses the stream channel and that portion of terrestrial landscape from the high water mark towards the uplands where vegetation may be influence by elevated water tables or flooding, and by the ability of soils to hold water." Previous studies have found richness can vary laterally across the width of the floodplain as a result of the differential influence of hydrologic and environmental variables (Brown and Peet 2003; Goebel et al. 2003; Augiar et al. 2006; Mouw et al. 2009); my primary focus here, however, is the longitudinal distribution of richness along rivers reaches of different size across the dendritic riparian landscape. Specifically, I address three questions in this paper. (1) How is plant species richness distributed across rivers of various sizes in the riparian landscape of the North Carolina Piedmont? (2) How do different species groups contribute to this pattern? (3) What environmental factors drive species richness in this system, and how are they related to river size?

Methods

Study area

The study area spans five North Carolina river basins: the Catawba, Yadkin, Cape Fear, Neuse, and Tar-Pamlico. Study sites were restricted to the Piedmont portion of each river basin, as defined by mapped geologic and soil units. Piedmont bedrock is largely composed of erosion-resistant metamorphic and igneous rocks, although a large southwest-northeast trending rift basin composed of Triassic sedimentary rock constitutes a prominent geologic feature of the lower Piedmont (Benedetti et al. 2006). Where Piedmont rivers cross the more resistant metamorphic and igneous bedrock, the river valley is relatively narrow and incised, whereas in the Triassic Basins, softer sedimentary rock and a long history of geomorphic development on an ancient landscape have resulted in wider floodplains.

The vegetation of the Southeastern United States floodplains is dominated by deciduous hardwood species (see Hodges 1998 and Kellison et al. 1998). There has been a long history of anthropogenic disturbance in the region, and the disturbances most likely to have affected riparian vegetation include sediment deposition, damming, and the subsequent regulation of downstream flow (Walter and Merritts 2008). The five rivers included in this study have all been influenced to some degree by these wide-spread disturbances, although I made an effort to exclude the most highly-altered regions of riparian vegetation from the dataset.

The rivers included in this study ranged in size from 1st to 7th order, with mean annual discharge ranging from < 1 to 220 cubic meters per second (cms). Watershed area ranged from 2.29 to 17,820 km^2. Where Piedmont rivers cross metamorphic and igneous bedrock the associated 100-year floodplain is relatively narrow ($\bar{x}$ = 340 m; 1st to 3rd quartile range: 150 - 450m), whereas the floodplains of the Triassic Basins are wider ($\bar{x}$ =

877.4m; 1st to 3rd quartile range: 500 - 1150m), with more variation in geomorphic setting.

Field methods

Sites were surveyed May through August in 2006, 2007, and 2008. Areas of high-quality natural vegetation were identified with assistance from state agencies such as the Natural Heritage Program and non-profit organizations, particularly local land trusts such as the Triangle Land Conservancy and the Land Trust for Central North Carolina. To various degrees, these organizations track natural areas of the state and were able to assist in locating and providing access to many of these sites. I selected sample sites in order to ensure representation from a broad geographic area within each of five river basins and to provide a good representation of various geologic features, geomorphic setting, stream order, and watershed area. In total, I established and recorded one hundred and eighty-two vegetation plots (Figure 3.1).

Vegetation was sampled following the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Vegetation plots were haphazardly established in areas of high-quality, homogenous vegetation. Plots ranged in size from $400m^2$ (typically 20m $\times$ 20m) to $1000m^2$ (typically 20m $\times$ 50m), depending upon the width of the floodplain; for consistency, I restricted the dataset for this study to the intensively sampled $400m^2$ area. All plots were located within the one-hundred year floodplain based upon NC floodplain maps and local vegetation composition; plots determined to be outside of the one-hundred year floodplain after field data collection were excluded from analyses. Each plot included four intensively sampled $100m^2$ modules (10m $\times$ 10m), with a smaller-scale observation in two corners encompassing a $10m^2$ nested sample area (Figure 3.2).

Plant taxa were identified to the finest taxonomic resolution possible. The definition of a "species" follows Weakley 2010, except for taxa that were impossible to correctly identify to the species-level as a result of the timing of field sampling and lack of floral parts. These taxa were grouped into lower resolution complexes (examples: *Rubus spp.*, *Oxalis spp., Carex* [*amphibola+grisea+corrugata*]; see Appendix 8), and each complex was treated as an individual taxon. Taxonomy was reviewed and standardized prior to analysis to account for differences due to plant identifications by a variety of individuals, both in the field and in the lab.

Observed taxa were partitioned into groups according to plant attributes. Three attributes were used to group species: (i) nativity (2 groups: exotic or native), (ii) growth form (6 groups: tree, shrub, subshrub, vine, forb, graminoid), and (iii) typical habitat association (8 groups: bottomland, upland, wet acidic, woodland, dry lowland acidic, mesic lowland, rich cove, ruderal), according to information obtained from regional floras, dissertations, and plant databases (Weakley 2005; USDA PLANTS 2010). Only native species were classified to a typical habitat association, and only habitats with a minimum of 10 associated species were included in the analyses. Classification of species to a habitat association follows the "90% rule," i.e., that 90% of the population of the taxon occurs in the habitat and up to 10% can occur in other habitats (Weakley 2005). The eight habitat-associations are defined as: *bottomland*, floodplains of large streams and rivers; *upland,* upland forests; *wet acidic,* boggy habitats; *woodland*, sunny habitats, including woodlands, glades, and prairies; *dry lowland acidic*, dry and dry-mesic forests of the Piedmont and less typically upper Coastal Plain, dominated by oaks and pines, and usually with extensive and diverse shrub cover of heaths; *mesic lowlands*, mesic lower

slopes and flats along small streams in the Piedmont and upper Coastal Plain, sometimes extending into mesic habitats in the mountains; *rich coves*, nutrient-rich, mesic forests of moderately high to low elevations in the Blue Ridge and the Blue Ridge escarpment, often occurring in "coves" or other "gathering" landforms, but can also be on open slopes or along small streams over the appropriate substrates; and *ruderal,* man-altered habitats. Taxa lacking attribute information were excluded from the richness by attribute-group analyses (see below). Composite taxa that spanned several attribute groups were also removed for these analyses (example: *Solidago spp.* complex with different habitat associations).

Environmental data collected in the field included percent slope and soil samples analyzed for texture and nutrient content. Soil samples included one surface sample from the top 10 cm of mineral soil in each intensive module, for a total of four surface samples, and one sub-surface sample from the center of each plot, 50 cm below the ground surface. Samples were analyzed by Brookside Laboratories, Inc., New Oxford, OH using the Mehlich 3 extraction method (Mehlich 1984). Exchangeable Ca, Mg, and K, pH, percent base saturation, extractable micronutrients (Fe, Cu, Zn, and Al), extractable P, bulk density, and percent organic matter were reported. Texture analyses included percent clay, silt, and sand. Samples from the four intensive modules were averaged for analysis.

Following field sampling, plot locations were mapped in a geographic information system (GIS) and additional environmental variables were calculated for each sample. These included stream order, cumulative drainage area, flow volume, and elevation. GIS analyses were based upon digital elevation models from the USGS

National Elevation Dataset (NED; http://ned.usgs.gov/), surface water themes from the

USGS National Hydrography Dataset (NHD; http://nhd.usgs.gov/), and additional

hydrologic variables from the NHDPlus dataset (http://www.horizon-

systems.com/nhdplus/). NED data were downloaded at a 30m resolution, and NHD data

were downloaded at the medium resolution (1:100,000-scale). Cumulative drainage area

and Strahler stream order were derived using the ArcHydro toolset (Strahler 1952). Flow

volume estimates for flowlines in the stream network were extracted from NHDPlus data.

Digital floodplain maps delineating the 100- year floodplain were downloaded from the

North Carolina Floodplain Mapping Program (http://www.ncfloodmaps.com/).

Quantitative analyses

I calculated total species richness at three scales: $10m^2$, $100m^2$ and $400m^2$. I

performed regression analyses to test for a relationship between species richness and

three hydrologic variables reflecting river size and location in the riparian network:

stream order, cumulative drainage area, and flow volume. As predicted by Shreve (1966),

the three hydrologic variables were highly correlated, and I present analyses related only

to stream order. Since the response data consisted of discrete species counts, I explored

both normal and negative binomial regression models. Model evaluation by AIC

suggested no difference in fit between the two models; mean-variance relationships

suggested that normal models were appropriate for these data. Richness patterns were

qualitatively equal at all three spatial scales, so I limited further analyses to the $400m^2$

scale. I tested for both linear and quadratic relationships in all regression analyses.

To explore how different species groups influence riparian richness patterns, I

also used regression models to examine the distribution of richness in the three sets of

species groups across stream orders, where groups were defined by nativity, growth form, and habitat affinity. I used two measures to examine the relationships between group richness and stream order: total richness and proportion of total richness in each category. For each group, I tested for a relationship between both floristic measures and stream order. Since there were more categories of growth form and habitat association, I also calculated and graphed the average total richness per plot and average proportion of richness contributed by species groups per plot to visually illustrate the distribution of all growth form and habitat association groups across stream orders. To examine the diversity of plant attribute groups found at each stream order, I calculated Simpson diversity indices using the average richness of growth form and habitat association groups.

I tested for correlations between 15 quantitative environmental variables and species richness using Pearson correlation coefficients. Environmental variables included 3 hydrologic variables (stream order, cumulative drainage area, and flow volume), 5 landscape descriptors (elevation, distance to mouth, slope, floodplain width, and distance to channel), and 7 edaphic variables (pH, % organic matter, bulk density, base saturation, Ca/Mg ratio, % sand, and % clay). To explore how environmental variables vary across the riparian landscape, I also tested for correlation between each of the environmental variables and stream order.

All analyses were performed in R (R Development Core Team 2010). Negative binomial models were fitted in the MASS package (Venables and Ripley 2002). Diversity indices were calculated using the vegan package (Oksanen et al. 2010).

Results

Floristic overview

I recognized a total of 530 vascular plant taxa in 121 families. Exotic species

comprised 6% of the dataset (34 species were identified as non-native according to

USDA Plants Database). The majority of taxa in the dataset were forbs (48%), followed

by graminoids (19%), trees (13%), shrubs (10%), vines (8%), and subshrubs ($< 2\%$). The

most common habitat associations were bottomland (28%) and lowland mesic (14%)

habitats, followed by upland (10%), ruderal (8%), wet acidic (7%), dry lowland acidic

(6%), woodland (5%), and rich cove (4%). The remaining 18% of species in the dataset

either were associated with a habitat-type rare in this dataset or were not classified to a

habitat due to a lack of sufficient data on the species.

Spatial richness patterns

Total species richness at the three spatial scales decreased with increasing stream

order (400m^2: $r^2 = 0.09$, $P < .0001$; 100m^2: $r^2 = 0.07$, $P < .001$; 100m^2: $r^2 = 0.06$, $P < .01$;

Figure 3.3). Native species richness showed a significant negative relationship with

increasing stream order ($r^2 = 0.10$, $P < .0001$), whereas exotic species did not exhibit any

significant relationship with stream order ($P = .25$; Figure 3.4). The proportion of exotic

species, on the other hand, increased with stream order ($r^2 = 0.07$, $P < 0.001$; Figure 3.5),

whereas the proportion of native species declined ($r^2 = 0.06$, $P < 0.001$; Figure 3.5).

Forb species richness showed the strongest decrease with increasing stream order

($y = 23.2 -1.45\text{x}$, $r^2 = .08$, $P < .001$; Figure 3.6)**,** although tree, subshrub, and graminoid

richness also significantly decreased with increasing stream order (Figure 3.6). I found no

significant relationship between species richness in the other growth form groups and

stream order. The proportion of forb, vine, and graminoid richness vary quadratically with stream order, with the lowest proportion of forb richness in the mid-order streams ($r^2 = .13$, $P < 0.001$) and the highest proportion of vine and graminoid richness in the middle to higher order streams (vine: $r^2 = .15$, $P < 0.003$; graminoid: $r^2 = .03$, $P = 0.023$; Figure 3.7). Proportion of subshrubs decreased monotonically with stream order. Simpson diversity indices for growth form diversity peaked in the mid-sized rivers (Figure 3.8).

Species richness associated with upland, wet acidic, woodland, dry lowland acidic, mesic lowland, and rich cove habitats all decreased significantly with increasing stream order (Figure 3.9). Neither richness of species associated with bottomland habitats nor ruderal habitats was significantly related to stream order. The proportion of richness of six habitat association groups was significantly related to stream order (bottomland; upland; wet acidic; dry lowland acidic; mesic lowland; rich cove; Figure 3.10). However, the bottomland habitat associated group was the only group that significantly increased in the proportion of richness with increasing stream order ($y = .35 + 0.02x$, $r^2 = .10$, $P < 0.0001$; Figure 3.10). Simpson diversity indices were highest in the lower order streams for the habitat association groups (Figure 3.11).

Relationship between vegetation and environment

The strongest correlation between total species richness and the environment was a negative correlation with floodplain width and clay content (floodplain width: $r = -.45$, $P < 0.0001$; clay: $r = -.41$, $P < 0.0001$; Table 3.1). Exotic richness, on the other hand, was positively correlated with edaphic variables associated with soil fertility, including pH, Ca/Mg ratio, and base saturation (pH: $r = .34$, $P < 0.001$; Ca/Mg: $r = .40$, $P < 0.001$;

base saturation: $r = .35$, $P < 0.001$; Table 3.1). Forb, tree, and upland richness correlations were very similar to those of the whole floristic dataset. Bottomland species richness was not significantly correlated to any environmental variables. Stream order was strongly correlated with the two additional hydrologic variables (cumulative drainage area: $r = .70$, $P < 0.001$; flow volume: $r = .77$, $P < 0.001$; Table 3.1) and was not significantly correlated with any of the soil fertility variables. Stream order was positively correlated with floodplain width and negatively correlated with elevation and distance to mouth (floodplain width: $r = .33$, $P < 0.001$; elevation: $r = -.19$, $P < 0.05$; distance to mouth: $r = -.17$, $P < 0.05$; Table 3.1).

Discussion

Floristic patterns

Piedmont floodplain plant species richness declines with increasing river size. This pattern was qualitatively consistent across all spatial scales examined in this study ($10m^2$, $100m^2$ and $400m^2$) and also when constrained to native taxa. However, in contrast to native diversity patterns, I found that larger-order rivers had a greater proportion of exotic plant taxa than smaller rivers.

The negative relationship between native species richness and river size found in Piedmont rivers contradicts earlier studies of riparian vegetation patterns in Europe (Nilsson et al. 1989; Nilsson et al. 1994; Planty-Tabacchi 1996). These studies found a mid-reach peak in richness along the larger order, main channel and higher richness in the main channel, when compared with smaller tributaries. However, results of these studies may not be directly comparable to the results presented here as the European

studies only examined richness in the narrow belt of streamside vegetation, known as the annual floodplain. On the other hand, studies that have focused on patterns across the larger riparian corridor in both arid and arctic systems have also found richness to increase in downstream riparian areas (Bendix 1997; Gould and Walker 1997). Alternatively, a more recent study of boreal rivers found a decrease in native species richness from the headwater to the coast, whereas ruderal species richness increased towards the mouth (Renofalt et al. 2005), results that are more consistent with those reported here. The fact that spatial richness patterns appear so variable across river systems in different geographic-climatic regions highlights the inherent complexity of riparian landscapes, where a wide variety of processes, many of which are unique to riparian systems, influence species richness. These unique riparian processes may include dispersal in a dendritically-arranged habitat, hydrologic movement of sediment and organisms, and seasonal flooding disturbances.

In this study, forb richness had the strongest negative relationship with stream order. Since forbs were the most common species in our dataset (48% of taxa), a strong decrease in forb richness substantially contributed to the overall decline in richness with increasing stream order (although tree, shrub, and graminoid richness also declined with increasing stream order). The proportion of forb taxa was lowest in the mid-order rivers, resulting in a greater diversity of growth forms. The proportion of vine taxa was highest in the mid to larger stream orders, where vines are known to be an important component of bottomland forest communities (Allen et al. 2007). Although the proportion of graminoid and subshrubs was also significantly related to stream order, the regression models explained only a small amount of the variation of these species groups.

Upland habitat species richness was highest in the small order streams, whereas the proportion of taxa associated with bottomland habitats was highest in the large-order streams. These results are consistent with earlier studies that found both a larger proportion of non-riparian species in areas of spatially constrained floodplain habitat, similar to small order stream floodplains, and decreased abundance of non-riparian species in downstream riparian areas (Tabacchi et al. 1996). The floodplain plant communities of smaller-order streams were also more diverse with regard to habitat associations of the resident species when compared to communities of large-order streams, where over 50% of species were associated with bottomland habitat. The decrease in bottomland-habitat associated species and increased diversity in the small order streams may reflect isolation from other riparian habitat, which might reduce dispersal of alluvial species into small-stream riparian areas. Additionally, small-stream habitats may be less affected by typical alluvial dynamics, such as flooding events, facilitating the long-term coexistence of non-alluvial species with the more typical alluvial species. Where coalescing rivers grow larger and fluvial landforms are better developed, species physiological tolerances to riparian processes like flooding may become more important, resulting in a species pool increasingly limited to alluvial species. In these larger-river floodplains, lower species richness may be a result of this physiological, flood-tolerance filter.

Relationships to the environment

Native and total richness exhibited similar relationships to environmental variation in the Piedmont riparian landscape. Richness was lowest in the wide floodplains, larger order streams, and soils high in clay content. In the Piedmont riparian

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landscape, fine textured soils most commonly occur on the low areas of wide floodplains where there are long, low-energy floods. The sustained flooding at these sites is stressful to many plant species and precludes species not adapted to these conditions from long term persistence. Alternatively, richness was positively correlated with sand and elevation. Sandy soils of the Piedmont riparian landscape frequently occur in the higher-elevation, small-stream forests and levee-flat geomorphic sites, where flooding is more rare and of short duration. These results are consistent with previous work in riparian systems that has also documented a significant relationship between richness and both substrate particle size and flow energy (Nilsson et al. 1989; Bendix 1997; Mouw et al. 2009).

Unlike native richness, however, exotic species richness was positively correlated with soil fertility, represented by pH, base saturation, and Ca/Mg ratio. Other studies in alluvial systems have also found soil pH, as a proxy for fertility, to have a positive effect on exotic species richness (Brown and Peet 2003; Vidra et al. 2006), whereas total richness is weakly or negatively correlated with pH (Renofalt et al. 2005; Vidra et al. 2006; however, Gould and Walker 1997 found a strong positive correlation between native richness and soil pH in an arctic riparian system). Additionally, recent studies in grassland and deciduous forest ecosystems have found a strong relationship between soil fertility and exotic richness (Thompson et al. 2001; Huebner and Tobin 2006; Huebner et al. 2009). These results are consistent with hypotheses that exotic invasions are promoted by resource availability and suggest that nutrient rich soils may be more prone to exotic invasion.

Stream order was significantly correlated with environmental variables that reflect expected changes in the riparian landscape as stream order increases. Stream order was positively correlated with cumulative drainage area, flow volume, and floodplain width, whereas it is negatively correlated with elevation and distance to the mouth. The positive correlation with floodplain width is partly due to the prominence of Triassic Basin bedrock the downstream, southeastern regions of the Piedmont river basins. The Triassic Basins sedimentary bedrock is less resistant than the bedrock of the inner Piedmont and allows erosion of wider floodplains in the same downstream region where the main channel of the Piedmont rivers has become a high-order river.

Synthesis: spatial patterns of alluvial plant community richness

This study demonstrates that the flora associated with different sized rivers in the Piedmont riparian landscape is distinctive. The flora of larger rivers is not simply a collection of the flora in smaller tributaries, a conclusion well supported by other riparian studies (Hupp 1986; Nilsson et al 1994; Chapter 2). The proportion of species groups based on nativity, life form, and habitat affinity all varied with stream order, as did total richness at three spatial scales. Additionally, none of our soil texture and chemistry variables were related to stream size, suggesting that they cannot explain the observed variation in richness across stream order.

These results are consistent with the view of riparian areas as both boundaries and corridors. The boundary concept is most appropriate in the small-order stream, headwater regions where the influence of surrounding uplands on the riparian flora is strongest. In contrast, the concept of the riparian zone acting as a corridor is more appropriate in the larger-order rivers where the influence of upstream riparian area is greatest. In low-order

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streams, propagule inputs of riparian species are limited by a small upstream watershed area. This is evident in the results presented here, where the lowest proportion of bottomland-associated species occurred in the small-stream floodplain forests, but total richness was high in these sites, augmented through floristic contributions from the surrounding uplands. In contrast, in larger-order rivers, the flora had a higher proportion of both exotic species and species associated with alluvial habitats, suggesting that these sites have accumulated alluvial species and exotic species as they move downstream from more extensive upstream watershed.

Downstream dispersal has commonly been proposed as an explanation for riparian diversity patterns (Johansson et al. 1996; Andersson et al. 2000; Renofalt et al. 2005); this study suggests that both location in the riparian landscape, which is related to downstream dispersal, and local environmental conditions are important drivers of richness in Piedmont riparian systems. Richness was significantly related to variables reflecting river size and position in the riparian landscape (stream order, upstream drainage area, elevation), but was also influenced by local edaphic conditions. Soil texture reflects site flood energy, with long, low-energy flood events resulting in fine-textured sediment deposition. A strong negative correlation between richness and fine-textured sediments suggests that local hydrology influences species richness. Soil nutrient variables were positively correlated to exotic richness further suggesting that local resource availability plays a role in driving richness patterns.

These results have implications for conservation and restoration practices in riparian areas in the Southeastern U.S. Other authors have argued for the important contribution of small-order and headwater streams to regional riparian diversity (Meyer

et al. 2007). This study supports this position by elucidating the spatial distribution of diversity across the riparian landscape and highlighting the importance of taking a landscape perspective in riparian conservation efforts. Streams of different sizes contribute differently to the regional diversity of these systems, and this study suggests a stronger emphasis on conservation and restoration of small streams and tributaries is appropriate.

Table 3.1. Correlations between richness and 15 environmental variables (Pearson's correlation coefficients). Table also includes correlation between stream order and the environmental variables. Variable codes include: Cum. drain.= cumulative drainage, Flow vol.= flow volume, Elev.= elevation, Dist. to mouth= river distance to mouth, Dist. to channel= distance to river channel, O.M.= % organic matter, Base. sat.= base saturation. Significance codes: *, $P < 0.05$; ***, $P < 0.001$.

Richness	Stream order	Cum. drain.	Flow vol.	Elev.	Dist. to mouth	Slope	Floodplain width	Dist. to channel	Sand	Clay	pH	O.M.	Dens.	Base sat.	Ca/Mg
Total	-0.29***	-0.20*	-0.27***	0.22*	0.13	0.20*	-0.45***	-0.22*	0.27***	-0.41***	0.07	-0.13	0.24*	0.08	-0.12
Native	-0.31***	-0.22*	-0.28***	0.19*	0.10	0.19*	-0.44***	-0.21*	0.26***	-0.38***	0.04	-0.11	0.21*	0.04	-0.17
Exotic	0.09	0.07	-0.01	0.15*	0.12	0.04	-0.31***	-0.19*	0.21*	-0.39***	0.34***	-0.21*	0.25*	0.35***	0.40***
Forb	-0.30***	-0.09	-0.25*	0.39***	0.31***	0.25*	-0.44***	-0.22*	0.17*	-0.30***	0.17*	-0.07	0.21*	0.17*	0.14
Graminoid	-0.19*	-0.20*	-0.18*	-0.04	-0.09	-0.03	-0.22*	-0.03	0.11	-0.11	-0.11	-0.08	0.16*	-0.10	-0.26***
Shrub	-0.06	-0.05	-0.09	0.01	-0.07	0.11	-0.16	-0.11	0.20*	-0.32***	0.12	-0.08	0.07	0.11	-0.09
Subshrub	-0.24*	-0.25*	-0.28*	0.14	0.08	0.16*	-0.26***	-0.06	0.24*	-0.26***	-0.10	-0.09	0.11	-0.10	-0.31***
Vine	0.02	-0.11	-0.05	0.04	0.00	0.12	-0.16*	-0.16*	0.26***	-0.33***	0.11	-0.08	0.14	0.11	-0.09
Tree	-0.24*	-0.21*	-0.20*	0.04	-0.02	0.13	-0.40***	-0.23*	0.25*	-0.4***	0.01	-0.13	0.13	0.02	-0.17*
Bottomland	0.03	-0.07	0.08	-0.08	-0.11	-0.10	-0.10	-0.04	-0.02	0.05	0.11	0.02	-0.03	0.11	-0.02
Upland forest	-0.30***	-0.25*	-0.31***	0.17*	0.09	0.19*	-0.33***	-0.20***	0.30***	-0.38***	-0.09	-0.09	0.20*	-0.09	-0.28***
Wet acidic	-0.21*	-0.20*	-0.16*	0.03	0.00	-0.14	-0.01	0.26***	0.04	0.15*	-0.36***	0.16*	-0.17*	-0.35***	-0.30***
Woodland	-0.17*	-0.09	-0.12	0.07	-0.02	0.04	-0.31***	-0.17*	0.14	-0.25*	-0.03	-0.14	0.20*	-0.02	-0.22*
Dry lowland acidic	-0.27***	-0.16*	-0.26***	0.13	0.10	0.16*	-0.28***	-0.12	0.19*	-0.26*	-0.15*	-0.10	0.15	-0.15*	-0.28***
Mesic lowland	-0.27***	-0.17*	-0.28***	0.22*	0.13	0.25*	-0.49***	-0.30***	0.28***	-0.54***	0.27***	-0.19*	0.27***	0.28***	0.11
Ruderal	-0.02	0.13	0.01	0.15*	0.15*	0.02	-0.09	-0.11	0.06	-0.01	0.08	-0.03	0.15	0.09	0.23*
Rich cove	-0.23*	-0.08	-0.24*	0.21*	0.25*	0.52***	-0.20*	0.00	0.10	-0.22*	0.02	-0.06	0.17*	0.03	-0.08
Stream Order	1***	0.70***	0.77***	-0.19*	-0.17*	-0.12	0.33***	-0.04	-0.02	0.08	0.11	-0.06	0.03	0.10	0.05
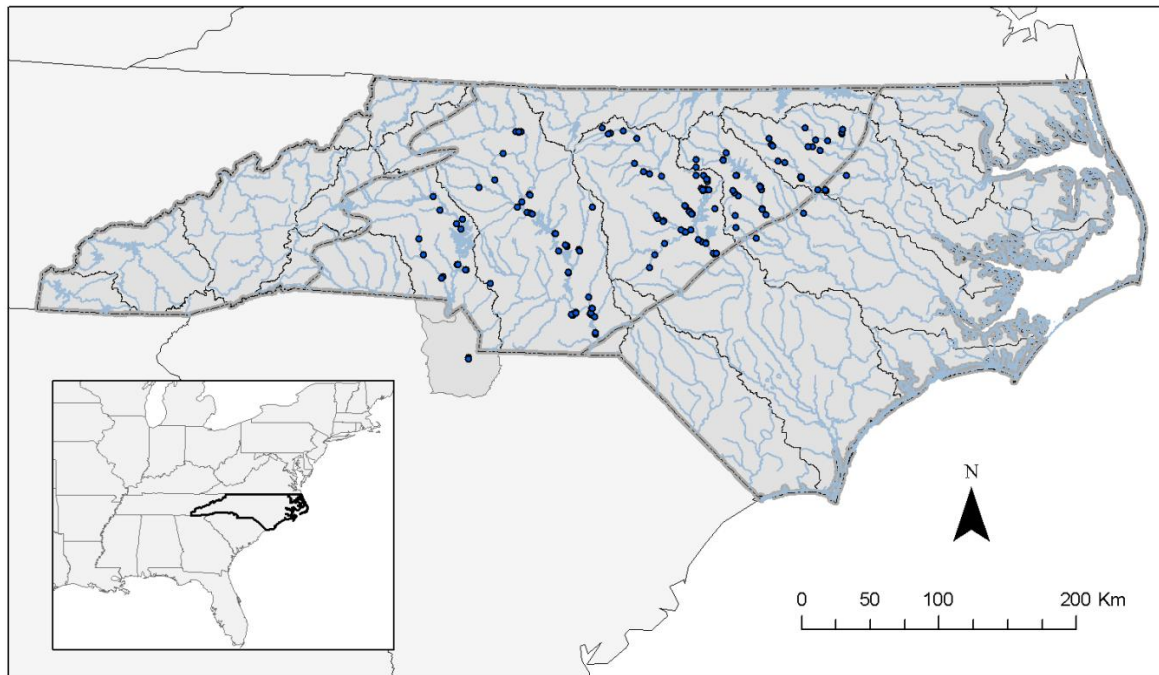
Figure 3.1: One hundred and eighty two vegetation plots across five river basins in the North Carolina Piedmont. Moving West to East, basins include the Catawba, Yadkin, Cape Fear, Neuse, and Tar-Pamlico. All plots are located within the one-hundred year floodplain of the nearest river channel.
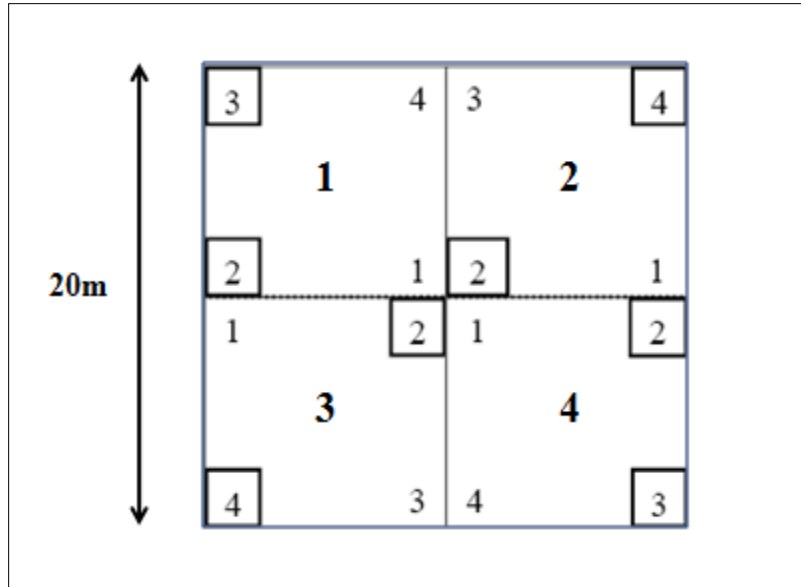
Figure 3.2: Nested quadrat vegetation plot design. 400m^2 plots of 20×20m included 4 modules of 10×10m, each with 2 nested subplots of 10m^2 (3.16×3.16m).
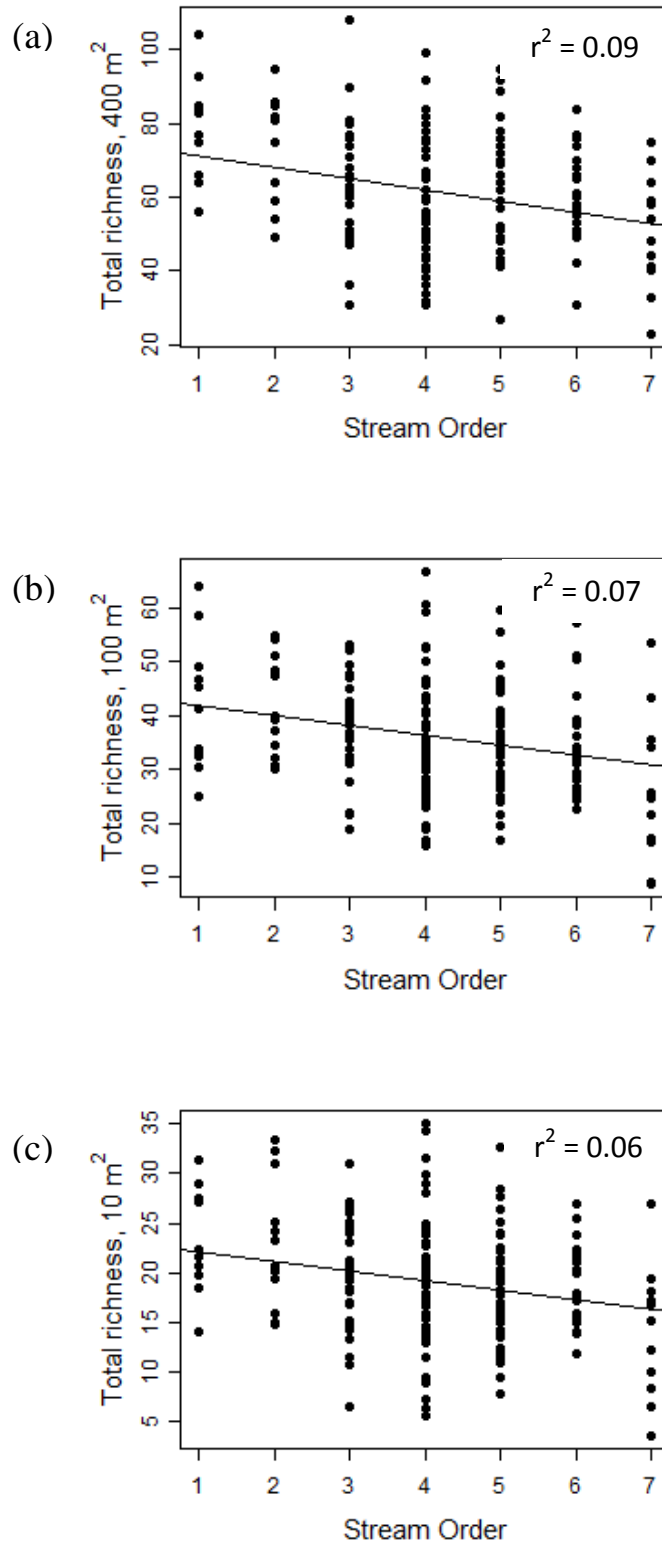
Figure 3.3: Total species richness across stream order at three scales: (a) 400m², (b) 100m², and (c) 10m². The equations for the regression lines are: (a) $y = 74.5 - 3.10x$; $P < 0.0001$; (b) $y = 43.7 - 1.83x$; $P < 0.001$; (c) $y = 23.1 - .96x$; $P < 0.002$.
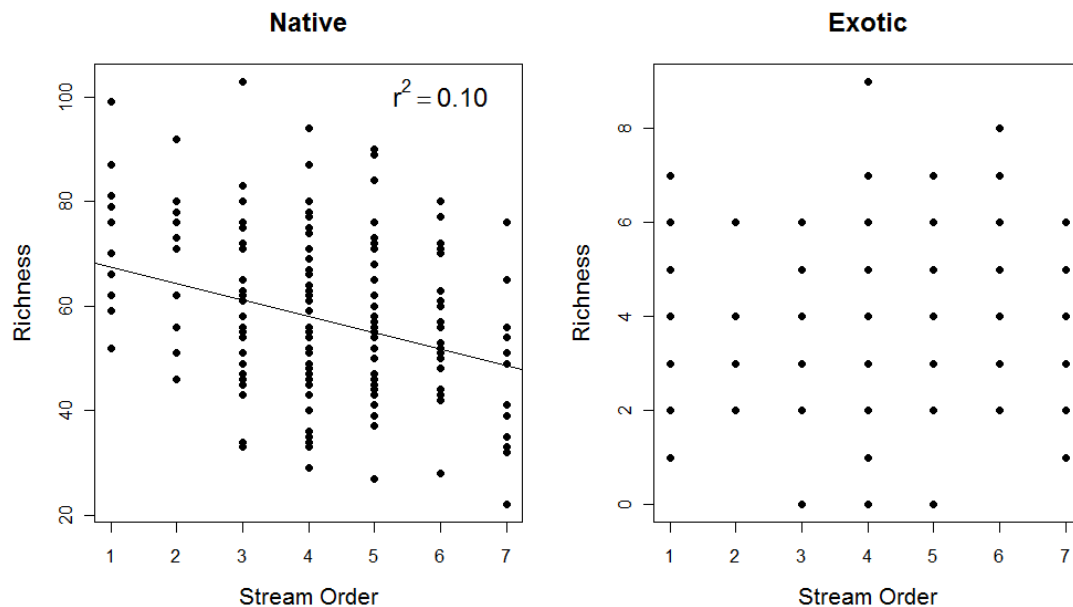
Figure 3.4: Total native species richness and exotic species richness across stream order (400m^2). Native species richness varies linearly with stream order ($y = 70.67 - 3.16x$; $P < 0.0001$). Exotic species richness is not significantly related to stream order ($P = .25$).
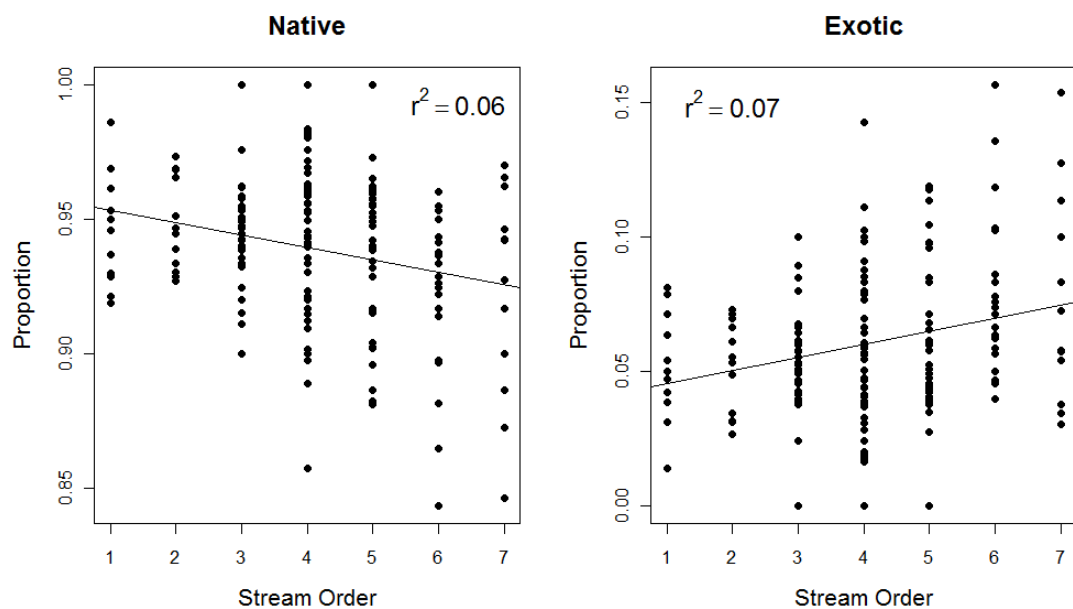
Figure 3.5: Proportion of native and exotic flora across stream order (400m^2). Both proportion of native and exotic species are linearly related to stream order (native equation: $y = .95 - .0045x$; $P < 0.001$; exotic equation: $y = .04 + .0048x$; $P < 0.001$).
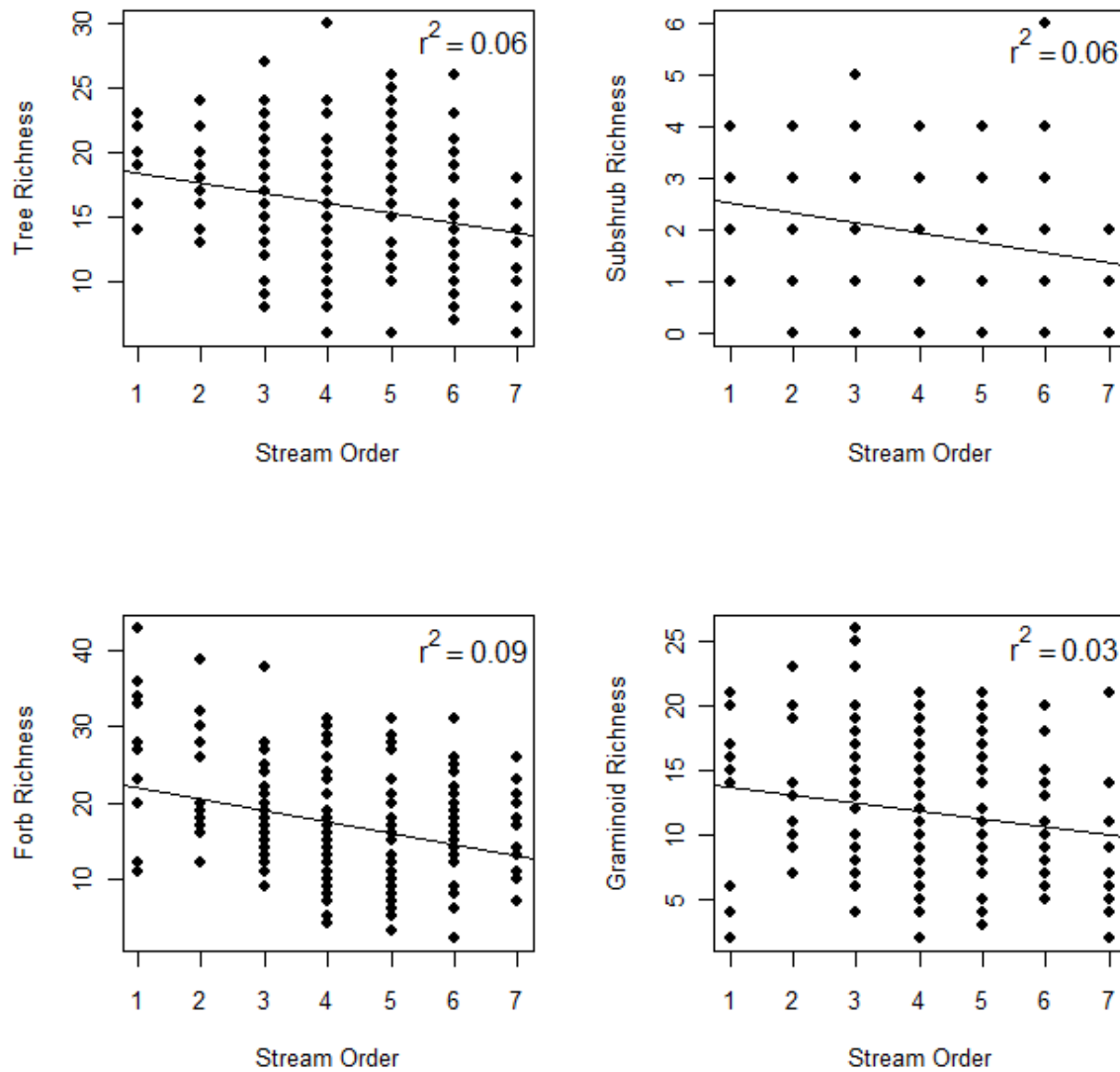
Figure 3.6: Growth form group richness with significant linear relationships to stream order (Tree: $y = 19.18 - .77x$, $r^2 = .06$, $P < 0.001$; Subshrub: $y = 2.72 - .20x$, $r^2 = .06$, $P < 0.002$; Forb: $y = 23.57 - 1.50x$; $r^2 = .08$, $P < 0.0001$; Graminoid: $y = 14.34 - .60x$, $r^2 = .03$, $P < 0.001$).
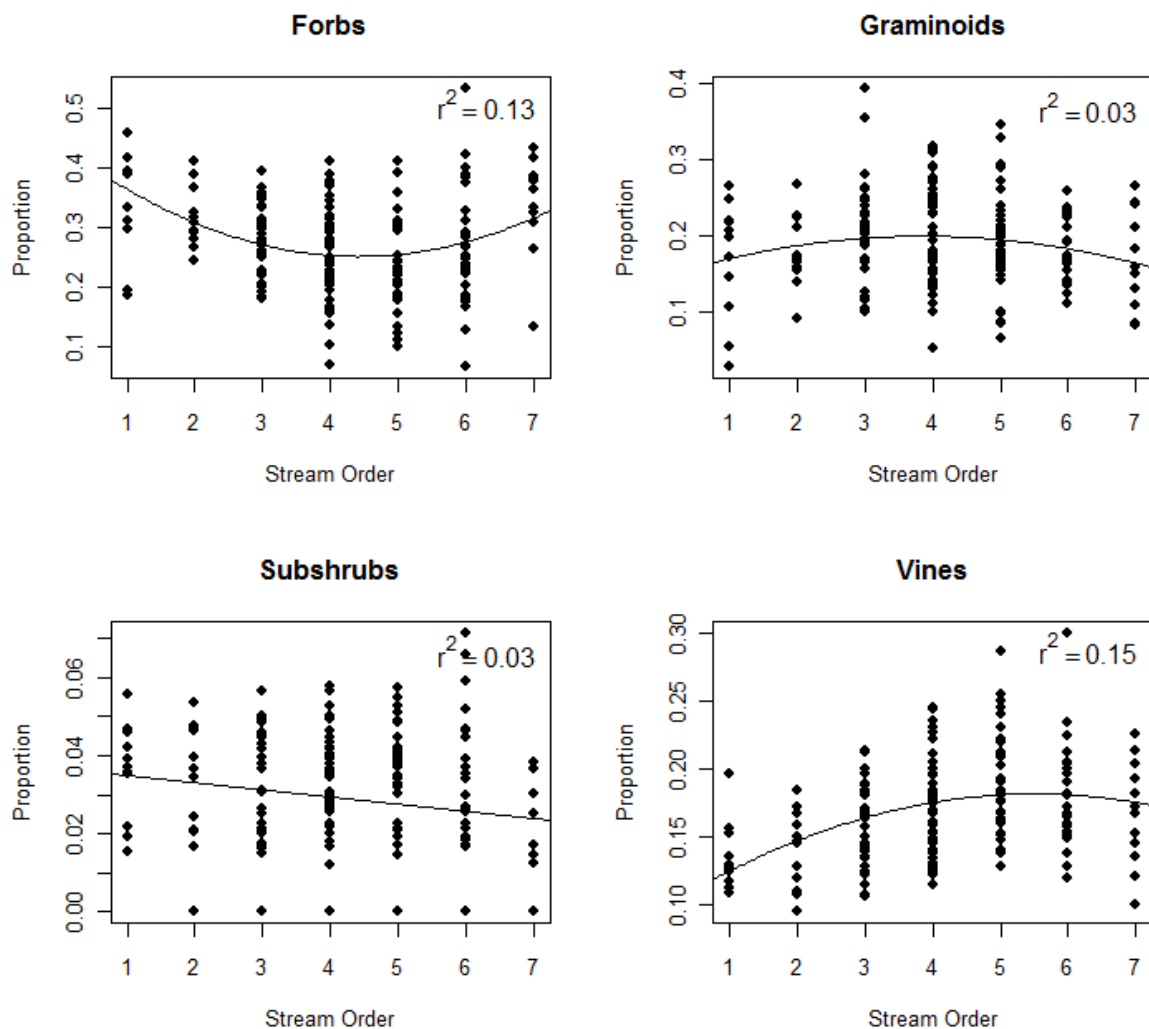
Figure 3.7: Proportion of growth form richness with significant relationships to stream order (Forbs: $y = .44 - .09x + .01x^2$, $r^2 = .13$, $P < 0.001$; Graminoids: $y = .15 + .03x - .003x^2$, $r^2 = .03$, $P = 0.023$; Subshrubs: $y = .04 - .002x$, $r^2 = .03$, $P = 0.028$; Vines: $y = .10 + .03x - .003x^2$, $r^2 = .15$, $P < 0.003$).
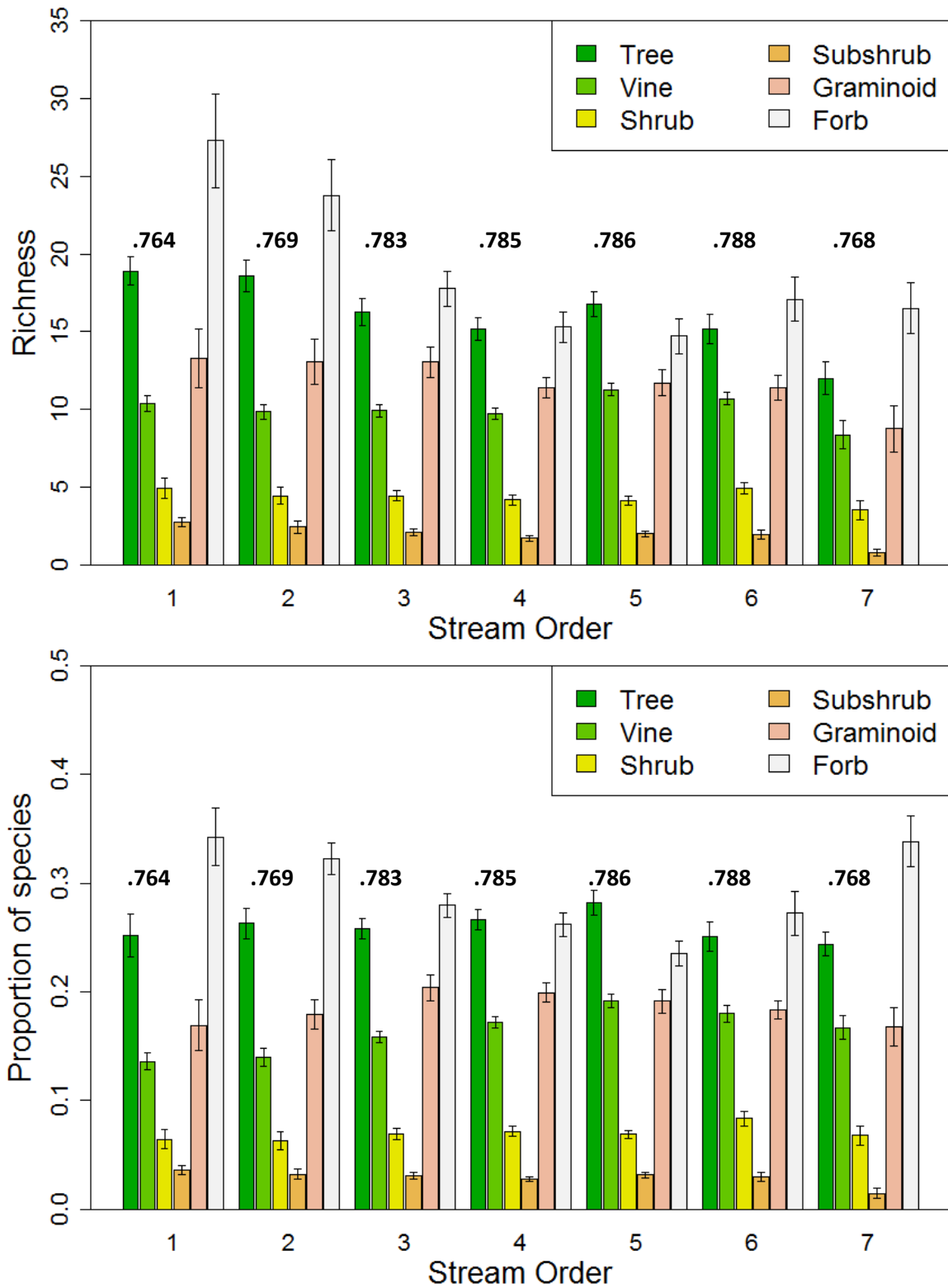
Figure 3.8: Richness (a) and proportion (b) of all growth form groups across stream order, with Simpson Diversity Index for each stream order. Error bars denote standard error.
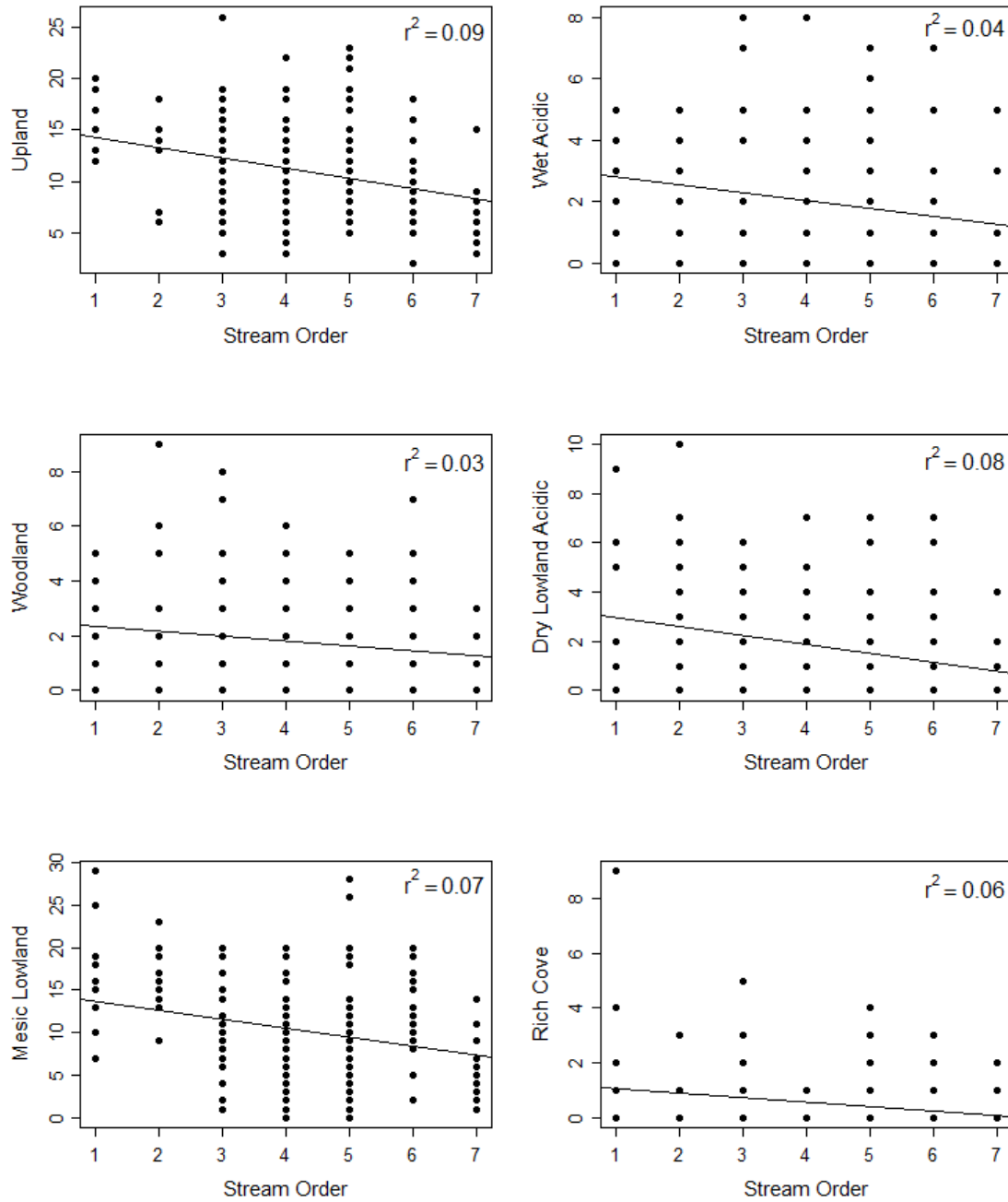
Figure 3.9: Richness of six habitat association groups is linearly related to stream order. Equations for the regressions lines are: upland: y= 15.28 - 1.0x; r^2= .09, $P < 0.0001$; wet acidic: y= 3.06 - .26x, r^2= .04, $P < 0.006$; woodland: y= 2.53 - .18x; r^2= .03, $P = 0.0259$; dry acidic lowland: y= 3.34 - .37x; r^2= .08, $P < 0.002$; lowland mesic: y= 14.78 -1.06x; r^2= .07, < 0.0001; and rich cove: y= 1.23 - .17x; r^2= .06, $P < 0.002$).
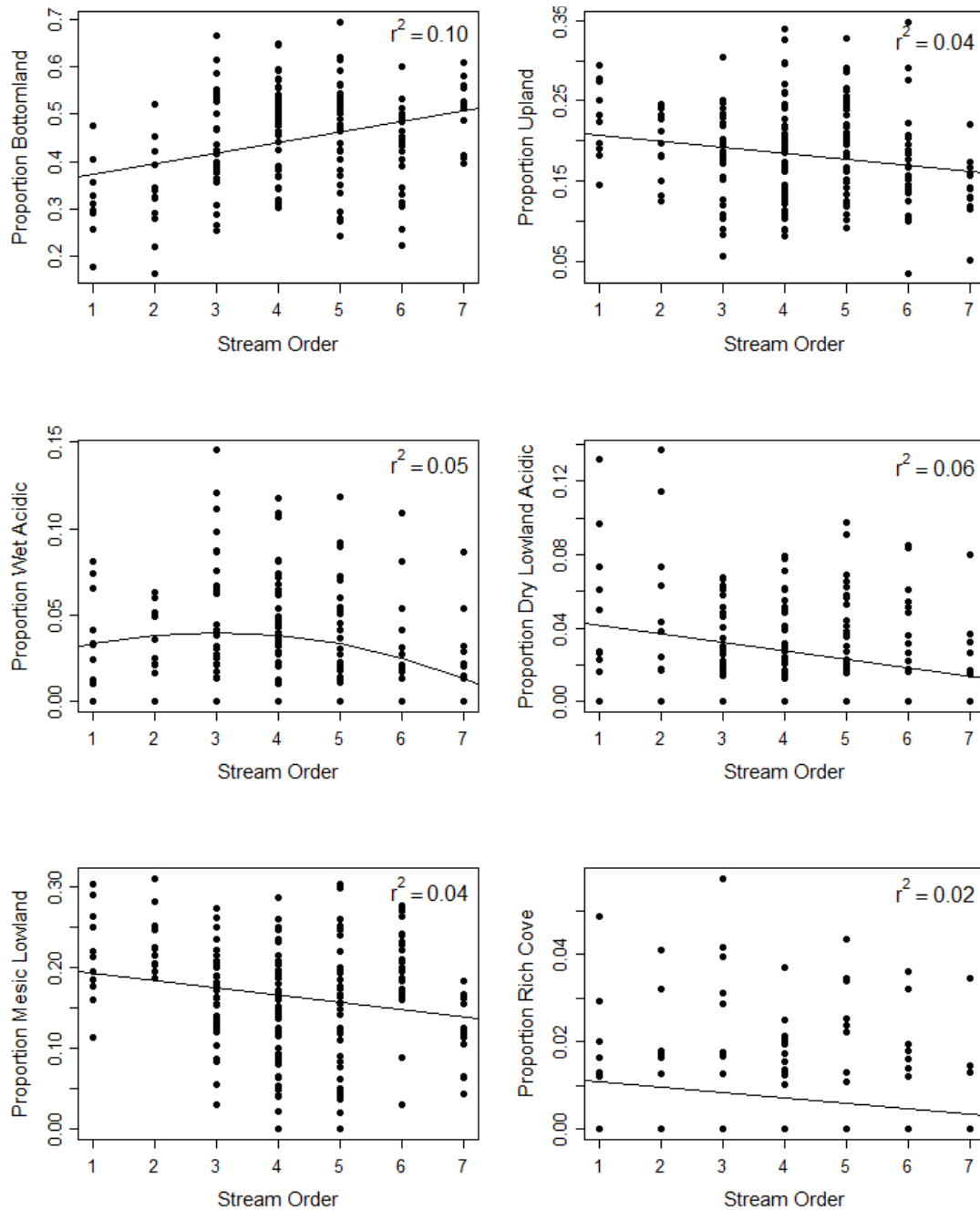
Figure 3.10: Proportion of richness of six habitat association groups significantly related to stream order. Four habitat association groups declined with increasing stream order (upland forest: $y = .21 - 0.01x$, $r^2 = .03$, $P = 0.012$; dry lowland acidic: $y = .05 - 0.005x$, $r^2 = .06$, $P < 0.001$; lowland mesic forest: $y = .20 - 0.01x$, $r^2 = .04$, $P = 0.009$; and rich cove: $y = .012 - 0.001x$, $r^2 = .02$, $P = 0.037$). The proportion of wet acidic species peaked at intermediate stream order (wet acid: $y = .02 + 0.01x - 0.001x^2$, $r^2 = .05$, $P = 0.042$). Only the proportion of bottomland species increased with increasing stream order ($y = .35 + 0.02x$, $r^2 = .10$, $P < 0.0001$).

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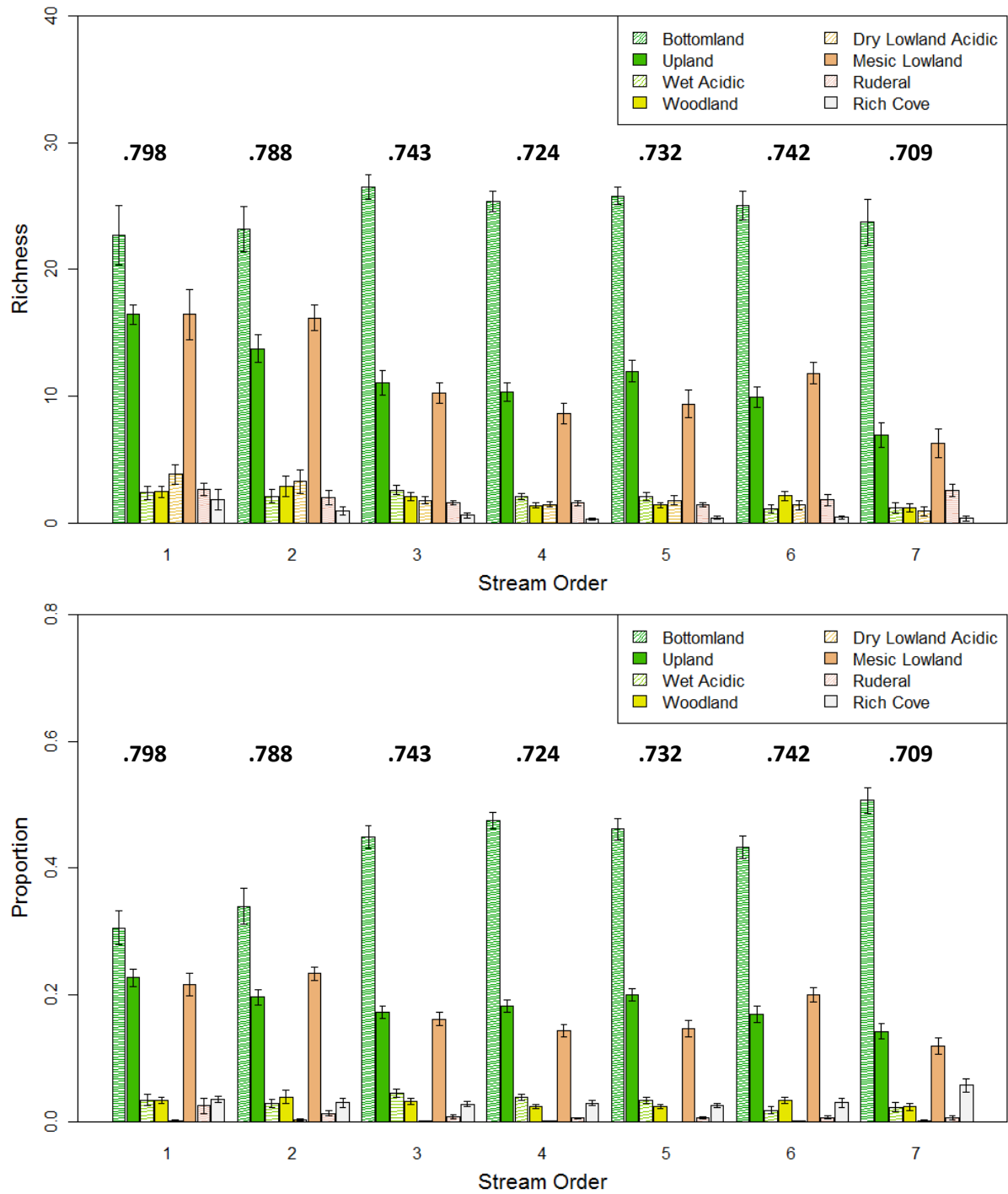
Figure 3.11: Richness and proportion of species in each habitat association group across stream order, with Simpson Diversity Index for each stream order. Error bars represent standard error.

References

Allen, B.P., Sharitz, R.R., and P.C. Goebel. 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecology and Management 242: 17-23.

Andersson, E., Nilsson, C. and M.E. Johansson. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. Journal of Biogeography 27: 1095-1106.

Augiar, F.C., Ferreira, M.T., and A. Albuquerque. 2006. Patterns of exotic and native plant species richness and cover along a semi-arid Iberian river and across its floodplain. Plant Ecology 184:189–202.

Bendix, J. 1997. Flood disturbance and the distribution of riparian species diversity. Geographical Review 87: 468-483.

Benedetti, M.M., Raber, M.J., Smith, M.S., and L.A. Leonard. 2006. Mineralogical indicators of alluvial sediment sources in the Cape Fear River Basin, North Carolina. Physical Geography 27: 258-281.

Brown, R. L. and R.K. Peet. 2003. Diversity and invasibility of Southern Appalachian plant communities. Ecology 84: 32-39.

Goebel, P.C., Palik, B.J., and K.S. Pregitzer. 2003. Plant diversity contributions of riparian areas in watersheds of the northern lake states, USA. Ecological Applications 13: 1595-1609.

Gould, W.A. and M.D. Walker. 1997. Landscape-scale patterns in plant species richness along an arctic river. Canadian Journal of Botany 75: 1748-1765.

Gregory, S.V., Swanson, F.J., McKee, S.W., and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41: 540-551.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest ecology and management 90:117-125.

Huebner, C.D., Morin, R.S., Zurbriggen, A., White, R.L., Moore, A., and D. Twardus. 2009. Patterns of exotic plant invasions in Pennsylvania's Allegheny National Forest using intensive Forest Inventory and Anlaysis plots. Forest Ecology and Management 257: 258-270.

Huebner, C.D., and P.C. Tobin. 2006. Invasibility of mature and 15-year-old deciduous forests by exotic plants. Plant Ecology 186: 57-68.

Hupp, C.R. 1986. Upstream variation in bottomland vegetation patterns, Northwestern Virginia. Bulletin of the Torrey Botanical Club 113: 421-430.

Johansson, M.E., Nilsson, C., and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? Journal of Vegetation Science 7: 593-598.

Kellison, R.C., Young, M.J., Braham, R.R., and Jones, E.J. 1998. Major alluvial floodplains. In: Messina, M.G., and Conner, W.H. (eds.) *Southern Forested Wetlands: Ecology and Management,* pp. 291-324. Lewis, Boca Raton, Florida, USA.

Khomo, L. and K.H. Rogers. 2009. Stream order controls geomorphic heterogeneity and plant distribution in a savanna landscape. Austral Ecology 34: 170-178.

Meyer, J.L, Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S., and N.E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association 43: 86-103.

Mouw, J.E.B., and P.B. Alaback. 2003. Putting floodplain hyperdiversity in a regional context: as assessment of terrestrial-floodplain connectivity in a montane environment. Journal of Biogeography 30: 87-103.

Mouw, J.E.B., Stanford, J.A., and P.B. Alaback. 2009. Influences of flooding and hyporheic excange on floodplain plant richness and productivity. River research and applications 25: 929-945.

Naiman, R.J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3: 209-212.

Naiman, R.J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. Ecology 70: 77-84.

Nilsson, C., Ekblad, A., Dynesius, M., Backe, S., Gardfjell, M., Carlberg, B., Hellqvist, S., and R. Jansson. 1994. A comparison of species richness and traits of riparian plants between a main river channel and its tributaries. Journal of Ecology 82: 281–295.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., O'Hara, R. B. , Simpson, G.L. , Solymos, P., Stevens, M.H.H., and H. Wagner. 2010. vegan: Community Ecology Package. R package version 1.17-3. http://CRAN.Rproject.org/package=vegan

Planty-Tabacchi, A.M., Tabacchi, E., Naiman, R.J., Deferrari, A. and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology 10: 598-607.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Renofalt, B.M., Nilsson, C., and R. Jansson. 2005. Spatial and temporal patterns of species richness in a riparian landscape. Journal of Biogeography 32: 2025-2037.

Renofalt, B.M., Jansson, R. , and C. Nilsson. 2005. Spatial patterns of plant invasiveness in a riparian corridor. Landscape Ecology 20: 165-176.

Richardson, J.S., Naiman, R.J., Swanson, F.J., and D.E. Hibbs. 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. Journal of the American Water Resources Association 41: 935-947.

Salinas, M.J. and J.J. Casas. 2007. Riparian vegetation of two semi-arid Mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. Wetlands 27: 831-845.

Shreve, R.L. 1966. Statistical law of stream numbers. Journal of Geology 75: 17-37.

Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosional topography. Geological Society of America Bulletin 63: 1117-1142.

Stromberg, J.C., Hazelton, A.F., and M.S. White. 2009. Plant species richness in ephemeral and perennial reaches of a dryland river. Biodiversity and Conservation 18:663-677.

Tabacchi, E., Planty-Tabacchi, A.M., Salinas, M.J., and H. Decamps. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. Regulated Rivers: Research and Management 12: 367-390.

Tabacchi, E., and A.M. Planty-Tabacchi. 2005. Exotic and native plant community distributions within complex riparian landscapes: A positive correlation. Ecoscience 12: 412-423.

Thompson, K., Hodgson, J.G., Grime, J.P., M.J.W. Burke. 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. Journal of Ecology 89: 1054-1060.

Townsend, P.A. 2001. Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. Plant Ecology 156: 43-58.

Venables, W. N. and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vidra, R.L., Shear, T.H., and T.R. Wentworth. 2006. Testing the paradigms of exotic species invasion in urban riparian forests. Natural Areas Journal 26: 339-350.

Walter, R.C., and D.J. Merritts. 2008. Natural streams and the legacy of water-powered mills. Science 319: 299- 304.

Ward, J.V., Tockner, K., Arscott, D.B., and C. Claret. 2002. Riverine landscape diversity. Freshwater Biology 47: 517-539.

Weakley, A.S. 2005. Change over time in our understanding of the flora of the southeastern United States: implications for plant systematics, bioinformatics, and conservation. Ph.D. dissertation, Duke University, Nicholas School of the Environment and Earth Sciences. 3240 pp.

Weakley, A. S. 2010. Flora of the Southern and Mid-Atlantic States. University of North Carolina at Chapel Hill Herbarium, Chapel Hill, North Carolina, U.S.A.

Wharton, C.H., Kitchens, W.M., Pendleton, E.C., and Sipe, T.W. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37. 133 pp.

CHAPTER 4

Riparian connectivity and the role of niche-assembly and dispersal-assembly processes in shaping alluvial metacommunity composition

Abstract

Although the metacommunity concept has received much attention as a framework in which to examine niche-assembly and dispersal-assembly processes, the relative influence of these processes remains a topic of debate. Niche-assembly and dispersal-assembly concepts can be interpreted as reflecting a gradient in connectivity, where higher connectivity is expected to result in local composition that closely tracks the abiotic environmental setting, whereas lower connectivity results in composition more strongly shaped by dispersal limitation and spatial structure. Metacommunity connectivity reflects both landscape-level attributes and organism-level traits.

In this chapter, I investigated how riparian connectivity affects the relative role of niche-assembly and dispersal-assembly processes in shaping alluvial plant communities. Whereas many metacommunity studies fail to account for the true habitat configuration and dispersal pathways in natural systems, I also explored two spatial models for the riparian system: one representing overland dispersal and the other representing dispersal in the dendritic riparian network. Since floodplain habitat is connected along the course of a river, I expect that dispersal limitation will not play a strong role in determining compositional

variation, and instead niche-assembly processes will dominate in these riparian plant communities. However, I also expect that the explanatory power of environmental variables will be stronger at higher connectivity. Finally, I hypothesize that accounting for network distance, expected to be an important dispersal pathway in riparian systems, will be important for identifying spatial structure within river basins.

I found that riparian plant communities are primarily shaped by niche processes, with environmental variables explaining the most compositional variation at all spatial scales and for all species groups. While landscape connectivity did not shift the influence of niche and dispersal processes, dispersal processes were influenced by landscape attributes, with the overland model explaining more compositional variation at the cross-basin spatial scale and the network model explaining more variation at the river basins scale. Distributions of species groups with facilitated dispersal were more strongly related to environmental variables compared with unassisted species, whose distributions were more strongly structured by spatial variables. Overall, even dispersal-limited species were more strongly structured by local environment and hydrological variables than spatial structure, suggesting that riparian connectivity is sufficient to produce communities primarily shaped by niche processes.

Introduction

A central theme of ecology is the identification and elucidation of processes that generate and maintain patterns of community composition (Watt 1947; Ricklefs 1987; Leibold et al. 2004). Traditional explanations focused on local processes that allow for the coexistence of species in a closed community, where local presence and abundance were interpreted to reflect underlying environmental gradients (Gleason 1926; Whittaker 1956; Grime 1974) or species interactions (Gause 1934; Tilman 1981). However, as the field of ecology developed from foundational concepts based on local processes in a closed community, there has been an increasing recognition that communities are open entities affected by processes operating at broader spatial scales. MacArthur and Wilson's theory of island biogeography (1967), for example, explicitly recognized the importance of processes occurring over larger spatial scales and highlighted the significance of distance and area measures in determining the movement and persistence of organisms, and subsequently local community patterns.

Theoretical developments in ecology have been derived from efforts to integrate processes acting at different scales, explicitly recognizing that processes operating at various scales are simultaneously driving patterns of local community composition. In particular, the metacommunity concept has provided a useful framework in which to examine the relative strength of local, niche-assembly processes and larger-scale, dispersal-assembly processes (Wilson 1992; Leibold et al. 2004; Cottenie 2005; Ozinga et al. 2005). It is well documented in the metacommunity literature that both niche-assembly and dispersal-assembly processes drive community patterns (*tropical forests*: Duque et al. 2002, Tuomisto et al. 2003, Powers et al. 2009; *lake plankton communities*: Cottenie et al. 2003, Soininen et al. 2007, Beisner et

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al. 2006; *macroinvertebrates*: Van de Meutter et al. 2007, Brown and Swan 2010; *temperate forests and grasslands*: Gilbert and Lechowicz 2004, Carr et al. 2009), but the relative influence of each process remains a topic of debate. Although documenting and comparing the relative strength of these processes across many different systems may lead to a better understanding of where to expect each process to dominate (Cottenie 2005), additional insight may also be gained by focusing on the landscape attributes and organism traits that influence the relative contribution of niche and dispersal processes in shaping local metacommunity composition (Driscoll and Lindenmayer 2009; Flinn et al. 2010).

The niche-assembly and dispersal-assembly concepts could be interpreted to reflect a gradient in connectivity, where connectivity is variously defined as "rates of dispersal among localities" (Chase and Ryberg 2004) and the "degree to which the landscape facilitates or impedes the movement of organisms among patches" (Rothley 2005). Higher connectivity is expected to result in more deterministic local community composition, heavily influenced by niche-assembly processes. Sufficient dispersal is necessary to provide the "fuel" for species distributions to closely track the abiotic setting in which they are most competitive (Cottenie and DeMeester 2004). Alternatively, metacommunities characterized by low connectivity are expected to be more heavily influenced by dispersal limitation, resulting in strong spatial structure and little influence of niche-assembly processes (Chase 2003; Cottenie and DeMeester 2004; Moore and Elmendorf 2006). Metacommunity connectivity, however, is related to both landscape-level attributes and organism-level traits. At the landscape level, greater habitat connectivity might be expected to reduce dispersal limitation and result in metacommunities more strongly structured by local niche processes (Cottenie and DeMeester 2004). At the species-level, better dispersed species might be expected to be less dispersal

limited and more closely track the local environment (Ozinga et al. 2005; Van de Meutter et al. 2007; Minor et al. 2009). In this chapter, I examine the influence of connectivity at both the landscape and organism levels in floodplain plant communities.

Floodplain habitats are an informative setting to examine the relationship between landscape connectivity and metacommunity processes. Floodplain habitat is, by definition, connected in a landscape context, longitudinally arranged along river channels (Figure 4.1). In this respect, the riparian landscape is fundamentally different from habitats associated with patchy geologic or soil attributes, such as rock outcrops or depression bogs. At the river basin-scale, both hydrologic dynamics and the movement of animals along the riparian corridor may serve to further increase the functional connectivity of floodplain habitat by acting as dispersal vectors (Naiman and Decamps 1997). In contrast, floodplain habits in separate river basins are explicitly not connected, requiring either dispersal through upland habitat or oceanic-estuarine environments at the river mouth. For these reasons, floodplain habitat offers a unique dichotomy of scales in which to examine the relative influence of niche and dispersal processes: within river basins, where habitat connectivity is higher, and across river basin boundaries, where connectivity is lower.

At the organism level, metacommunity connectivity is related to the dispersal ability of individual species. Less motile species are more dispersal limited, and compositional patterns of these taxa have been found to be more strongly shaped by spatial structure (Beisner et al. 2006; Van de Meutter et al. 2007; Minor et al. 2009; Flinn et al. 2010). However, certain dispersal modes may be more conducive to mobility in specific systems. In riparian ecosystems, the movement of water along the riparian corridor might be expected to facilitate the movement of plant propagules adapted for aquatic dispersal (hydrochory),

resulting in compositional patterns that closely track the local environment. However, plant

dispersal by animals (zoochory) and wind (anemochory) may also be important for propagule

movement in riparian corridors, although it is unclear what the relative effect of hydrochory,

zoochory, and anemochory might be in the riparian zone (Naiman and Decamps 1997; Imbert

and Lefevre 2003). Alternatively, plant species with no adaptations for assisted dispersal are

likely to be the most dispersal limited taxa of the floodplain plant community, resulting in

compositional patterns strongly shaped by spatial structure.

Recent studies have highlighted the critical role that the spatial model plays when

analyzing metacommunity structure (Beisner et al. 2006; Jones et al. 2008; Minor et al.

2009). However, few researchers have explicitly incorporated habitat configuration and

theorized dispersal pathways of natural systems into the spatial model used in

metacommunity analyses (except see: Beisner et al. 2006; Urban et al. 2006; Minor et al.

2009; Nabout et al. 2009; Brown and Swan 2010). In riparian systems, connectivity is

influenced by river basin boundaries, as discussed above, but may also be influenced by the

dendritic configuration of riparian habitat (Figure 4.1). The dendritic arrangement may

influence the functional dispersal pathway between floodplain locations within a river basin.

For organisms that disperse within the riparian corridor, the true distance between local

floodplain sites might best be represented by a network distance-based spatial model, as

opposed to the Euclidean distance-based model often used in metacommunity analyses. In a

riparian system, Euclidean distance would suggest overland dispersal through the upland

habitat matrix. While strictly aquatic species might be limited to the network dispersal

pathway (Beisner et al. 2006; Urban et al. 2006), both overland and network dispersal

pathways are potential dispersal routes for floodplain plants and both might be considered viable spatial models.

In this chapter, I examine the influence of riparian connectivity on the relative strength of niche-assembly and dispersal-assembly processes in floodplain plant communities. While past studies have examined metacommunity dynamics in alluvial systems (Urban et al. 2006; Nabout et al. 2009; Brown and Swan 2010), this approach has not previously been applied to floodplain plant communities. I also investigate how the spatial model, representing dispersal pathways, affects the results of metacommunity analyses in riparian systems. I address three questions:

(1) What is the relative influence of niche-assembly and dispersal-assembly processes in alluvial plant metacommunities?

(2) How is the relative strength of niche-assembly and dispersal-assembly processes affected by different levels of connectivity, represented by two spatial scales (across river basins and within river basins) and four species groups defined by dispersal mechanism (wind, vertebrate, water, and unassisted)?

(3) How sensitive are the results of metacommunity analyses to the spatial model employed to represent dispersal pathways? Does variation in riparian plant community composition relate more strongly to Euclidean distance (overland dispersal) or network distance (riparian-zone dispersal) and does this change at different spatial scales?

I hypothesize that niche-assembly processes will dominate in riparian plant communities due to the inherently connected arrangement of floodplain habitat. However, I hypothesize that the explanatory power of environmental variables will be stronger with higher connectivity,

both within river basin boundaries and for species groups with facilitated dispersal mechanisms. Finally, I hypothesize that accounting for network distance, expected to be an important dispersal pathway in riparian systems, will be important for identifying spatial structure at the within river basin scale, where the network dispersal pathway may be most important.

Methods

Study area

The study area spans five North Carolina river basins (Figure 4.2). Study sites were restricted to the Piedmont portion of each river basin, as defined by mapped geologic and soil units. Piedmont bedrock is largely composed of erosion-resistant metamorphic and igneous rocks, although a large southwest-northeast trending rift basin composed of Triassic sedimentary rock is a prominent geologic feature of the lower Piedmont (Benedetti et al. 2006). Where Piedmont rivers cross the more resistant metamorphic and igneous bedrock, the resulting river valley is relatively narrow and incised; in contrast, the softer sedimentary bedrock that dominates the ancient Triassic Basin landscape, has allowed for the development of wider floodplains.

High-quality natural vegetation was identified with assistance from state agencies such as the Natural Heritage Program and non-profit organizations, particularly local land trusts such as the Triangle Land Conservancy and the Land Trust for Central North Carolina. To various degrees, these organizations track natural areas of the state and were able to assist in locating and providing access to many of these sites. Sample sites were selected in order to ensure representation from a broad geographic area within each of the river basins and to

provide a good representation of various geologic features, geomorphic settings, stream

order, and watershed area. In total, one hundred and eighty-two vegetation plots were

established and recorded (Figure 4.2).

Vegetation and environmental data

Vegetation was surveyed May through August 2006-2008, following the Carolina

Vegetation Survey protocol (Peet et al. 1998). Six alluvial plots surveyed by CVS prior to the

2006-2008 field seasons were exported from the archived CVS database and included in this

dataset. Plots ranged in size from $400m^2$ (typically 20m × 20m) to $1000m^2$ (typically 20m ×

50m), depending upon the width of the floodplain, and all plots included four $100m^2$

intensively sampled subplots (10m × 10m). For consistency, I restricted this dataset to the

intensively sampled $400m^2$ area. Cover was estimated for all vascular plant taxa in each of

the four subplots, following the CVS cover class scale: 1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-

5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, 10 = >95%. All plots

were located within the one-hundred year floodplain of the nearest creek, determined using

floodplain maps and local vegetation composition; plots determined to be outside of the one-

hundred year floodplain after field data collection were excluded from this analysis.

At each plot, slope, aspect, and geomorphic position were recorded in the field.

Geomorphology was identified to one of five settings: small stream forests, alluvial flats,

levees, bottomlands, and backswamps (see in-depth descriptions of geomorphic settings in

Chapter 2). Soil samples were collected for nutrients and texture analysis. Soil samples

included one surface sample (top 10cm of mineral soil) from each of the four intensive

modules and one sub-surface sample from the center of each plot, collected approximately 50

cm below the ground surface. Samples were analyzed by Brookside Laboratories, Inc., New

Oxford, OH using the Mehlich III extraction method (Mehlich 1984). Chemical analyses included pH, percent base saturation, exchangeable Ca, Mg, K, and Na, total cation exchange capacity, extractable micronutrients (B, Fe, Mn, Cu, Zn, and Al), soluble sulfur, estimated N-release, extractable P, bulk density, and percent organic matter. Texture analyses included percent clay, silt, and sand. Soil samples from the four intensive modules were averaged for analysis.

Following field sampling, plot locations were mapped in a geographic information system (GIS) and additional environmental variables were calculated for each sample. These included stream order, upstream area drained, distance to river mouth, the width of the one hundred year floodplain, and elevation. GIS analyses were based upon digital elevation models from the USGS National Elevation Dataset (NED; http://ned.usgs.gov/) and surface water themes from the USGS National Hydrography Dataset (NHD; http://nhd.usgs.gov/). NED data were downloaded at a 30m resolution, and NHD data were downloaded at the medium resolution (1:100,000-scale). Upstream area drained and stream order were derived using the ArcHydro toolset. Width of the one hundred year floodplain was determined using the North Carolina digital floodplain maps (NC Floodplain Mapping Program; http://www.ncfloodmaps.com/). PRISM mean annual temperature and mean annual precipitation were extracted from the NHD Plus dataset (PRISM and NHD Plus; http://www.prism.oregonstate.edu/ and http://www.horizon-systems.com/nhdplus/).

Plant taxa were identified to the finest taxonomic resolution possible, following Weakley 2010. Taxa that were difficult to identify to species without fruit or flower due to the timing of field sampling were grouped into lower resolution complexes (examples: *Viola spp.*, *Oxalis spp., Solidago spp., Carex* [*amphibola+grisea+corrugata*]; see Appendix 8).

Taxonomy was reviewed and standardized to account for differences due to plant identifications determined by a variety of individuals, both in the field and in the lab. The final floristic dataset contained 530 consistently recorded taxonomic units. Plant taxa were classified by dispersal mode based on information obtained from the literature and plant databases (Appendix 8). Taxa were assigned to four dispersal modes: wind, water, vertebrate, or unassisted, although some taxa were characterized by more than one dispersal mode. Taxa that were dispersed by gravity or small invertebrates (e.g. ants) were grouped with the unassisted species.

Analytical methods

There has been some debate in the literature about the best methods for investigating metacommunity structure. This debate has primarily centered on the advantages of distance approaches, e.g. Mantel tests, versus the raw-data approaches, e.g. variation partitioning with canonical analysis (Tuomisto and Ruokolianen 2006; Legendre et al. 2008; Tuomisto and Ruokolianen 2008; Pelissier et al. 2008; Laliberte 2008). However, many authors have suggested that the two methods are complementary and each approach yields results that may provide insights into the drivers of metacommunity structure (Borcard et al. 1992; Jones et al. 2006; Tuomisto and Ruokolainen 2006; Vanschoenwinkel et al. 2007). I used the distance-based Mantel test approach to test for correlations between floristic, environmental, and spatial distance or dissimilarity matrices to answer two questions: (1) do environmentally similar sites have similar species composition, while environmentally different sites have dissimilar species composition? and (2) are samples located closer together (i.e., a smaller spatial distance between samples) more similar than sites farther apart? Simple Mantel correlations indicate which explanatory dataset might best explain overall variation in

floristic composition. I then used a raw-data variation partitioning approach to quantify the proportion of floristic variation independently explained by spatial and environmental variables.

Three data sets were created for these analyses: floristic, spatial, and environmental matrices. For the floristic matrices, species importance values were calculated as the geometric mean of the cover values in the four intensive modules ($400m^2$). Four floristic matrices were restricted to subsets of taxa defined by the four dispersal modes (wind, vertebrate, water, and unassisted). Floristic dissimilarity was computed using the Bray-Curtis dissimilarity index.

The environmental data matrix included 29 variables: all 22 soil chemistry and texture variables, 2 climate variables (mean annual temperature and precipitation), and 5 variables related to the local geomorphic setting (stream order, upstream area drained, distance to river mouth, floodplain width, and geomorphic position). Soil chemistry variables were log transformed and the categorical geomorphic settings were coded as dummy variables prior to analysis. To account for environmental variables with varying scales of measurement, all variables were standardized to z-scores before analysis (Legendre and Legendre 1998). Environmental dissimilarity was computed using Euclidean distance.

Two spatial matrices were computed for each landscape scale, one using Euclidean distance and one using network distance. For Mantel correlations, Euclidean distance was calculated from UTM coordinates of each plot, whereas network distance was calculated at the river basin-scale in a GIS using the FLoWS toolbox (Theobald et al. 2005). Network distance is defined as the symmetric instream distance between two sample locations. Network distance matrices that included samples across river basins required special

consideration, since sites located in separate river basins have no network distance yet cannot be represented by a zero in the distance matrix (which would suggest the sites are in the same location). Therefore, network distance of sites in different river basins was calculated as 4* the maximum within-basin network distance, following standard practice in metacommunity spatial models (Borcard and Legendre 2002; Dray et al. 2006; Urban et al. 2006; Van de Meutter et al. 2007). For variation partitioning analyses, Moran's eigenvector maps (MEM) were used to generate spatial predictor matrices. MEM spatial matrices were constructed in two ways: the principal coordinates of neighborhood matrices (PCNM) approach was used to generate predictors based on Euclidean distance, while a distance-based eigenvector map was used to generate spatial predictors based on network distance (PCNM: Borcard and Legendre 2002; Dray et al. 2006; dbMEM: Dray et al. 2006; Griffith and Peres-Neto 2006; Beisner et al. 2006). MEMs are an improvement over the traditional trend-surface spatial model, which can only model broad-scale spatial structure, whereas MEMs can identify spatial patterns across a range of scales perceptible in a given dataset (Legendre and Legendre 1998; Borcard and Legendre 2002; Jones et al. 2008).

To compare the floristic dissimilarity with environmental dissimilarity and spatial distance, simple Mantel tests were carried out at two levels of habitat connectivity, across river basins and within river basins, using both Euclidean and network spatial distance matrices (Mantel 1967). Bootstrapped confidence intervals for the Mantel r statistic were generated based on 500 iterations of resampling, without replacement (Goslee and Urban 2007).

To quantify the proportion of floristic variation explained by environmental and spatial variables, I used variation partitioning based upon partial redundancy analysis

(pRDA; Borcard et al. 1992; Legendre et al. 2005; Jones et al. 2006; Peres-Neto et al. 2006; Legendre 2008). The total variation in the response floristic matrix was partitioned into four fractions representing the effects of environmental conditions, the effects of spatial structure, the shared effects environment and space, and unexplained variation. Results of variation partitioning reflect the adjusted R^2 values developed by Peres-Neto et al. (2006); negative R^2_{adj} values were interpreted as a zero value (Peres-Neto et al. 2006; Satller et al. 2010). To prevent overestimation of explained variance, forward selection of explanatory variables was used to select significant environmental and spatial predictors before all variation partitioning analyses (Blanchet et al. 2008). The number of forward selected environmental variables ranged from 6-27 variables; selected variables in each analysis can be found in Appendix 2. To better illustrate the relative importance of environmental and spatial variables in structuring community composition, I calculated the ratio of variation explained by spatial variables to variation explained by environmental variables for each analysis. Variation partitioning was performed at the two spatial scales and for the four subsetted floristic matrices; all analyses were performed with both Euclidean and network distance models.

All statistical analyses were carried out in the R statistical language (R Development Core Team 2007). Mantel tests were computed in the "ecodist" package (Goslee and Urban 2007). The canonical analyses, variation partitioning, and tests of significance of the fractions were computed using the ''vegan'' library (Oksanen et al. 2007). PCNM eigenfunctions were created using the package "PCNM" (Legendre et al. 2009) and MEM eigenfunctions for network analyses were created using the "spacemakeR" package (Dray 2008). Forward selection procedures were carried out using the ''packfor'' package (Dray et al. 2009).

Results

Of the 182 vegetation plots sampled, the geographic distribution of the plots across the five river basins included 19 plots in the Catawba basin, 49 plots in the Yadkin basin, 57 plots in the Cape Fear basin, 30 in the Neuse basin, and 27 in the Tar basin. Of the 530 taxa identified in the field sampling, 381 were categorized by their dispersal modality (72 % of the taxa observed): 86 (16%) were wind-dispersed, 149 (28%) were vertebrate-dispersed, 63 (12%) were water-dispersed, and 132 taxa (25%) were classified as taxa with unassisted dispersal (some taxa were characterized by more than one dispersal mode).

Mantel tests

Mantel test results indicate that floristic dissimilarity was more strongly related to environmental dissimilarity at both spatial scales, regardless of the spatial model employed (Figure 4.3). In examining the full floristic dataset across all river basins, the Mantel correlation with environment was significantly higher than the correlation with either spatial distance matrix, as indicated by non-overlapping 95% confidence intervals (environment: Mantel $r = .407$, $P \le 0.001$; Euclidean distance: Mantel $r = .139$, $P \le 0.001$; network distance: Mantel $r = .096$, $P \le 0.001$; Figure 4.3). Within river basins, the qualitative pattern remained the same, with environmental dissimilarity more strongly correlated with floristic dissimilarity than either spatial distance model (the Tar Basin is the only basin in which overlapping confidence intervals indicate that the correlation with environmental dissimilarity is not significantly different than the correlation with spatial distance). The strength of the correlation between floristic and environmental dissimilarity did not change substantially at the two spatial scales; in contrast, the correlation between floristic

dissimilarity and spatial distance increased slightly at the river basin scale. Overlapping confidence intervals for the two spatial distance models suggests that the Mantel results are not sensitive to the spatial model. The Euclidean distance model was at least as strongly correlated to floristic dissimilarity as the network model, and in two basins (Neuse and Tar) it was the only spatial model significantly correlated with floristic dissimilarity (Figure 4.3).

Variation partitioning

Environmental predictors consistently explained more variation in community composition (Table 4.1; Table 4.2). The ratio of space to environment (S:E) was < 1 in all analyses, reflecting the dominant influence of the environmental variables. When all species and plots were considered together, environmental variables alone explained over 18% of the variation in community composition, whereas spatial variables explained less than 5%. The strongest environmental predictors of alluvial plant community composition were Ca/Mg ratio, % clay, geomorphic position, floodplain width, distance to river mouth, and exchangeable Fe (Appendix 9).

Consistent with the Mantel results, there was no substantial change in the relative influence of spatial and environmental variables at the two spatial scales (Table 4.1). Additionally, the total variation explained ([E+S]; Table 4.1) did not differ at the two scales of landscape connectivity; [E+S] was somewhat higher at the river basin scale for three basins (Yadkin, Cape Fear and Neuse basins) and lower for two basins (Catawba and Tar). In three basins, neither the Euclidean nor network distance spatial models were significant. However, in the two basins with significant spatial structure, the Yadkin and Cape Fear basins, the ratio of spatial:environmental variation (S:E) was higher for the network distance spatial model compared with the Euclidean distance model. Alternatively, when all river

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basins were considered together, the ratio of S:E based on Euclidean distance was higher than the ratio for network distance. The highest ratio of S:E based on Euclidean distance was found at the broader spatial scale, and consistently decreased at the scale of a single basin (reflecting both an increase in E and a decrease in S). In contrast, the S:E ratio for the network distance spatial model had the highest values at the river basin scale.

When considering the species grouped by dispersal mode across all river basins, the lowest S:E ratio occurred in the species with facilitated dispersal, reflecting the importance of niche-assembly processes (Table 4.2). The distributions of unassisted species were more strongly related to spatial variables (higher S:E ratios), although environmental variables still explained more variation in composition. The Euclidean model explained more compositional variation at this scale for the wind-dispersed, animal-dispersed, and unassisted species, while the network model was a stronger predictor of water- dispersed species distributions. At the scale of the single river basins, many of the spatial models were not significant predictors of floodplain plant community composition. However, the general patterns evident at the cross-basin scale remained, with floristic variation more strongly related to environmental variables and the highest S:E ratios, where significant, associated with unassisted dispersal species. Floristic composition for each of the species groups at the river basin scale was also more strongly related to network distance than Euclidean distance.

Discussion

Compositional variation of Piedmont riparian plant communities is primarily driven by niche processes. Local environmental and hydrologic setting consistently explained more variation in community composition than spatial structure, regardless of the analytical

approach, the spatial scale, the dispersal mechanism, or the spatial model employed. The strong influence of environmental variables is consistent with the hypothesis that the configuration of floodplain habitat along the river channel results in sufficient connectivity for plant communities to be primarily structured by niche processes; indeed, prior research in riparian systems has found high rates of plant dispersal along the riparian corridor (Johannsson et al. 1996; Brown and Peet 2003). In contrast, plant metacommunities associated with patchy wetland habitats might be expected to be more strongly shaped by dispersal limitation and spatial structure, and this has been documented in recent studies in seeps on serpentine outcrops (Freestone and Inouye 2006) and wetlands within an old growth forest matrix (Flinn et al. 2010).

The strongest environmental predictors of compositional variation in Piedmont floodplain plant communities were relatively consistent across all analyses and confirmed environmental drivers of vegetation patterns identified in previous work (see Chapter 2 results). Soil texture (% Clay) was commonly among the forward selected environmental variables, as was geomorphic position and floodplain width. These variables reflect the local hydroperiod, long known to be an important driver of floodplain plant community composition (Wharton et al. 1982). Other important environmental variables included those reflecting local soil fertility (Ca/Mg ratio) and location within the river basins (distance to river mouth).

The dominant influence of environmental variables in floodplain forests is also consistent with studies conducted in other contiguous forested systems (Tuomisto et al. 2003; Jones et al. 2006; Powers et al. 2009). However, the results of observational ecological studies must always be interpreted in light of their spatial scale. Even with advances in

spatial modeling tools that allow for the assessment of a multitude of scales in a single analysis (e.g. eigenvectors maps), inference is not possible outside the spatial scales at which data were collected. In this study, I did not examine variation in community composition at small spatial scales (<1,000m), and many past studies of contiguous forested systems have examined compositional variation at similar spatial scales to those investigated here (1km to 1000 km). However, there is some evidence that plant metacommunity structure is more strongly influenced by dispersal processes at small spatial scales (<200m; Karst et al. 2005), where two opposing dispersal-processes, dispersal limitation and mass effects, could result in stronger spatial structure. The dominant processes driving metacommunity structure, therefore, may change depending upon the spatial scale, and the results of metacommunity studies should be interpreted in light of the observed spatial scale.

At the scales examined here, there was little evidence for my second hypothesis, that landscape-scale connectivity affects the relative influence of niche-assembly and dispersal-assembly processes in shaping floodplain plant community composition. However, landscape-scale connectivity does appear to influence dispersal processes, a conclusion that is only evident when accounting for the two possible dispersal pathways at each spatial scale. While Mantel results suggested there is little difference between the two spatial models, variation partitioning results suggest that community composition is more strongly related to a specific spatial model at each scale. At the cross basin boundary scale, the Euclidean spatial model almost always explained more floristic variation than the network model (the one exception was for water-dispersed species), but its explanatory power decreased at the within-basin scale. Alternatively, the network spatial model was more important at the river basin scale, consistently explaining more variation in composition than the Euclidean model;

when expanding the spatial scale across river basin boundaries, the strength of the network model tended to decrease.

These results suggest that both overland and network dispersal are influencing community composition, and each is more important at a different scale. At the cross-basin scale, the importance of the Euclidean model suggests that at least some riparian plants disperse across the upland habitat. Indeed some plant species found in riparian communities also occur in upland habitats and are not restricted to riparian zones; overland dispersal between floodplain habitats in separate river basins would likely occur most frequently for these species. Alternatively, at the scale of a single river basin, the network spatial model explains more variation than Euclidean distance, suggesting that within river basins, at least part of the riparian plant community disperses within the riparian corridor. Species that are restricted to the riparian corridor are more likely to include taxa less ubiquitous in the upland Piedmont landscape and taxa with dispersal traits that facilitate movement within the corridor (e.g. water and animal dispersed species; see discussion below). While past studies have found that both overland and network dispersal were equally important in riparian landscapes (Beisner et al. 2006), these results suggest that each form of dispersal is dominant at a different spatial scale.

In contrast to the effects of landscape-scale connectivity, the relative influence of niche-assembly and dispersal-assembly processes depended on organism traits. At the broader cross-basin scale, the results support the hypothesis that dispersal limited species are more strongly influenced by dispersal processes, while species with facilitated dispersal more closely track the local environment (Ozinga et al. 2005; Van de Meutter et al. 2007; Minor et al. 2009). Within river basins, the spatial model was rarely significant, suggesting little

influence of dispersal processes at this scale. This was particular true for water-dispersed species, whose distributions were significantly related to spatial structure in only one river basin.

The true dispersal pathway, as represented by a spatial model, was important to consider. While the Euclidean model was stronger for most species groups at the cross-basin scale, water-dispersed species were more strongly related to network spatial structure, reflecting the dominant influence of the network dispersal pathway for these species; this is not surprising in light of past research suggesting hydrochory is an important dispersal mechanism in riparian systems (Jansson et al. 2005; Chambert and James 2009). Similar to the results for all species at the single river basin scale, composition of animal-dispersed and unassisted species were also more strongly related to network spatial structure, suggesting that network dispersal is also important for these taxa. While animal-dispersed species may be dispersed by animals moving within the riparian corridor, past research has suggested that even species without specific adaptations for hydrochory are often dispersed by water in riparian systems (Danvind and Nilsson 1997; Hampe 2004). In the two river basins where wind-dispersed species distributions were significantly related to spatial structure, on the other hand, network distance was more important in one basin and Euclidean and network dispersal were equally important in the other, suggesting that dispersal of these species may not be restrained to the riparian corridor.

Overall, accounting for network distance did not qualitatively alter the interpretation of the results: niche-processes dominate over dispersal-processes in shaping Piedmont alluvial plant metacommunities. In many cases, the overall difference between Euclidean and network-distance spatial models was small, and often, neither spatial model was a significant

predictor of community composition. However, the two spatial models did make additional insights into the processes structuring alluvial communities possible, suggesting that overland dispersal and network dispersal are each important in this system, although perhaps at different spatial scales.

Metacommunity studies aimed at increasing our understanding of where to expect niche-assembly and dispersal-assembly processes to dominate can benefit conservation planning and restoration design. Successful conservation and restoration of degraded communities requires information about the processes that determine natural plant community composition (Chase 2003; Mouillot et al. 2007). For riparian systems, strong control by niche-processes, where composition is more predictable based upon local environment, lends itself well to describing repeatable vegetation units and developing restoration reference conditions based upon environmental variables. Alternatively, systems characterized by low connectivity and high dispersal limitation, likely resulting in less predictable community composition, common management practices, such as community classification and restoration target design, may prove more difficult.

Table 4.1: Redundancy analysis (RDA) variation partitioning of plant community composition into fractions explained by environmental and spatial variables. Floristic composition data includes all species at two spatial scales, across river basins and within river basins. Spatial distance was computed using Euclidean (Euc) distance and network (Net) distance. The different components are: total explained variation [E + S], variation explained by environmental variables [E], variation explained by spatial variables [S], variation explained by environmental variables independent of space [E|S], variation explained by spatial variables independent of environment [S|E], and variation jointly explained by environment and space [E∩S]. S:E is the ratio of spatial to environmental variation. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

	All plots		Catawba				Yadkin				Cape Fear				Neuse				Tar			
	Euc	Net	Euc	P	Net	P	Euc	P	Net	P	Euc	P	Net	P	Euc	P	Net	P	Euc	P	Net	P
[E+S]	30.43 ***	29.08 ***	26.28 ***		27.93 ***		36.23 ***		36.49 ***		31.35 ***		33.73 ***		37.02 ***		37.44 ***		28.08 ***		26.87 ***	
[E]	26.04 ***	26.04 ***	24.75 ***		24.75 ***		31.77 ***		31.77 ***		29.52 ***		29.52 ***		35.95 ***		35.95 ***		26.37 ***		26.37 ***	
[S]	11.66 ***	9.29 ***	4.8 *		9.56 ***		11.97 ***		17.87 ***		6.76 ***		15.58 ***		7.39 ***		5.4 ***		11.63 ***		3.77 **	
[E|S]	18.81 ***	19.78 ***	21.48 ***		18.38 ***		24.26 ***		18.63 ***		24.58 ***		18.15 ***		29.63 ***		32.04 ***		16.44 ***		23.1 ***	
[S|E]	4.4 ***	3.05 ***	1.53 n.s.		3.18 n.s.		4.47 ***		4.73 ***		1.83 *		4.22 **		1.07 n.s.		1.49 n.s.		1.7 n.s.		.51 n.s.	
[E∩S]	7.23	6.25	3.28		6.48		7.5		13.14		4.93		11.37		6.31		3.91		9.93		3.27	
S:E	0.23	0.15	n.s.		n.s.		0.18		0.25		0.07		0.23		n.s.		n.s.		n.s.		n.s.	

Table 4.2: Redundancy analysis (RDA) variation partitioning of plant community composition into fractions explained by environmental and spatial variables. Floristic composition data includes all species grouped by dispersal mode (wind, animal, water, and unassisted) at two spatial scales, across river basins and within river basins. Spatial distance was computed using Euclidean (Euc) distance and network (Net) distance. The different components are: total explained variation [E + S], variation explained by environmental variables [E], variation explained by spatial variables [S], variation explained by environmental variables independent of space [E|S], variation explained by spatial variables independent of environment [S|E], and variation jointly explained by environment and space [E∩S]. S:E is the ratio of spatial to environmental variation. * $P \leq$ 0.05; ** $P \leq 0.01$; *** $P \leq 0.001$

Wind-dispersed

	All plots Euc P	All plots Net P	Catawba Euc P	Catawba Net P	Yadkin Euc P	Yadkin Net P	Cape Fear Euc P	Cape Fear Net P	Neuse Euc P	Neuse Net P	Tar Euc P	Tar Net P
[E+S]	34.67 ***	30.99 ***	32.61 ***	30.97 ***	38.25 ***	39.15 ***	35.79 ***	34.96 ***	42.31 ***	40.25 ***	38.13 ***	39.37 ***
[E]	30.99 ***	33.7 ***	32.43 ***	32.43 ***	34.08 ***	34.08 ***	32.33 ***	32.33 ***	39.92 ***	39.92 ***	37.78 ***	37.78 ***
[S]	12.9 ***	11.58 ***	5.69 *	6.85 *	16.52 ***	23.28 ***	10.44 ***	14.77 ***	10.11 **	3.12 **	7.74 *	7.66 **
[E|S]	21.77 ***	22.12 ***	26.93 ***	24.12 ***	21.73 ***	15.86 ***	25.36 ***	20.19 ***	32.21 ***	37.13 ***	30.39 ***	31.71 ***
[S|E]	3.68 ***	2.7 ***	0.18 n.s.	-1.5 n.s.	4.17 *	5.07 *	3.46 **	2.63 *	2.39 n.s.	0.33 ***	0.35 n.s.	1.59 n.s.
[E S]	9.22	8.87	5.5	8.31	12.35	18.21	6.98	12.15	7.71	2.78	7.39	6.07
1- [E+S]	65.33	66.3	67.39	63.1	61.75	60.85	64.21	65.04	57.69	59.71	61.87	60.63
S:E	0.17	0.12	n.s.	n.s.	0.19	0.32	0.14	0.13	n.s.	0.01	n.s.	n.s.

Animal-dispersed

	All plots Euc P	All plots Net P	Catawba Euc P	Catawba Net P	Yadkin Euc P	Yadkin Net P	Cape Fear Euc P	Cape Fear Net P	Neuse Euc P	Neuse Net P	Tar Euc P	Tar Net P
[E+S]	30.31 ***	28.81 ***	22.67 ***	21.79 ***	28.11 ***	28.2 ***	24.25 ***	26.21 ***	29.39 ***	32.12 ***	23.05 ***	20.37 ***
[E]	26.99 ***	26.99 ***	21.31 ***	21.31 ***	26.11 ***	26.11 ***	22.22 ***	22.22 ***	25.32 ***	25.32 ***	20.32 ***	20.32 ***
[S]	10.57 ***	7.95 ***	2.87 n.s.	3.49 *	11.82 ***	17.13 ***	2.44 **	10.97 ***	8.56 ***	9.23 **	10.92 ***	3.09 *
[E|S]	19.75 ***	20.85 ***	18.79 ***	18.3 ***	16.29 ***	11.07 ***	21.81 ***	15.24 ***	20.83 ***	22.9 ***	12.13 ***	17.29 ***
[S|E]	3.32 ***	1.82 ***	1.35 n.s.	0.48 n.s.	2.01 **	2.1 *	2.03 **	3.98 **	4.06 n.s.	6.8 **	2.73 n.s.	0.06 n.s.
[E S]	7.24	6.14	1.52	3.01	9.81	15.04	0.41	6.99	4.5	2.43	8.19	3.03
1- [E+S]	69.69	71.19	77.33	78.21	71.89	71.8	75.75	73.79	70.62	67.88	76.95	79.63
S:E	0.17	0.09	n.s.	n.s.	0.12	0.19	0.09	0.26	n.s.	0.30	n.s.	n.s.

Table 4.2, continued:

Unassisted dispersal

	All plots Euc	P	Net	P	Catawba Euc	P	Net	P	Yadkin Euc	P	Net	P	Cape Fear Euc	P	Net	P	Neuse Euc	P	Net	P	Tar Euc	P	Net	P
[E+S]	24.02	***	23.68	***	31.07	***	29.94	***	27.029	***	31.91	***	19.79	***	22.84	***	16.74	***	14.68	***	34.99	***	33.7	***
[E]	17.46	***	17.46	***	27.78	***	27.78	***	25.98	***	25.98	***	18.19	***	18.19	***	15.07	***	15.07	***	32.8	***	32.8	***
[S]	10.89	***	9.98	***	5.7	n.s.	8.83	**	5.85	***	13.33	***	4.96	***	11.99	***	7.63	*	3.97	*	10.5	***	11.46	***
[E|S]	13.13	***	13.71	***	25.37	***	21.11	***	21.18	***	18.58	***	14.82	***	10.85	***	9.11	***	10.71	***	24.5	***	22.24	***
[S|E]	6.56	***	6.23	***	3.3	n.s.	2.16	n.s.	1.05	n.s.	5.93	***	1.59	n.s.	4.65	***	1.68	n.s.	0.39	n.s.	2.2	n.s.	0.91	n.s.
[E S]	4.33		3.75		2.41		6.67		4.8		7.4		3.37		7.34		5.95		4.35		8.3		10.56	
1- [E+S]	75.98		76.32		68.93		70.06		72.97		68.09		80.22		77.16		83.26		85.32		65.01		66.3	
S:E	0.50		0.45		n.s.		n.s.		n.s.		0.32		n.s.		0.43		n.s.		n.s.		n.s.		n.s.	

Water- dispersed

	All plots Euc	P	Net	P	Catawba Euc	P	Net	P	Yadkin Euc	P	Net	P	Cape Fear Euc	P	Net	P	Neuse Euc	P	Net	P	Tar Euc	P	Net	P
[E+S]	27.43	***	28.56	***	54.84	***	54.69	***	37.29	***	38.25	***	24.38	***	23.41	***	30.54	***	32.84	***	33.83	***	29.78	***
[E]	24.74	***	24.74	***	53.69	***	53.69	***	34.62	***	34.62	***	23.68	***	23.68	***	30.94	***	30.94	***	30.41	***	30.41	***
[S]	10.87	***	11.04	***	-2.01	n.s.	5.5	n.s.	15.78	***	19.91	***	1.11	n.s.	3.87	**	2.87	n.s.	3.81	*	13.37	**	5.51	***
[E|S]	16.56	***	17.52	***	56.85	***	48.82	***	21.52	***	18.34	***	23.28	***	19.53	***	27.67	***	29.03	***	20.46	***	24.27	***
[S|E]	2.69	***	3.83	***	1.15	n.s.	0.63	n.s.	2.67	*	3.63	***	0.7	n.s.	-0.28	*	-0.41	n.s.	1.9	n.s.	3.42	n.s.	-0.63	n.s.
[E S]	8.17		7.22		-3.17		4.87		13.1		16.28	***	0.04		4.15		3.27		1.91		9.95		6.14	
1- [E+S]	72.57		71.45		45.16		45.69		62.71		61.75	***	75.62		76.59		69.47		67.16		66.17		70.22	
S:E	0.16		0.22		n.s.		n.s.		0.12		0.20		n.s.		-0.01		n.s.		n.s.		n.s.		n.s.	
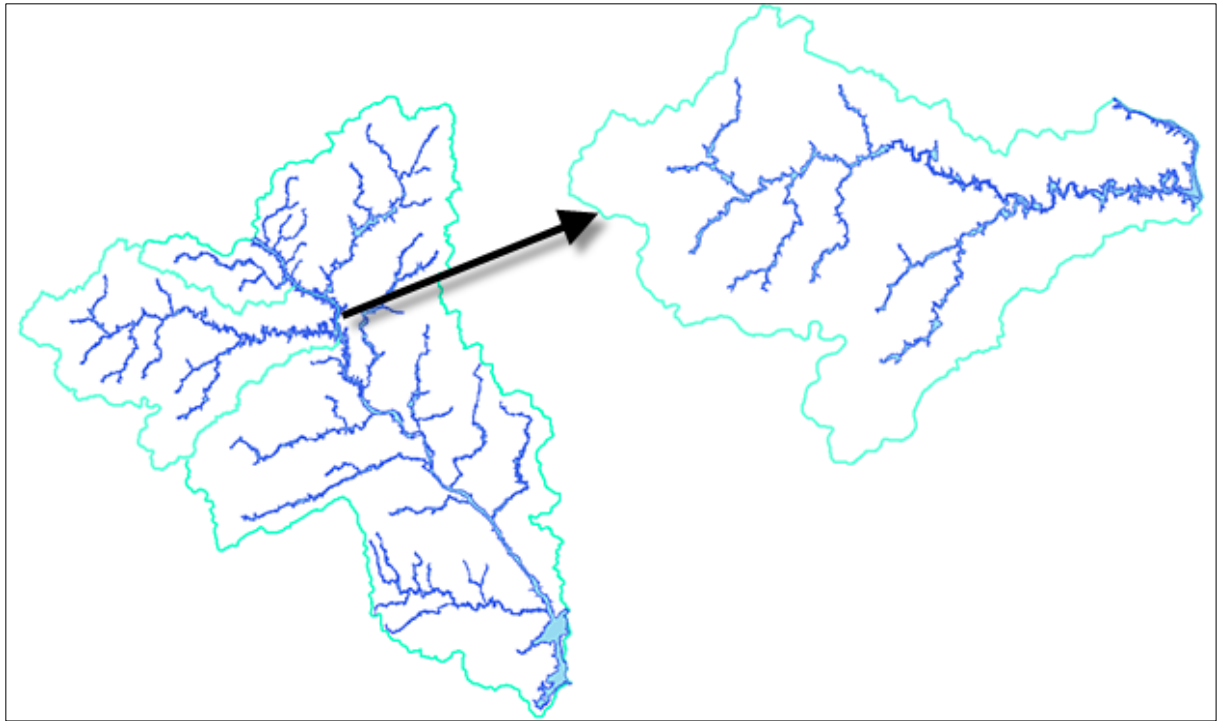
Figure 4.1: Sub-basins within the Cape Fear River Basin. The aquamarine lines are USGS Hydrologic Unit sub-basin boundaries. The dark blue lines indicate the outer-edge of the 100-year floodplain of the nearest river channel, and the lighter blue shading within the dark blue lines indicates floodplain habitat.
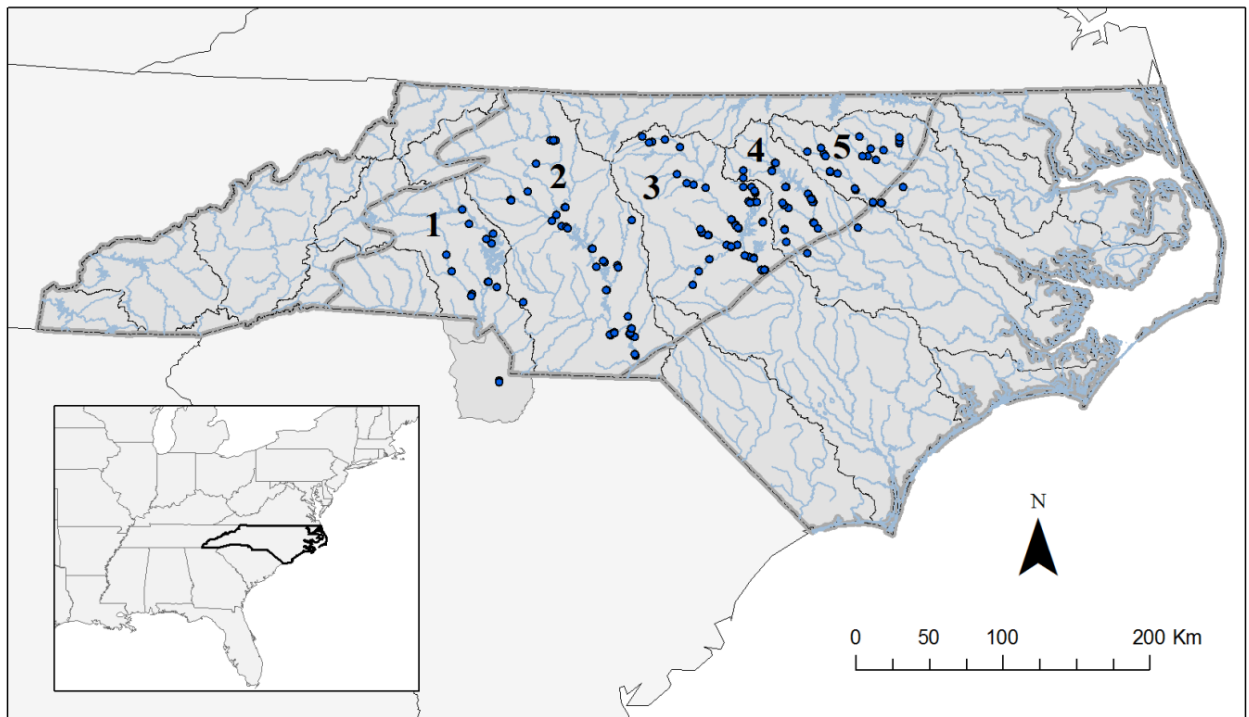
Figure 4.2: Distribution of 182 forested vegetation plots recorded in five Piedmont river basins. The inset map identifies the location of North Carolina. In the North Carolina state map, the wide grey lines delineate the three broad physiographic regions of North Carolina (left mountains, center Piedmont, right Coastal Plain). The narrow dark grey lines delineate river basin boundaries: 1. Catawba, 2. Yadkin- PeeDee, 3. Cape Fear, 4. Neuse, and 5. Tar-Pamlico River Basins.
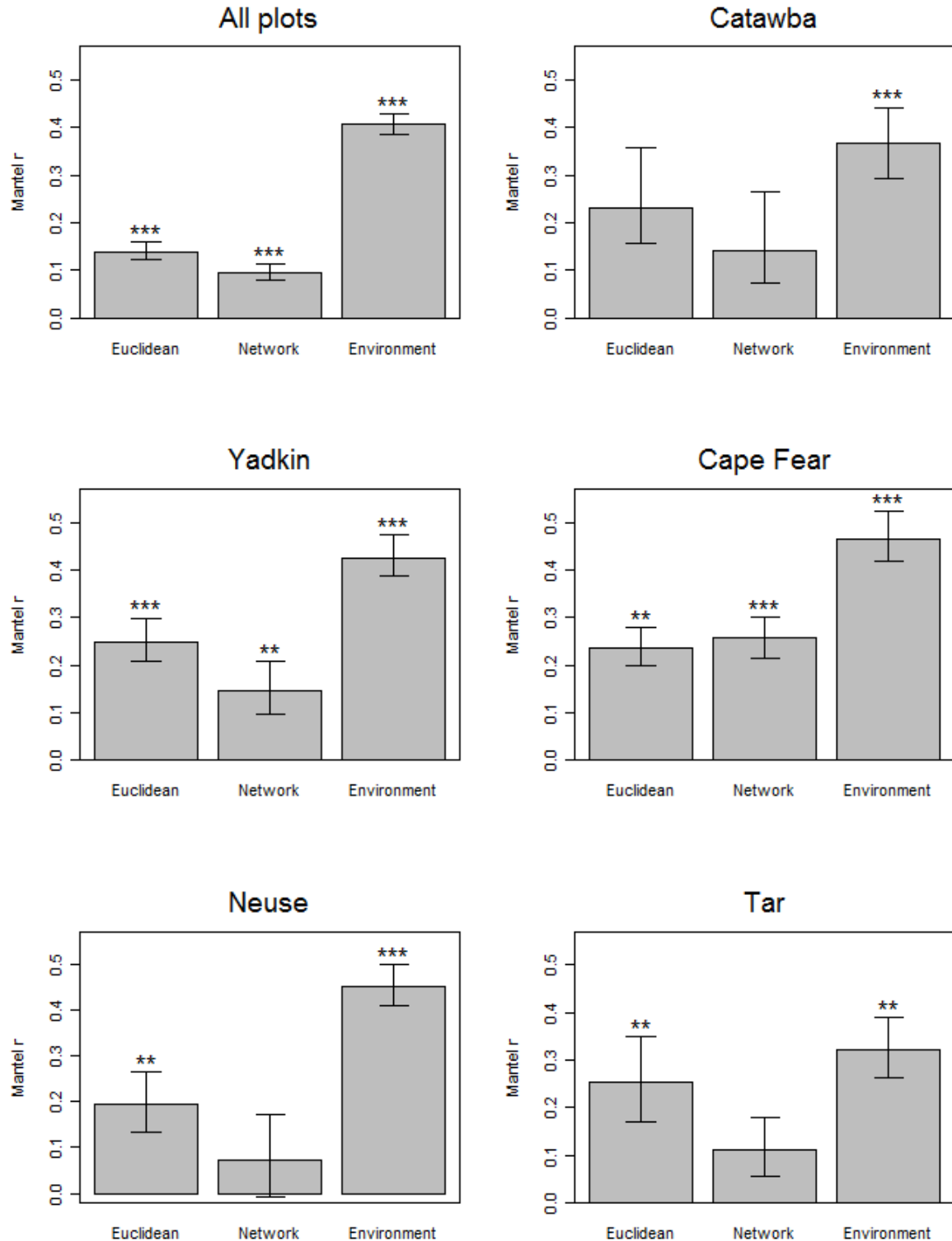
Figure 4.3: Mantel correlations (Mantel r) for riparian plant community composition at two scales, across river basins and within river basins. Floristic dissimilarity is compared to Euclidean spatial distance, network spatial distance, and environmental dissimilarity. Environmental dissimilarity is most strongly correlated to floristic dissimilarity at both scales. Error bars reflect the 95% confidence interval for the Mantel r statistic. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

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References

Benedetti, M.M., Raber, M.J., Smith, M.S., and Leonard, L.A. 2006. Mineralogical indicators of alluvial sediment sources in the Cape Fear River Basin, North Carolina. Physical Geography 27: 258-281.

Beisner, B.E., Peres-Neto, P.R., Lindstrom, E.S., Barnett, A., and M.L. Longhi. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87: 2985-2991.

Blanchet, F.G., Legendre, P., and D. Borcard. 2008. Forward selection of explanatory variables. Ecology 89: 2623-2632.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Borcard, D. and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. Ecological Modeling 153: 51-68.

Brown, B.L., and C.M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79: 571-580.

Carr, S.C., Roberston, K.M., Platt, W.J., and R.K. Peet. 2009. A model of geographical, environmental, and regional variation in vegetation composition of pyrogenic grasslands of Florida. Journal of Biogeogrpahy 36: 1600-1612.

Chambert, S. and C.S. James. 2009. Sorting of seeds by hydrochory. River research and applications 25: 48-61.

Chase J. M. 2003. Community assembly: when should history matter? Oecologia 136:489-498.

Chase, J.M., and W.A. Ryberg. 2004. Connectivity, scale-dependence, and the productivity-diversity relationship. Ecology Letters 7: 676-683.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175-1182.

Cottenie, K., and L. De Meester. 2004. Connectivity and cladoceran species richness in a metacommunity of shallow lakes. Freshwater Biology 48:823-832.

Cottenie, K., Michels, E., Nuytten, N., and L. DeMeester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. Ecology 84: 991-1000.

Danvind, M. and C. Nilsson. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. Journal of Vegetation Science 8: 271-276.

Dray, S. 2008. SpacemakeR: Spatial modeling. R package version 0.0-5.

Dray, S., Legendre, P., and G. Blanchet. 2009. packfor: Forward Selection with permutation (Canoco p.46). R package version 0.0-7/r58.

Dray, S., Legendre, P., and P.R. Peres-Neto. 2006. Spatial modeling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). Ecological Modelling 196: 483-394.

Driscoll, D.A. and D.B. Lindenmayer. 2009. Empirical tests of metacommunity theory using an isolation gradient. Ecological Monographs 79: 485-501.

Duque, A., Sanchez, M., Cavelier, J., and J.F. Duivenvoorden. 2002. Different floristic patterns of woody understory and canopy plants in Columbian Amazonia. Journal of Tropical Ecology 18: 499-525.

Flinn, K.M., Gouhier, T.C., Lechowicz, M.J., and M.J, Waterway. 2010. The role of dispersal in shaping plant community composition in wetlands within an old-growth forest. Journal of Ecology 98: 1292-1299.

Freestone, A.L. and B.D Inouye. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology 87: 2425-2432.

Gause, G.F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, M.D.

Gilbert B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences of the United States of America 101:7651-7656.

Gleason, H.A., 1026. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Society 53: 7-26.

Goslee, S.C. and D.L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22: 1-19.

Griffith, D.A. and P.R. Peres-Neto. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology 87: 2603-2613.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250: 26-31.

Hampe, A. 2004. Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a 'bird-dispersed' riparian tree. Journal of Ecology 92: 797-807.

Imbert, E. and F. Lefevre. 2003. Dispersal and gene flow of *Populus nigra* (Salicaceae) along a dynamic river system. Journal of Ecology 91: 447-456.

Jansson R., Zinko, U., Merritt, D.M., and C. Nilsson. 2005. Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. Journal of Ecology 93:1094-1103.

Johansson, M.E., Nilsson, C., and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? Journal of Vegetation Science 7: 593-598.

Jones, M.M., Tuomisto, H., Clark, D., and P. Olivas. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. Journal of Ecology 94: 181-195.

Jones, M.M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D.B., and P.C. Olivas. 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155: 593-604.

Karst, J., Gilbert, B., and M.J. Lechowicz. 2005. Fern community assembly: the role of chance and the environment at local and intermediate scales. Ecology 86: 2473-2486.

Laliberte, E. 2008. Analyzing or explaining beta-diversity? Comment. Ecology 89: 3227-3232.

Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology 1: 3-8.

Legendre, P. and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam, The Netherlands.

Legendre, P., Borcard, D., Blanchet, G., and S. Dray. 2009. PCNM: PCNM spatial eigenfunction and principal coordinate analyses. R package version 1.9/r75. http://R-Forge.R-project.org/projects/sedar/

Legendre, P., Borcard, D., and P.R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75: 435-450.

Legendre, P., Borcard, D., and P.R. Peres-Neto. 2008. Analyzing or explaining beta diversity? Comment. Ecology 89: 3238-3244.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M. , Hoopes, J. M. , Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601-613.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

McCune, B. and Grace, J.B.. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, USA.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 201-218.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis 15: 1409-1416.

Minor, E.S., Tessel, S.M., Engelhardt, A.M., and T.R. Lookingbill. 2009. The role of landscape connectivity in assembling exotic plant communities: a network analysis. Ecology 90: 1802-1809.

Moore, K.A. and S.C. Elmendorf. 2006. Propagule vs. niche limitation: untangling the mechanisms behind plant species' distributions. Ecology Letters 9:797-804.

Mouillot, D. 2007. Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. Journal of Applied Ecology 44: 760-767.

Nabout, J.C., Sequeira, T., Bini, L.M., and I. de S. Nogueira. 2009. No evidence for environmental and spatial processes in structuring phytoplankton communities. Acta Oecologica 35: 720-726.

Naiman, R.J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

Oksanen, J., F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, R. G. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens and Helene Wagner (2010). vegan: Community Ecology Package. R package version 1.17-0. http://CRAN.R-project.org/package=vegan

Ozinga, W.A., Schaminee, J.H.J., Bekker, R.M., Bonn, S., Poschlod, P., Tackenberg, O., Bakker, J., and J.M. van Groenendael. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos 108: 555-561.

Peet, R. K., T. R. Wentworth, and White, P. S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262–274.

Pelissier, R., Couteron, P., and S. Dray. 2008. Analyzing or explaining beta-diversity? Comment. Ecology 89: 3227-3232.

Peres-Neto, P.R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614-2625.

Powers, J.S, Becknell, J.M., Irving, J., and D. Perez-Aviles. 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. Forest Ecology and Management 258: 959-970.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for CI Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org.

Ricklefs, R. E. 1987. Community diversity - relative roles of local and regional processes. Science 235: 167-171.

Rothley, K. 2005. Finding and filling the "cracks" in resistance surfaces for least-cost modeling. Ecology and Society 10(1):4. [online] URL: http://www.ecologyandsociety.org/vol10/iss1/art4/

Royal Botanic Gardens Kew. (2008) Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (May 2008)

Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M.K., and M. Moretti. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology 91: 3343-3353.

Soininen J., M. Kokocinski, S. Estlander, J. Kotanen, and J. Heino. 2007. Neutrality, niches, and determinants of plankton metacommunity structure across boreal wetland ponds. Ecoscience 14:146-154.

Theobald, D.M., J.B. Norman, E. Peterson, S. Ferraz, A. Wade, and M.R. Sherburne. 2005. FLoWS v1: Functional Linkage of Watersheds and Streams tools for ArcGIS v9. Natural Resource Ecology Lab, Colorado State University. http://www.nrel.colostate.edu/projects/starmap/flows_index.htm

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62: 802-815

Tuomisto, H., Ruokolainen, K., and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. Science 299:241-244.

Tuomisto, H., and K. Ruokolainen. 2006. Analyzing or explaining beta-diversity? Understanding the targets of different methods of analysis. Ecology 87: 2697-2708.

Tuomisto, H., and K. Ruokolainen. 2008. Analyzing or explain beta-diversity? Reply. Ecology 89: 3244-3256.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-197.

Urban, M.C., Skelly, D.K., Burchsted, D., Price, W., and S. Lowry. 2006. Stream communities across a rural-urban landscape gradient. Diversity and Distributions 12: 337-350.

Van de Meutter, F., De Meester, L., and R. Stoks. 2007. Metacommunity structure of pond macroinvertebrates: effects of dispersal mode and generation time. Ecology 88: 1687-1695.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1-22.

Weakley, A. S. 2010. Flora of the Carolinas, Virginia, and Georgia, northern Florida, and surrounding areas. http://www.herbarium.unc.edu/flora.htm/. University of North Carolina at Chapel Hill Herbarium, Chapel Hill, North Carolina.

Wharton, C.H., Kitchens, W.M., Pendleton, E.C., and Sipe, T.W. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37. 133 pp.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26: 1-80.

Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73: 1984-2000.

CHAPTER 5

Application of Quantitative Vegetation Descriptions to Restoration

Abstract

The definition of reference conditions is a vital step in restoration projects. However, as a result of resource constraints, adequate descriptions of reference conditions are rarely feasible. Past studies have suggested that vegetation databases and plant community descriptions may be able to provide this essential reference information, but a methodology for matching new restoration sites to vegetation descriptions is not readily available for resource managers. I present an approach for matching restoration sites to quantitative vegetation descriptions based on a reference dataset from North Carolina. The Southeastern U.S., and North Carolina in particular, are active regions for restoration of stream ecosystems, and we illustrate our approach with six sites in North Carolina. I develop a prototype matching tool that is flexible and is able to match restoration sites to the most similar quantitative plant community descriptions based on easily obtainable, common environmental data. I then illustrate the usability of this tool with a set of restoration sites from the North Carolina Piedmont. I expect that this approach and infrastructure can be readily applied to other locations and vegetation types as data become available. My goal is to provide an approach that might be implemented in other regions where quantitative vegetation descriptions are available.

Introduction

Reference information is an important component of ecological restoration projects (Brinson and Rheinhardt 1996; White and Walker 1997; Harris 1999; Stephenson 1999; de Gruchy et al. 2001; Hughes et al. 2005; Rheinhardt et al. 2007; Lane and Trexler 2009). The description of reference conditions aids in the design of restoration projects, the establishment of restoration goals, and the assessment of restoration success (Lane and Trexler 2009; Rheinhardt et al. 2009). While incorporating natural variation of ecological systems into reference condition descriptions is a vital part of this process, this often proves to be challenging in practice. Many restoration projects proceed with insufficient reference information because of limited time, limited funding, or difficulty in identifying appropriate reference sites (White and Walker 1997; Hughes et al. 2005; Lane and Trexler 2009). Activities commonly associated with restoration projects include riparian buffer creation, buffer maintenance, and revegetation projects (Palmer et al. 2007). However, resource constraints often result in planting lists that are either developed based upon a single, local reference site, or developed by scientists and then planted indiscriminately across ecosystems (Lane and Trexler 2009).

Vegetation databases and plant community descriptions may be able to provide high-quality reference information for restoration activities. Quantitative vegetation descriptions offer a financially feasible way to include natural variation of plant communities into conservation and restoration activities (Harris 1999; Lane and Trexler 2009; Rheinhardt et al. 2009). Quantitative descriptions of plant communities are being developed and archived in publicly available databases on both a nation-wide scale, such as the U.S. National Vegetation Classification (NVC; Jennings et al. 2009), and a regional-scale, such as the

Carolina Vegetation Survey database (http://cvs.bio.unc.edu/). The vegetation plot data used in community descriptions are frequently collected at a larger spatial and temporal scale than typical restoration reference data, which is often collected at a single, opportunistic sampling location. In addition, plant community descriptions generally include a more complete list of species, are more likely to contain information about the average abundance and frequency of species across large spatial extents, and are more likely to represent natural vegetation with minimal human impacts.

While the concept of applying quantitative vegetation descriptions to restoration activities is not new (Harris 1999; Lane and Trexler 2009; Rheinhardt et al. 2009), few authors have discussed how quantitative descriptions are matched to restoration sites. A methodology for matching sites to quantitative vegetation descriptions should be cheap, efficient, and based on data that are readily accessible to resource managers and restoration practitioners. In this paper, we present an approach for matching new restoration sites to appropriate vegetation descriptions based on quantitative environmental data associated with each type description. As quantitative vegetation descriptions become more readily available, this methodology for matching sites to community descriptions will provide savings to the user by preventing the need for field work beyond the restoration site. We developed a matching tool that can be readily accessible to resource managers and restoration practitioners over the web.

We illustrate our approach with a case study in the Piedmont region of North Carolina. The Southeastern United States, and North Carolina in particular, are active regions for stream restoration (Sudduth et al. 2007). We utilize quantitative plant community descriptions developed from high-quality alluvial vegetation plot data, outline an approach

for matching the community descriptions to new restoration sites, and demonstrate this process with a set of pre-construction restoration sites in North Carolina. We expect that this approach and infrastructure can be readily applied to other locations and vegetation types as data become available.

Methods

Case study

Our case study uses two datasets. The first is a quantitative classification of the alluvial vegetation types of the North Carolina Piedmont. The classification is based on 182 vegetation plots documenting high-quality natural vegetation. These plots have been classified to twelve forested vegetation types, each with a quantitative description that includes average cover and constancy values for each taxon occurring in the type. The classification spans five river basins in the Piedmont region in the Southeastern United States, the Catawba, Yadkin, Cape Fear, Neuse, and Tar-Pamlico (Figure 5.1), and was developed using standard quantitative techniques, including cluster analyses, random forests, and ordination (Chapter 2). The twelve forested types are comparable to NVC associations in terms of compositional variation and consistency, and in fact, have been proposed as possible revisions of the NVC alluvial associations. These types reflect the level of resolution that we expect would be most useful in guiding restoration practices and in the design of restoration targets.

Environmental data associated with the described vegetation types includes both field-collected data and data derived using a geographic information system (GIS). These data characterize the environmental setting of each type and include variables that have been

shown to be important drivers of Piedmont alluvial vegetation (Chapter 2). Field-based environmental variables include geomorphic position, slope, geographic coordinates, and soil nutrient and texture variables. GIS-derived variables include elevation, stream order, cumulative upstream area drained (watershed area), width of the 100-year floodplain, distance to channel, mean annual temperature and precipitation, mapped soil unit, and bedrock formation. All GIS-derived variables were extracted from readily available spatial data or basic GIS analyses; data sources include the National Elevation Dataset (NED; http://ned.usgs.gov/), the USGS National Hydrography Dataset (NHD; http://nhd.usgs.gov/), and the USDA-NRCS Soil Survey Geographic Database (SSURGO; http://soildatamart.nrcs.usda.gov/). Width of the one hundred year floodplain was determined using the North Carolina digital floodplain maps (http://www.ncfloodmaps.com/).

The second dataset includes six pre-production restoration sites in the North Carolina Piedmont (Figure 5.1). These sites were identified by the North Carolina-Ecosystem Enhancement Program (EEP), the state agency that oversees wetland conservation and restoration in North Carolina. The six sites were visited in the fall of 2009 to characterize the geomorphic setting. Following field visits, restoration sites were mapped in a GIS and supplementary environmental data were gathered; the GIS-derived variables extracted for each restoration site matched those extracted for the reference vegetation plots. Larger restoration sites were divided into separate units corresponding to different environmental-geomorphic settings. Where restoration sites included streams of various stream order, each stream was treated as an independent restoration unit.

Quantitative analysis

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We summarized the environmental data associated with each vegetation type. The environmental dataset included 14 variables: cumulative drainage area, distance to river mouth (km), elevation (m), latitude (decimal degrees), longitude(decimal degrees), distance to channel (m), one-hundred year floodplain width (m), mean annual temperature (C), mean annual precipitation (mm), stream order, and four categorical variables: mapped soil unit, geologic bedrock, river basin, and general geomorphic position. We calculated the mean value for each group for six variables: distance to river mouth, latitude, longitude, one-hundred year floodplain width, and mean annual temperature and precipitation. We reported the median value for two variables, cumulative drainage area and stream order, in order to minimize the influence of outlier values. Categorical variables were summarized by the percentage of plots associated with each category; only categories that included >10% of the vegetation plots were reported.

We employed classification methods to identify key environmental variables in discriminating between potential vegetation types. Classification results would allow restoration professionals to focus on a subset of the potential environmental site data. Classification techniques are particularly appropriate for identifying key variables in predicting the potential vegetation type because they do not require assumptions of normally distributed variables and can easily handle both categorical and continuous predictor data (Byrd and Kelly 2006; Cutler et al. 2007). We used random forests classification methods as implemented in R to identify the key environmental variables in discriminating between the plant community descriptions of our model system (Breiman 2001; R Development Core Team 2010). Both R and the "randomForests" package are free statistical software.

Environmental variables were evaluated in the "randomForests" package via the permutation importance measure. This measure is computed from permuted out-of-bag predictor data (oob; out-of-bag data are those data left out of the training dataset for each tree, typically one third of the dataset; Breiman 2001). For each tree, the oob data is run through the trees produced by the random forests algorithm and the prediction error rate is recorded. This procedure is then repeated, with the values of each predictor variable randomly permuted. The number of correct classifications from the permuted oob data is subtracted from the correct classifications from the unpermuted oob data. The difference between the two values is then averaged across all trees grown in the forest and becomes the raw importance score for each variable. Variables are ranked by their importance score.

We developed a tool in Microsoft Access (Microsoft Corporation 2007) to match new restoration sites to described vegetation types based upon similarity of environmental variables. The tool is flexible and will determine the most similar vegetation types based upon any set of user-supplied environmental data. However, when many predictor variables are available, resource manager may choose to restrict predictors to those identified by the random forests variable importance analyses. User-supplied environmental variables are compared to the average group variables using similarity metrics. Any similarity or dissimilarity metric could be utilized for this matching process, based upon user-preferences and metrics most appropriate for the available quantitative data. To compare the environmental settings at new restoration sites with environmental variables for described vegetation types, we used a dissimilarity metric defined as

$$\frac{\Sigma \, |N_i - G_i| * w_i}{\Sigma \, (N_i + G_i) * w_i}$$

where $N_i = i$ [th] environmental variable at the new site, $G_i =$ group average for i [th] environmental variable, $w_i =$ weight for i[th] environmental variable.

Various data transformations and standardizations may be required prior to analysis, either to satisfy assumptions for quantitative analyses or to adjust the influence of specific variables. For this case study, we transformed all categorical variables (geomorphic position, river basin, mapped soil unit, and geologic bedrock formation) to dummy variables. We also square root transformed cumulative drainage area to down-weight high outliers. We calculated G_i as the arithmetic average; all environmental variables were relativized by the maximum observed value in this dataset to standardize all variables to a 0-1 scale. All variables included the same weight ($w = 1$) for this analysis.

We then used the tool to generate reference community descriptions for each of the six restoration sites identified by EEP. Described vegetation types were ranked by dissimilarity metric, with the three least dissimilar (most similar) groups identified and reported by the tool. The reference community descriptions include the floristic information for each of the most similar vegetation types, consisting of average percent cover where present and constancy (the percent of plots in which the taxon occurs). The vegetation type species information reported by the tool can also be filtered by constancy and species attributes to include only prevalent (sensu Curtis 1959) and woody species. Prevalent species are identified by ranking species by constancy and selecting the most common species such that the total number of prevalent species equals average species richness.

Results

The environmental descriptors of our restoration sites fell well within the range of variation captured in the fourteen community descriptions (Table 5.1; Table 5.2). The six

restoration sites identified covered a variety of environmental settings, from 1st to 5th order

rivers, across a range of geomorphic settings, bedrock, and soil units. The restoration sites

were all located within the Piedmont sections of the Cape Fear and Yadkin River Basins

(Figure 5.1). All but one of the sites spanned more than one geomorphic setting and were

treated as multiple sites in the matching approach.

Random forest analysis identified geomorphic position as the strongest environmental

predictor of vegetation type (Figure 5.2). Distance to mouth, longitude, and elevation were

the next three strongest predictors, followed by the two climatic variables (temperature and

precipitation) and watershed area. Mapped soil unit, latitude, stream order, and floodplain

width were also identified as useful predictors of vegetation types.

We created a user interface that allows the user to input predictor environmental

variables (Figure 5.3). We also incorporated input space for additional environmental

variables not used in this analysis, but often associated with vegetation descriptions (e.g., soil

texture and nutrient descriptions). The tool interface generates a list of the most similar

communities in the reference dataset, as well as a panel that summarizes the floristic data of

the matched community type. Predictor variables can also be color coded to reflect their

influence on the predicted community.

We generated restoration targets for each of the six restoration sites based upon the 14

descriptor variables (Table 5.2; Table 5.3). We present the single most similar community

type, although the tool ranked all described community types by their dissimilarity and

identified the three most similar types.

Discussion

Using environmental descriptors of restoration sites, we were able to generate reference condition descriptions from quantitative community classifications and their associated floristic information. We created a tool that matches new restoration sites to the most similar described vegetation type based on a user-supplied set of environmental variables describing the restoration site. The tool is flexible and does not require a full set of environmental variables to match restoration sites to vegetation types. We also demonstrated how classification techniques can be used to rank environmental variables by their ability to predict the natural vegetation on a site.

We illustrated the usability of the matching tool with a set of restoration sites from the North Carolina Piedmont. The highest-ranked vegetation types for the restoration sites were often associated with similar geomorphic settings and characterized by similar species composition. The two most similar community types for the Mill Creek, Uwharrie River site, for example, are both oak-hickory dominated flats (Figure 5.3). Even the third most similar vegetation type is commonly found on both alluvial flats and small stream riparian areas (Table 5.1); while slightly more common along small streams, this type includes many of the dominant species found in the oak-hickory flat vegetation types (*Carpinus caroliniana, Carya cordiformis, Ulmus americana)*. As illustrated by this example, the tool was able to match a single best vegetation type and two additional, often geomorphically and floristically similar, communities to the restoration site, suggesting that other high-ranked types might also provide useful floristic reference information for restoration sites.

Detailed floristic descriptions that accompany quantitative vegetation classifications often include data on species composition, abundance, constancy, and diagnostic value. These data can be used as the basis for designing planting species mixes that reflect species

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most likely to naturally occur on site and, hence, might be most likely to be successful after restoration activities are complete. Restoration practitioners may chose species for planting based upon the floristic descriptions, although the tool-generated lists may be edited to emphasize both dispersal-limited species that are unlikely to colonize restoration sites unassisted and species that are rare on the landscape. Restoration sites that are matched to community types that include early successional, well-dispersed species at high cover, such as *Liquidambar styraciflua,* may be edited in the creation of planting lists, perhaps directing resources towards less common or dispersal-limited species, such as heavy-seeded *Quercus* and *Carya* species. Many of the smaller restoration sites included in our case study were matched to a vegetation type described by high constancy and cover of early successional species (Ia. *Liriodendron tulipifera – Liquidambar styraciflua / Lindera benzoin/ Amphicarpaea bracteata* Forest). However, two *Carya* species (*C. cordiformis* and *C.ovata)* also contribute high cover, although at a lower constancy, to this vegetation type. Planting lists might emphasize these species over the smaller-seeded, early-successional dominants.

Quantitative community descriptions generated using our approach can also provide the multivariate data necessary to both characterize the restoration target and assess the success of restored vegetation communities using multivariate analyses (Rheinhardt et al. 2008). Vegetation monitoring data can be used to track the long-term recovery trajectory of restoration sites after planting. The combination of quantitative reference data and monitoring data may also suggest taxa that remain underrepresented in restored sites, taxa that might need to be introduced later in the successional recovery of restoration sites.

In this study, the environmental predictor dataset was limited to easily obtainable data, requiring only short field visits to the restoration site and spatial analyses in a

geographic information system (GIS). All GIS analyses were restricted to free and readily accessible spatial data. We further demonstrated that restoration practitioners can utilize classification methods to rank environmental variables by their predictive power; as a result, restoration professionals can focus limited resources toward the collection of a smaller, yet more powerful set of predictor environmental data. In our case study we found geomorphic setting to be the strongest predictor of vegetation type; it is well-established that vegetation varies with geomorphology in the riparian landscape (Wharton et al. 1982; Hupp and Osterkamp 1985; Hupp 2000; Chapter 2). The next three strongest predictors of vegetation, distance to mouth, longitude, and elevation, all reflect the location of the vegetation type within the river basin. High values for each of these variables indicate a position higher in the basin and more distant from the river mouth. Watershed size (cumulative are drained), stream order, and floodplain width all reflect the size of the stream. Climatic variables were also useful in predicting vegetation, as was the mapped soil unit.

It is important to note that the variables best able to discriminate between potential vegetation types will be different for each system, possibly for similar habitats in different climatic regions (temperate riparian systems vs. desert riparian system), and will likely change with the spatial extent of the reference dataset. The initial phase of gathering appropriate environmental predictors must be carefully executed and must reflect both the ecological context and the resources available for restoration projects. The primary ecological considerations when gathering predictor variables include an effort to incorporate variables known to be important drivers of vegetation patterns in the system. These drivers may be identified based upon past field work, expert knowledge of the system, published literature, and the reference classifications and quantitative community descriptions.

Choosing among potential environmental variables is a vital step in this process and should be carefully considered before continuing with classification methods or matching techniques. More disturbed restoration sites may require more complex assessment of appropriate environmental predictors as the setting before and after restoration may change substantially. Stream size and soil properties, for instance, may be altered in a large restoration project. Financial resources and time constraints may also play a role in determining the set of environmental variables appropriate; however, we have shown here that there are many freely available data and software resources that might alleviate financial restrictions. Additionally, the matching tool presented here is flexible and is able to match restoration sites to the most similar quantitative plant community descriptions even when limited to easily obtainable environmental data.

Because both the reference dataset and the restoration sites of this study were confined to a single physiographic region in the Southeastern U.S., we were able to utilize local to regional scale environmental variables in the matching process. However, as the spatial extent of the reference dataset expands towards regional or national-scale databases, a preliminary filter based upon physiognomy, biogeographic history, or bioclimatic variables will be necessary (Hughes et al. 2005). These filters may reflect higher levels already recognized in classification systems, such as the NVC's Formation level (e.g., *Temperate Shrublands and Grasslands*) or U.S. Environmental Protection Agency Level III Ecoregions (e.g., *Central Great Plains*).

The application of quantitative community descriptions to the development of restoration targets allows relatively easy generation of otherwise unattainable, state-of-the-art predictions of the natural vegetation of a site. We expect these targets should satisfy the most

stringent current and future restoration guidelines. As a consequence, the application of the vegetation databases can greatly increase the efficiency and effectiveness with which agencies and contractors conduct restoration work while significantly reducing their costs. We expect that this approach and infrastructure can be readily applied to other locations and vegetation types as they become available, increasing restoration efficiency and success beyond North Carolina.

Table 5.1: Summary of environmental variables for vegetation types and restoration sites. Unless otherwise noted, quantitative variables are summarized by their arithmetic mean. Cumulative drainage and stream order are summarized by their median values. River basin includes all basins where present, listed in order of abundance. Geologic bedrock includes all bedrock with >10% of occurrences. Mapped soil unit in which greater than 25% of the plots in a group occur are listed, with percentage of plots. ** indicates that no mapped soil unit occurred at more than 25% of the plots. Codes used in table include: MAT= mean annual air temperature; MAP= mean annual precipitation.

vegetation type	cumu. drainage	distance to river mouth (km)	elevation (m)	lat.	long.	distance to channel (m)	100 year floodplain width (m)	MAT (C)	MAP (mm)	mapped soil unit	geologic bedrock	stream order	river basin	geomorphic position
Ia. *Liriodendron tulipifera – Liquidambar styraciflua / Lindera benzoin/ Amphicarpaea bracteata* **Forest**	61.3	454	175	35.81	-80.03	37.9	171.5	14.5	1177	**	CZ (78%)	3	all	SS(50%); flat(45%)
Ib. *Liriodendron tulipifera - Betula nigra / Cornus florida / Sanicula canadensis var. canadensis* **Forest**	26.1	391	121	35.60	-79.57	29.2	118.8	15	1160	Ch(50%)	CZ(100%)	2	Cat; CF; Neu	SS(100%)
IIa. *Liquidambar styraciflua - Quercus nigra / Carpinus caroliniana / Mitchella repens* **Forest**	300.2	334	91	35.72	-79.12	37.3	419.5	14.8	1161	Ch(44%)	CZ(63%); TR(22%)	4	all	flat(56%); bottom (22%)
IIb. *Liquidambar styraciflua- Quercus pagoda- Carya cordiformis/ Asimina triloba/ Arundinaria tecta* **Forest**	427.9	340	60	35.06	-80.05	36.7	1150.0	16.1	1200	Ch(100%)	TR(100%)	4	Yad	bottom(66%)
IIc. *Carya carolinae-septentrionalis - Acer floridanum / Aesculus sylvatica/ Zizia aurea* **Forest**	896	364	118	35.55	-79.76	29.7	141.6	15.1	1175	Ok (63%)	CZ(100%)	3	Yad; CF	flat(63%)
IIIa. *Ulmus americana - Celtis laevigata/ Lindera benzoin / Osmorhiza longistylis* **Levee Forest**	3347	350	89	35.61	-79.38	37.8	488.5	14.5	1170	Ch(30%); RvA(27%)	CZ(54%); PPg(21%); TR(18%)	6	CF; Yad; Neu: Cat	levee (67%)
IIIb. *Fraxinus pennsylvanica- Platanus occidentalis / Acer negundo/ Chasmanthium latifolium* **Levee Forest**	1150	394	129	35.87	-79.48	34.5	369.8	14.3	1156	Ch(43%)	CZ(43%); PPg(27%)	5	all	levee(70%)
IVa. *Quercus (phellos-pagoda-michauxii)- Ulmus americana / Ilex decidua / Arisaema triphyllum* **Bottomland Forest**	146.8	347	78	35.76	-79.07	89.1	624.5	14.7	1157	Ch(82%)	TR (53%); CZ (41%)	4	CF; Neu; Tar; Yad	bottom(76%)
IVb. *Fraxinus pennsylvanica -Acer rubrum-Ulmus americana/ Ilex decidua / Saururus cernuus* **Swamp Forest**	231.5	339	82	35.82	-78.95	97.6	639.0	14.7	1149	Ch(63%)	CZ (33%); PPg(33%); TR(25%)	4	all	BS(58%); bottom(29%)
IVc. *Fraxinus pennsylvanica -Betula nigra-Platanus occidentalis/ Alnus serrulata / Boehmaria cylindrica* **Forest**	2532	481	212	35.78	-80.59	64.7	470.8	13.9	1224	**	CZ (83%)	3	Yad; Cat; CF	BS(83%)
IVd. *Quercus lyrata- Fraxinus pennsylvanica/ Saururus cernuus* **Swamp Forest**	144.7	370	74	35.47	-79.40	93.0	603.3	15.6	1171	Ch(33%); Co(33%); CoA(33%)	TR (100%)	4	CF; Neu; Yad	BS(100%)
IVe. *Carya aquatica- Nyssa aquatica* **Swamp Forest**	17381	316	55	35.07	-79.90	35.5	1100.0	14.6	1189	Ch(100%)	TR (100%)	7	Yad	BS(100%)

Table 5.2: Environmental descriptors for the six NC-EEP restoration sites.

restoration site	cumu. drainage	distance to river mouth (km)	elevation (m)	lat.	long.	distance to channel (m)	100- yr floodplain width (m)	MAT (C)	MAP (mm)	mapped soil unit	geologic bedrock	stream order	river basin	geomorphic position
Morgan Creek														
	112	345	70	35.890	-79.910	<50	760	14.5	1168	Cp; Ch	TR	4	CF	levee
	112	345	70	35.890	-79.910	50-150+	760	14.5	1168	Ch	TR	4	CF	bottom; BS
Wells Creek #2														
	<10	383	180	35.919	-79.466	0-40	30-50	14.7	1155	Cf; Hd; Ce	CZ	2 (UT,1)	CF	SS; flats
UT to West Fork of Deep River (G)														
UTA	<10	501	260	36.055	-80.04	<10	NA	14.7	1111	Ha	PPg	1	CF	SS
UTB	<10	501	260	36.055	-80.04	<10	10	14.7	1111	Ha	PPg	1	CF	SS
UTC	<10	501	260	36.055	-80.04	<10	NA	14.7	1111	Ha	PPg	1	CF	SS
main channel, West Fork Deep	<10	501	260	36.055	-80.04	<25	16	14.7	1111	Ha	PPg	2	CF	SS; flats
Sandy Creek														
UT	74	451	170	35.827	-79.646	0-80+	180-220	14.7	1159	Ch	CZ	2	CF	SS;BS
	74	451	170	35.827	-79.646	0-40	150	14.7	1159	Ch	CZ	2	CF	levee; flat
Sandy Creek	89	451	170	35.827	-79.646	0-40	120	14.7	1159	Ch	CZ	4	CF	flat
Ut to Haw (Beckom)													CF	
	<10	389	194	36.153	-79.464	0-40	40-50	14.7	1134	Lc	CZ	1	CF	BS
	<10	389	194	36.149	-79.464	0-40	40-50	14.7	1134	Lc; EeD2	CZ	1	CF	SS; flat
Mill Creek														
Uwharrie River	767	406	112	35.556	-79.976	<150	220	15.2	1156	Ch; DoB	CZ	5	Yad	flat
Mill Creek	<10	406	**112**	35.556	-79.971	<45	50-60	15.4	1173	BtC	CZ	1	Yad	SS
UT2	<10	406	118	35.558	-79.974	<20	0-30	15.2	1156	DoB; MeC	CZ	1	Yad	SS
UT4	<10	406	120	35.555	-79.968	<20	NA	15.4	1173	BtC	CZ	1	Yad	SS
UT5	<10	406	120	35.557	-79.971	<20	0-30	15.4	1173	BtC	CZ	1	Yad	SS

Table 5.3: Restoration sites and matched vegetation type generated by tool.

Restoration site name	Geomorphic position	Matched vegetation type ID	Dissimilarity
Morgan Creek			
	levee	IIIa	0.118
	bottom; BS	IVd.	0.086
Wells Creek #2			
	SS; flats	Ib.	0.102
UT to West Fork of Deep River (G)			
UTA	SS	Ia.	0.187
UTB	SS	Ia.	0.194
UTC	SS	Ia.	0.187
West Fork Deep	SS; flats	Ib.	0.123
Sandy Creek			
UT	SS;BS	IVc.	0.161
	levee; flat	Ia.	0.163
Sandy Creek	flat	IIc.	0.128
Ut to Haw (Beckom)			
	BS	Ib.	0.193
	SS; flat	Ib.	0.114
Mill Creek			
Uwharrie River	flat	IIb.	0.145
Mill Creek	SS	Ib.	0.051
UT2	SS	Ib.	0.054
UT4	SS	Ib.	0.048
UT5	SS	Ib.	0.054
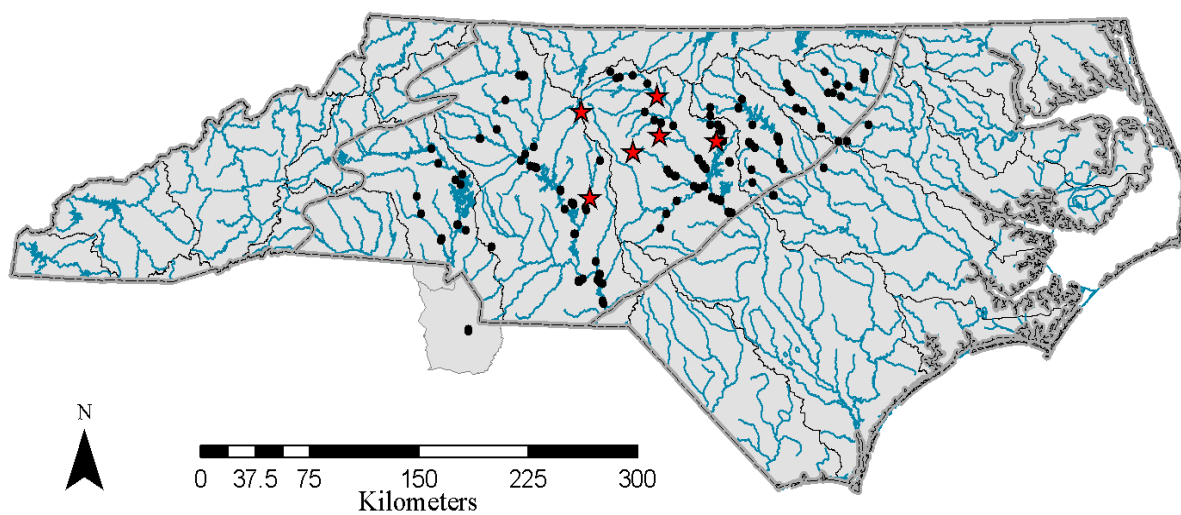
Figure 5.1: 182 reference floodplain forest vegetation plots and 6 restoration sites identified by NC-EEP for this case study.
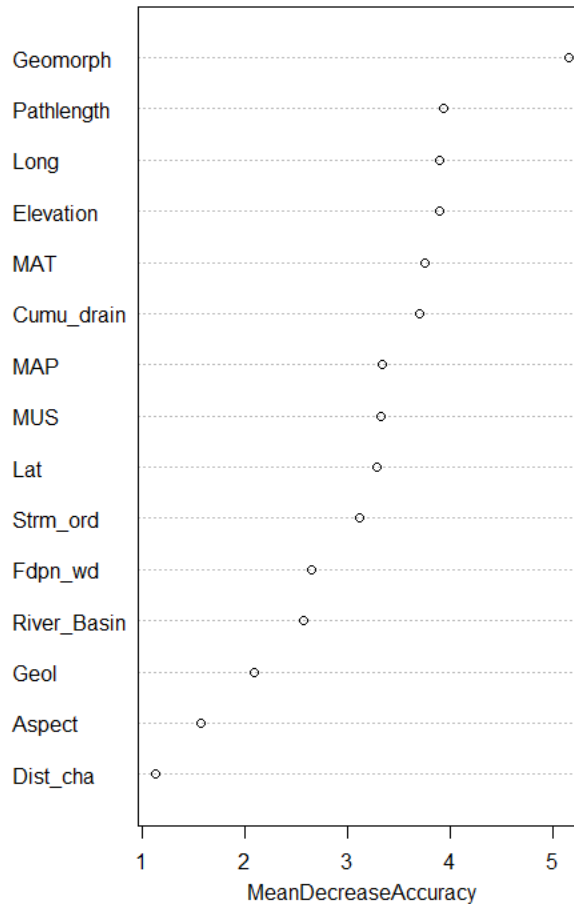
Figure 5.2: Environmental variables ranked by importance in discriminating between vegetation groups: (a) the four broad geomorphic-floristic groups and (b) the twelve finer-scale vegetation types. Code for the environmental variable are: Geomorph= geomorphic position, Long= longitude, Lat= latitude, Pathlength= distance to river mouth, MAT= mean annual temperature, MAP= mean annual precipitation, Cumu_drain= watershed area, Strm_ord= stream order, Fdpn_wd= one-hundred year floodplain width, Dist_cha= distance to channel, and MUS= mapped soil unit.

Figure 5.3: Screenshot of the restoration tool to match restoration sites with described vegetation types. Screen shot shows results for the Mill Creek, Uwharrie River restoration site.

References

Berk, Richard. 2008. Statistical Learning from a Regression Perspective. Springer, New York.

Bragg, D. C. 2002. Reference conditions for old-growth pine forests in the Upper West Gulf Coastal Plain. Journal of the Torrey Botanical Society 129:261–288.

Breiman, L. 2001. Random forests. Machine Learning 45:15–32.

Brinson M.M., and R. Rheinhardt. 1996. The role of reference wetlands in functional assessment and mitigation. Ecological Applications 6:69–76.

Byrd, K.B. and M. Kelly. 2006. Salt marsh vegetation response to edaphic and topographic changes from upland sedimentation in a pacific estuary. Wetlands 26: 813-829.

de Gruchy, M. A., U. Matthes, J. A. Gerrath, and D. W. Larson. 2001. Natural recovery and restoration potential of severely disturbed talus vegetation at Niagara Falls: assessment using a reference system. Restoration Ecology 9:311–325.

Harris, R.R. 1999. Defining reference conditions for restoration of riparian plant communities: examples from California, USA. Environmental Management 24:55-63.

Hastie, Trevor, Robert Tibshirani, and Jerome Friedman. 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer, New York.

Hughes, F.R., Colston, A., and J.O. Mountford. 2005. Restoring riparian ecosystems: the challenge of accommodating variability and designing restoration trajectories. Ecology and Society 10(1):12. Available at: http://www.ecologyandsociety.org/vol10/iss1/art12/.

Hupp, C.R. and Osterkamp, W.R. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.

Hupp, C.R. 2000. Hydrology, geomorphology and vegetation of Coastal Plain rivers in the south-eastern USA. Hydrological Processes 14, 2991-3010.

Jennings, M.D., Faber-Langendoen, D., Loucks, O.L., Peet, R.K., and D. Roberts. 2009. Standards for associations and alliances of the U.S. National Vegetation Classification. Ecological Monographs 79: 173-199.

Lane, C.P. and H.D. Trexler. 2009. Generating quantitative regional plant community descriptions for restoration. Restoration Ecology 17: 42-50.

Microsoft Corporation. 2007. Microsoft Access 2007. http://office.microsoft.com

Nilsson, C., Jansson, R., Malmqvist, B., and R. Naiman. 2007. Restoring riverine landscapes: the challenge of identifying priorities, reference states, and techniques. Ecology and Society 12: 16. Available at: http://www.ecologyandsociety.org/vol12/iss1/art16/.

Palmer, M., Allan, J.D., Meyer, J., and E.S. Bernhardt. 2007. River restoration in the twenty-first century: data and experiential knowledge to inform future efforts. Restoration Ecology 15: 472-481.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262–274.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rheinhardt, R.D., Brinson, M.M., Christian, R.R., Miller, K.H., and G.F. Meyer. 2007. A reference-based framework for evaluating the ecological condition of stream networks in small watersheds. Wetlands 27: 524-542.

Rheinhardt, R.D., Brinson, M.M., and T.R. Wentworth. 2008. Developing and testing multivariate approaches for evaluating success of restored vegetation communities. Report to the Ecosystem Enhancement Program, N.C. Department of Environment and Natural Resources, Raleigh, N.C. Available at: http://www.nceep.net/resources/papers/Rheinhardt_et_al_EEP_Final_Report.pdf

Rheinhardt, R.D., McKenney-Easterling, M., Brinson, M.M., Masina-Rubbo, J., Brooks, R.P., Whigham, D.F., O'Brien, D., Hite, J.T., and B.K. Armstrong. 2009. Canopy composition and forest structure provide restoration targets for low-order riparian ecosystems. Restoration Ecology 17: 51-59.

Sudduth, E.B., Meyer, J.L., and E.S. Bernhardt. 2007. Stream restoration practices in the Southeastern United States. Restoration Ecology 15: 573-583.

Stephenson, N. L. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecological Applications 9:1253–1265.

Wharton, C.H., Kitchens, W.M., Pendleton, E.C., and Sipe, T.W. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37. 133 pp.

White, P.S. and J.L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5:338-349.

Zuur, Alain F., Elena N. Ieno, Graham M. Smith. 2007. Analysing Ecological Data. Springer, New York.

CHAPTER 6
Conclusion

Summary of conclusions

The research presented in this dissertation provides documentation and description of North Carolina's Piedmont alluvial vegetation, an understudied yet ecologically important Southeastern ecosystem. This work substantially advances our understanding of the major drivers of diversity in this system and outlines an approach for using vegetation descriptions in the restoration of degraded alluvial vegetation. The major conclusions of this dissertation work include:

1. Piedmont riparian vegetation can best be represented in a hierarchical framework, where higher-level vegetation groups reflect broad geomorphic-floristic patterns and lower-level vegetation types reflect finer-scale floristic variation. These lower-level groups are comparable to National Vegetation Classification (NVC) associations in terms of compositional variation and consistency and may be used to guide revisions to currently recognized NVC concepts. Compositional variation is strongly related to local hydrogeomorphic setting and soil fertility.

2. Richness of Piedmont riparian forests is highest in the small-stream floodplain forests. However, floodplain forests associated with different river sizes are characterized by distinct plant communities, where the total abundance or proportion of the community represented by species groups defined by plant attributes (nativity, habitat association and growth form) varies with river size.

3. Piedmont alluvial vegetation can be viewed as a metacommunity, where local

sites are linked by both overland and riparian network dispersal. Compositional

patterns of Piedmont alluvial metacommunities, however, are primarily shaped by

local environmental setting, with dispersal processes playing a relatively small role in

determining local composition.

4. By utilizing quantitative environmental variables of both vegetation types and

restoration sites, it is possible to match restoration sites to described vegetation types.

Floristic descriptions of the matched vegetation type provide the necessary reference

information for guiding restoration action. As a result of using site-specific variables,

matched vegetation type descriptions can increase the likelihood of restoration

success when compared with current restoration protocols.

Implications for conservation and restoration

The results of this work have various implications for the conservation and restoration

of North Carolina's Piedmont alluvial vegetation. The classification presented in Chapter 2

can inform revisions of vegetation classifications used by state agencies, conservation

organizations, and federal land management agencies, improving the ability of managers to

efficiently engage in management action. Comparison of the vegetation units presented in

Chapter 2 with those currently recognized in the U.S. National Vegetation Classification

suggests that revisions of the NVC are necessary to better represent Piedmont alluvial

vegetation. Additionally, Piedmont alluvial vegetation in North Carolina is now documented

by substantial plot data, allowing for both more complete explorations of patterns across the

state and reclassification by future researchers in developing vegetation types at broader

spatial scales. In addition, results presented in Chapter 3 suggest that conservation and restoration activities should take a broader view of riparian systems and include efforts focused on both small stream alluvial forests and larger-river bottomland habitat, as each contributes a unique set of species to the riparian flora. The work presented in Chapter 4 demonstrates that NC piedmont riparian plant communities are largely structured by local environmental setting, and Chapter 5 illustrates that in a system predominately structured by local environmental variables, restoration practitioners can employ these variables and using matching criteria generate reference information from quantitative community classifications.

Future needs

Although this research expands the body of knowledge related to Southeastern alluvial vegetation, there are still gaps in our knowledge that need to be addressed. In particular, while the spatial extent of this work was motivated by ecological and biogeographic factors (e.g. river basin boundaries, Piedmont physiographic region), it also reflects political borders (e.g. the North Carolina state border). Alluvial plant communities, however, likely respond to these boundaries as either fuzzy edges, in the case of ecological and biogeographic boundaries, or nonexistent edges, in the case of political borders. Future research should address how vegetation patterns respond to and change at these boundaries and how vegetation scientists and plant ecologists should handle boundary issues in classification and description. These questions are of vital importance for management and remain unanswered and under-investigated. A variety of questions related to the issue of boundaries are of interest for understanding alluvial vegetation of the Southeast, including:

How do riparian plant communities within the same river basin change across biogeographical boundaries, such as the fall line of the Southeastern U.S.? Do the major drivers of community composition vary across physiographic boundaries (Mountains, Piedmont, Coastal Plain)? How do riparian communities vary across the remainder of the Southeastern Piedmont region, which crosses many political borders? Are the types defined here sufficient in capturing variation in riparian plant communities across the Southeastern Piedmont? If not, how might they be integrated with other classifications, which are often conducted at spatial scales smaller than the entire ecological region due to resources constraints?

I expect that as the spatial scale of study increases to include the entire Piedmont, unique histories, unique combinations of environmental settings, and perhaps unique spatial constraints will result in distinct alluvial vegetation types, perhaps structured by distinct drivers. In addition to dealing with the variation across boundaries, applied ecologists and natural resource managers must also address how to reconcile patterns described at one spatial scale with variation occurring over a wide range of scales, often in the face of insufficient data for adequately describing variation across these scales. With limited resources available for description and classification of natural systems, methods that utilize available data to "fill in the gaps" are essential. Many of these issues are apparent in current efforts to describe North American vegetation; regional and national-scale vegetation classification is approached at a wide variety of scales and by a wide variety of practitioners (e.g., National Park-scale vegetation classifications and state-wide classifications, such as those developed by the California Native Plant Society and being developed by the Carolina Vegetation Survey). How these descriptions, developed at very different spatial and

temporal scales, will be reconciled, however, is not obvious, and is of fundamental

importance for successful implementation of large-scale natural resource management.

Appendix 1

Means and standard errors (±SE) of soil variables by vegetation type and soil horizon. Texture variables (sand, silt, and clay) are reported as %, and all nutrients (Ca, Mg, K, Na, Fe, Mn, and Al) are reported in ppm. Codes used in table: H= horizon, Or= organic matter, exc= cation exchange capacity, base= base saturation, dens= density.

Type	H	Sand	±SE	Silt	±SE	Clay	±SE	Or	±SE	pH	±SE	exc	±SE	base	±SE	Ca	±SE	Mg	±SE	K	±SE	Na	±SE	Fe	±SE	Mn	±SE	Al	±SE	den	±SE
Ia.	A	47	5	38	4	15	2	5.6	0.5	5.1	0.1	11.8	0.8	52.6	2.8	955	114	170	18	65	7	29	1	185	15	124	18	623	26	0.85	0.04
Ib.	A	70	5	18	5	11	1	4.1	0.8	5.1	0.2	8.1	0.7	51.9	4.7	585	108	113	5	56	11	29	5	201	31	109	30	526	76	0.86	0.04
IIa.	A	45	3	36	3	18	1	5.9	0.3	4.9	0.0	9.4	0.5	45.4	1.2	564	44	143	10	69	4	31	2	229	12	132	11	704	24	0.78	0.02
IIb.	A	17	4	39	1	44	4	5.9	1.1	4.9	0.2	21.7	2.6	47.0	5.5	1240	336	445	61	90	9	28	3	145	11	269	25	850	94	0.77	0.03
IIc.	A	37	10	45	7	17	3	4.4	0.6	4.9	0.2	8.6	1.0	46.9	4.1	502	107	151	21	50	5	31	1	211	12	115	13	667	70	0.89	0.03
IIIa.	A	34	4	45	3	20	2	5.9	0.4	5.4	0.1	15.2	0.7	59.5	2.1	1385	89	228	14	55	4	29	1	183	8	129	8	500	26	0.77	0.02
IIIb.	A	44	5	34	3	22	2	4.9	0.3	5.2	0.1	13.9	1.1	53.5	1.6	1083	86	181	16	65	5	34	2	257	13	107	12	551	30	0.83	0.03
IVa.	A	23	2	50	2	27	2	6.2	0.3	4.7	0.0	13.2	1.1	42.0	1.1	741	87	189	15	65	3	35	1	249	27	150	23	691	28	0.69	0.01
IVb.	A	28	3	37	2	36	2	7.6	0.5	4.8	0.1	14.9	1.5	44.4	1.6	914	122	216	31	84	6	45	3	328	18	99	12	764	32	0.68	0.02
IVc.	A	31	6	38	1	31	6	7.4	0.9	4.6	0.1	8.7	0.9	39.4	2.0	437	33	106	17	58	5	35	3	351	56	48	5	802	49	0.75	0.04
IVd.	A	14	3	50	6	36	4	6.0	0.4	4.8	0.2	14.6	5.6	42.9	5.5	755	276	182	18	76	3	35	10	373	52	94	52	840	111	0.70	0.05
IVe.	A	16	4	40	4	44	0	5.0	0.3	4.8	0.1	11.5	1.9	43.5	1.9	636	93	177	62	67	13	46	8	275	68	90	42	907	53	0.71	0.00
Type	H	Sand	±SE	Silt	±SE	Clay	±SE	Or	±SE	pH	±SE	exc	±SE	base	±SE	Ca	±SE	Mg	±SE	K	±SE	Na	±SE	Fe	±SE	Mn	±SE	Al	±SE	den	±SE
Ia.	B	52	5	31	4	16	2	1.7	0.1	5.1	0.1	5.6	0.5	52.5	2.3	396	48	96	11	30	2	29	2	167	22	106	17	764	26	1.03	0.03
Ib.	B	64	7	23	5	13	3	1.5	0.3	4.9	0.0	6.8	1.2	45.0	1.0	448	107	74	16	31	5	31	5	255	101	106	33	765	101	1.01	0.04
IIa.	B	45	4	32	3	23	2	2.0	0.1	4.9	0.0	6.1	0.6	46.6	1.1	337	40	108	11	36	3	33	2	162	7	128	18	861	39	0.97	0.02
IIb.	B	16	2	51	5	34	6	2.5	0.4	4.7	0.1	14.4	1.9	41.0	2.2	523	72	351	37	69	12	37	3	158	7	356	57	1264	74	0.87	0.02
IIc.	B	35	9	42	7	23	4	3.2	0.6	5.1	0.2	8.6	1.0	51.0	4.6	541	112	175	15	40	5	30	2	180	19	102	15	714	83	0.93	0.04
IIIa.	B	39	4	39	3	22	1	2.2	0.2	5.2	0.1	9.7	0.7	53.7	2.1	736	65	156	11	30	2	31	2	171	8	112	12	678	31	0.92	0.02
IIIb.	B	50	5	28	3	22	2	2.1	0.1	5.0	0.1	9.6	0.9	49.9	1.6	680	72	140	16	38	3	32	1	216	12	80	9	703	27	0.97	0.02
IVa.	B	25	3	46	2	29	2	2.3	0.2	4.9	0.1	9.9	0.9	45.2	1.3	546	76	177	15	34	2	46	5	199	15	139	24	849	29	0.86	0.03
IVb.	B	33	5	34	3	33	3	2.4	0.2	4.9	0.1	11.2	1.3	45.9	1.6	633	87	205	32	44	4	51	6	250	21	90	15	867	37	0.88	0.02
IVc.	B	44	9	28	6	28	4	2.8	0.5	5.0	0.1	7.1	0.9	48.8	2.3	449	54	103	15	38	7	39	3	209	17	57	15	826	79	0.94	0.05
IVd.	B	12	3	48	4	40	6	2.3	0.4	4.9	0.1	13.2	3.2	45.4	1.3	774	264	222	47	44	1	49	6	298	44	85	34	843	45	0.80	0.04
IVe.	B	17	5	52	8	31	3	2.0	0.0	4.9	0.2	12.5	0.5	44.3	3.3	679	99	224	19	36	3	42	8	490	112	110	7	805	35	0.81	0.03

Appendix 2

Average constancy (%) and basal area of woody vegetation in each type (BA = basal area m2/ha). Species list includes species with constancy >25% in at least one group. Non-native species are identified with an *. Rhododendron group 1 = periclymenoides + arborescens + viscosum + calendulaceum.

	I. Small streams and narrow floodplain forests		II. Oak-hickory flats			III. Large river levees		IV. Swamps				
Types	Ia.	Ib.	IIa.	IIb.	IIc.	IIIa.	IIIb.	IVa.	IVb.	IVc.	IVd.	IVe.
Plot Count	18	6	32	3	8	33	30	17	24	6	3	2
taxon name	const BA	const BA	const BA	const BA	const BA	const BA	const BA	const BA	const BA	const BA	const BA	const BA
Acer floridanum	44 0.99	-- --	31 1.26	-- --	100 1.59	64 1.61	23 1.45	29 0.46	8 0.13	-- --	-- --	-- --
Acer negundo	22 1.63	-- --	6 0.00	33 0.06	-- --	73 0.78	90 3.07	29 0.10	-- --	-- --	-- --	-- --
Acer rubrum	78 1.37	100 2.63	88 1.72	100 1.73	50 0.72	21 0.11	17 3.03	82 1.48	100 4.79	83 9.93	67 9.06	100 3.41
Aesculus sylvatica	6 0.00	-- --	6 0.00	-- --	13 0.45	33 0.08	13 0.02	12 0.01	-- --	-- --	-- --	-- --
Alnus serrulata	11 0.19	-- --	-- --	-- --	-- --	-- --	3 0.24	-- --	-- --	50 0.39	-- --	-- --
Asimina triloba	11 0.15	-- --	6 0.03	100 0.17	-- --	42 0.19	7 0.01	29 0.19	8 0.01	-- --	-- --	-- --
Betula nigra	44 6.98	67 6.19	13 4.48	-- --	-- --	12 1.35	23 3.01	35 0.65	25 5.35	83 3.32	-- --	50 2.87
Bignonia capreolata	44 0.00	-- --	78 0.03	100 0.01	25 0.00	52 0.01	43 0.01	71 0.01	58 0.00	33 0.00	-- --	-- --
Campsis radicans	28 0.18	-- --	13 0.06	-- --	-- --	12 0.10	37 0.15	59 0.04	25 0.01	33 0.13	-- --	50 0.00
Carpinus caroliniana	83 1.26	83 1.37	97 1.69	100 1.18	75 0.95	64 0.66	40 0.58	71 0.40	63 0.54	50 0.68	67 0.09	50 3.28
Carya alba	28 0.15	17 0.01	28 0.79	-- --	13 1.19	-- --	-- --	6 0.01	-- --	-- --	-- --	-- --
Carya aquatica	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-- --	100 1.81
Carya carolinae-septentrionalis	-- --	-- --	-- --	-- --	75 6.03	-- --	-- --	-- --	-- --	-- --	-- --	-- --
Carya cordiformis	44 2.35	17 0.00	28 1.02	67 1.03	13 0.24	70 1.69	13 1.20	-- --	-- --	-- --	-- --	-- --
Carya glabra	6 0.00	33 0.03	16 0.83	-- --	25 1.39	-- --	-- --	6 0.40	-- --	-- --	-- --	-- --
Carya ovata	17 0.24	-- --	34 1.06	33 0.02	13 0.49	12 1.23	3 0.83	35 0.63	13 0.50	-- --	-- --	-- --
Celtis laevigata	28 0.10	-- --	-- --	33 0.04	-- --	76 3.96	60 1.05	35 0.22	8 0.20	-- --	-- --	-- --
Cornus florida	89 0.73	83 0.33	44 0.10	-- --	38 0.16	36 0.16	13 0.13	18 0.04	-- --	17 0.01	-- --	-- --
Crataegus viridis	-- --	-- --	-- --	-- --	-- --	-- --	-- --	-- --	17 0.17	-- --	-- --	50 0.04
Diospyros virginiana	11 0.24	33 0.44	13 0.62	-- --	13 0.59	3 0.00	-- --	-- --	-- --	17 0.04	-- --	-- --
*Elaeagnus umbellata**	-- --	17 0.01	9 0.05	-- --	38 0.07	18 0.04	-- --	-- --	4 0.04	-- --	-- --	-- --
Fagus grandifolia	44 6.41	50 0.06	47 2.26	-- --	25 0.02	9 0.42	10 0.17	18 0.02	4 0.11	-- --	-- --	-- --
Fraxinus pennsylvanica	56 0.48	33 0.01	50 0.55	67 0.12	88 0.90	45 1.15	87 6.25	82 0.80	88 2.94	100 4.42	100 2.38	50 1.19
Ilex decidua	11 0.04	-- --	63 0.13	-- --	38 0.18	30 0.03	17 0.11	82 0.26	58 0.07	-- --	67 0.22	50 0.06
Ilex opaca var. opaca	61 0.26	67 0.85	78 1.30	-- --	25 0.02	48 0.49	10 0.43	41 0.15	13 1.69	33 0.01	-- --	-- --
Ilex verticillata	-- --	-- --	3 0.00	-- --	-- --	-- --	-- --	6 0.00	-- --	-- --	33 0.00	-- --
Juglans nigra	22 1.37	-- --	-- --	-- --	13 0.02	33 1.25	20 1.57	-- --	-- --	-- --	-- --	-- --

	I. Small streams and narrow floodplain forests				II. Oak-hickory flats						III. Large river levees				IV. Swamps									
Juniperus virginiana	33	0.33	--	--	28	0.46	--	--	50	0.80	15	0.31	3	0.40	--	--	--	--	--	--	--	--	--	--
*Ligustrum sinense**	6	0.00	--	--	22	0.00	33	0.01	--	--	52	0.14	63	0.06	35	0.02	25	0.01	67	0.06	--	--	--	--
Lindera benzoin	56	0.18	--	--	16	0.00	--	--	--	--	58	0.12	30	0.11	18	0.00	8	0.01	17	1.02	--	--	--	--
Liquidambar styraciflua	67	4.60	100	1.84	94	4.82	67	0.05	88	3.82	88	2.98	43	2.44	100	4.56	75	3.62	67	3.78	100	2.19	50	5.38
Liriodendron tulipifera	89	6.74	67	3.53	50	2.80	--	--	25	3.87	42	4.16	20	5.34	24	0.84	--	--	17	4.88	--	--	--	--
*Lonicera japonica**	67	0.02	17	0.00	63	0.07	--	--	25	0.00	79	0.03	60	0.08	76	0.02	33	0.00	33	0.09	--	--	--	--
Morus rubra	28	0.33	--	--	3	0.12	--	--	--	--	21	0.40	13	0.62	24	0.35	--	--	--	--	--	--	--	--
Nyssa aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100	31.10
Nyssa sylvatica	22	0.04	50	0.35	63	0.54	33	4.98	38	0.20	12	0.20	--	--	35	0.08	13	2.07						
Ostrya virginiana	17	0.77	50	0.36	25	0.79	--	--	25	1.34	12	0.40	7	0.57	6	0.02								
Oxydendrum arboreum	33	1.64	50	0.48	16	0.15	--	--	13	0.07	--	--	--	--										
Parthenocissus quinquefolia	39	0.06	17	0.00	47	0.02	67	0.00	38	0.01	79	0.07	50	0.04	94	0.01	63	0.01	33	0.01	--	--	--	--
Pinus taeda	6	3.91	33	9.35	16	5.08	--	--	25	4.92	9	4.09	10	4.92	6	2.21	4	1.77	--	--	--	--	--	--
Platanus occidentalis	17	13.43	33	0.80	9	8.56	--	--	13	1.10	33	4.52	53	13.97	12	0.46	21	2.04	50	2.18	--	--	--	--
Populus deltoides	--	--	--	--	--	--	--	--	--	--	3	1.10	13	10.01	6	2.66	--	--	--	--	--	--	50	5.19
Prunus serotina	22	0.18	17	0.03	19	0.38	--	--	--	--	18	0.19	10	0.38	--	--								
Quercus alba	28	0.24	17	0.01	34	1.88	--	--	38	0.83	6	0.75	--	--	18	0.40								
Quercus lyrata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	12	9.31	13	2.44	--	--	100	8.23	100	4.30
Quercus michauxii	--	--	17	3.27	25	1.69	67	1.33	--	--	24	4.98	3	1.56	35	0.69	29	0.46	--	--	33	0.00	--	--
Quercus nigra	6	5.84	17	4.24	53	3.76	33	5.85	13	1.10	12	2.92	7	6.44	24	1.63	13	0.04	33	2.11	--	--	--	--
Quercus pagoda	6	1.50	17	2.51	28	2.21	33	5.88	--	--	--	--	--	--	29	4.57	13	1.36	--	--	--	--	--	--
Quercus phellos	--	--	--	--	47	3.56	--	--	38	2.67	6	0.31	--	--	59	4.24	33	3.26	--	--	100	5.13		
Quercus rubra	22	1.86	--	--	9	1.52	--	--	--	--	6	0.01	--	--	--	--	--	--	17	0.11	--	--	--	--
Quercus shumardii	33	7.60	--	--	9	2.97	--	--	50	6.34	3	1.78	--	--	12	2.61	--	--	17	0.03	--	--	--	--
Quercus stellata	6	0.30	17	0.03	--	--	--	--	25	1.32	3	0.40	--	--										
Rhododendron group 1[1]	--	--	33	0.16	6	0.01	--	--	--	--	--	--	--	--										
Smilax bona-nox	28	0.00	--	--	16	0.01	33	0.00	13	0.01	27	0.01	23	0.01	--	--	8	0.00	17	0.00	--	--		
Smilax [rotundifolia + walterii]	44	0.00	17	0.00	59	0.01	33	0.00	13	0.01	21	0.01	43	0.02	76	0.01	71	0.00	67	0.01	67	0.00	--	--
Toxicodendron radicans	78	0.12	33	0.02	66	0.03	100	0.01	38	0.21	64	0.05	70	0.17	100	0.08	75	0.06	83	0.15	33	0.00	50	0.06
Ulmus alata	39	0.34	17	0.06	69	0.63	--	--	75	0.59	45	0.73	27	1.23	94	0.81	63	0.44	--	--	--	--	--	--
Ulmus [americana +rubra]	44	0.47	17	0.01	41	0.62	--	--	25	1.50	67	0.84	67	2.35	82	1.17	79	0.83	33	0.18	67	0.48	--	--
Viburnum dentatum	6	0.01	--	--	16	0.00	--	--	--	--	3	0.00	3	0.01	6	0.00	13	0.02	33	0.01	--	--	--	--
Viburnum prunifolium	22	0.05	--	--	41	0.02	33	0.04	38	0.13	21	0.02	7	0.00	53	0.01	25	0.04	17	0.44	--	--	--	--
Vitis [cinerea + vulpina]	39	0.18	--	--	13	0.03	33	0.36	25	0.03	24	0.21	40	0.15	18	0.04	4	0.00	17	0.14	--	--	--	--
Vitis aestivalis var. aestivalis	--	--	--	--	--	--	33	0.00	--	--	12	0.09	3	0.11	6	0.00	4	0.01	--	--	--	--	--	--
Vitis rotundifolia	61	0.05	83	0.19	94	0.05	--	--	38	0.05	67	0.08	20	0.29	59	0.06	25	0.01	33	0.11	--	--	--	--

Appendix 3

Average cover by strata, constancy (const.), fidelity, diagnostic value (DV), and indicator value (IV) of prevalent species in the two small stream, narrow floodplain forest types. Prevalence is calculated separately for each stratum, and species must be prevalent in at least one type to be included in table (see text for definition of terms and calculation of metrics). Species may be in the table more than once as they receive cover in every stratum in which they were observed. Non-native species are identified by an *.

Type	Ia.					Ib.				
Plot Count	18					6				
Avg Spp Richness (400m^2)	79.3					70.5				
Avg Spp Richness (100m^2)	43.0					42.5				
Avg Spp Richness (10m^2)	24.4					22.1				
Avg Spp Richness (1m^2)	10.6					9.6				
Homotoneity	61					60				
Tree stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	33	8	11	4	--	17	2	2	0	--
Acer rubrum	83	6	13	11	--	100	7	5	5	--
Betula nigra	56	6	16	9	--	67	8	7	4	--
Carpinus caroliniana	78	7	13	10	--	67	7	4	2	--
Carya cordiformis	39	6	13	5	--	33	4	4	1	--
Carya glabra	6	4	8	0	--	33	4	15	5	--
Carya ovata	33	6	15	5	--	--	--	--	--	--
Cornus florida	89	6	27	24	--	100	6	10	10	30.5
Fagus grandifolia	56	6	29	16	--	33	3	6	2	--
Fraxinus pennsylvanica	44	5	6	3	--	33	3	2	1	--
Ilex opaca var. opaca	17	6	7	1	--	67	6	9	6	--
Juglans nigra	44	5	24	10	--	--	--	--	--	--
Liquidambar styraciflua	78	6	9	7	--	67	6	3	2	--
Liriodendron tulipifera	100	6	23	23	27.6	67	6	5	3	--
Morus rubra	28	3	24	7	--	17	4	5	1	--
Nyssa sylvatica	6	5	2	0	--	50	5	6	3	--
Ostrya virginiana	22	5	16	4	--	67	6	16	11	28.0
Oxydendrum arboreum	39	5	44	17	--	50	5	19	9	--
Pinus taeda	11	6	8	1	--	33	6	8	3	--
Platanus occidentalis var. occidentalis	22	7	5	1	--	50	5	4	2	--
Quercus alba	22	5	11	2	--	33	5	5	2	--
Quercus nigra	6	7	2	0	--	33	5	4	1	--
Quercus shumardii var. shumardii	33	6	19	6	--	33	5	6	2	--
Toxicodendron radicans	56	4	9	5	--	33	3	2	1	--
Ulmus alata	39	5	9	4	--	--	--	--	--	--
Ulmus [americana + rubra]	44	5	7	3	--	33	4	2	1	--
Vitis rotundifolia var. rotundifolia	33	4	8	3	--	83	4	6	5	--
Shrub stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	44	4	14	6	--	--	--	--	--	--
Acer rubrum	56	4	13	7	--	67	3	5	3	--
Carpinus caroliniana	78	6	11	9	--	67	4	3	2	--

Type		Ia.					Ib.			
Carya cordiformis	28	3	20	6	--	17	2	4	1	--
Cornus florida	61	4	28	17	--	50	4	8	4	--
Corylus americana	28	5	63	17	--	--	--	--	--	--
Fagus grandifolia	44	4	21	9	--	33	4	5	2	--
Fraxinus pennsylvanica	44	3	9	4	--	17	2	1	0	--
Ilex opaca var. opaca	44	4	10	4	--	83	5	6	5	--
Juniperus virginiana	33	4	26	9	--	--	--	--	--	--
Lindera benzoin	56	7	18	10	--	--	--	--	--	--
Liquidambar styraciflua	44	3	12	5	--	33	2	3	1	--
Liriodendron tulipifera	17	3	19	3	--	67	2	25	17	35.5
Lonicera japonica*	39	2	9	4	--	17	2	1	0	--
Ostrya virginiana	11	4	11	1	--	67	4	22	15	33.6
Quercus alba	17	2	21	4	--	33	2	14	5	--
Toxicodendron radicans	56	2	9	5	--	33	2	2	1	--
Ulmus alata	44	5	10	4	--	--	--	--	--	--
Ulmus [americana + rubra]	28	5	8	2	--	17	2	2	0	--
Vaccinium elliottii	--	--	--	--	--	33	4	100	33	33.3
Viburnum prunifolium	50	4	14	7	--	--	--	--	--	--
Vitis [cinerea + vulpina]	33	2	19	6	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	61	3	12	7	--	67	4	4	3	--
Herb stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acalypha rhomboidea	--	--	--	--	--	50	2	17	8	--
Acer floridanum	50	3	12	6	--	33	2	3	1	--
Acer negundo var. negundo	56	2	10	6	--	--	--	--	--	--
Acer rubrum	89	2	13	12	--	100	2	5	5	--
Amphicarpaea bracteata	89	3	25	23	--	50	2	5	2	--
Anemonella thalictroides	33	2	46	15	--	17	2	8	1	--
Arisaema triphyllum	78	2	19	15	--	50	2	4	2	--
Athyrium asplenioides	28	3	15	4	--	33	2	6	2	--
Betula nigra	--	--	--	--	--	33	2	22	7	--
Bignonia capreolata	56	2	7	4	--	33	2	1	0	--
Boehmeria cylindrica	67	2	10	6	--	50	2	2	1	--
Botrypus virginianus	83	2	28	23	31.0	33	2	4	1	--
Brachyelytrum erectum	22	2	33	7	--	33	2	17	6	--
Bromus [nottowayanus + pubescens]	39	2	24	9	--	--	--	--	--	--
Campsis radicans	83	2	12	10	--	50	2	2	1	--
Carex [amphibola+grisea+corrugata]	72	3	12	9	--	17	2	1	0	--
Carex [radiata + rosea]	89	3	16	14	--	83	2	5	4	--
Carex blanda	61	3	14	9	--	50	2	4	2	--
Carex debilis	39	3	13	5	--	50	2	5	3	--
Carex intumescens	6	2	3	0	--	33	1	5	2	--
Carex laxiculmis var. laxiculmis	17	3	20	3	--	33	2	13	4	--
Carex oxylepis	39	3	19	7	--	50	2	8	4	--
Carex tribuloides	33	2	7	2	--	17	1	1	0	--
Carpinus caroliniana	83	2	11	9	--	100	2	4	4	--
Carya alba	17	2	12	2	--	33	1	8	3	--
Carya cordiformis	56	2	10	6	--	17	2	1	0	--
Carya glabra	11	2	11	1	--	33	2	11	4	--

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Type	Ia.					Ib.				
Carya ovata	39	2	14	6	--	17	1	2	0	--
Celtis laevigata	72	2	11	8	--	50	2	3	1	--
Cercis canadensis var. canadensis	50	2	39	20	--	17	1	4	1	--
Chasmanthium latifolium	50	3	9	4	--	--	--	--	--	--
Chasmanthium [sessiliflorum + laxum]	11	3	9	1	--	50	4	13	7	--
Cornus florida	100	2	27	27	29.1	100	2	9	9	--
Desmodium paniculatum var. paniculatum	6	1	8	0	--	33	2	17	6	--
Dichanthelium boscii	22	2	25	6	--	33	4	13	4	--
Dichanthelium commutatum var. commutatum	72	2	14	10	--	83	2	5	4	--
Dichanthelium laxiflorum	28	2	19	5	--	33	2	7	2	--
Dichanthelium yadkinense	6	2	7	0	--	33	4	14	5	--
Diospyros virginiana	28	2	11	3	--	50	2	7	3	--
Elaeagnus umbellata	28	2	19	5	--	17	1	4	1	--
Elephantopus tomentosus	6	1	13	1	--	33	1	25	8	--
Elymus [glabriflorus + macgregorii + virginicus]	33	2	7	2	--	50	2	3	2	--
Elymus hystrix	33	4	19	6	--	33	3	6	2	--
Endodeca serpentaria	44	2	25	11	--	33	2	6	2	--
Erechtites hieracifolia	22	2	6	1	--	33	1	3	1	--
Eubotrys racemosa	--	--	--	--	--	33	2	15	5	--
Euonymus americanus	100	2	14	14	--	100	2	5	5	--
Eurybia divaricata	39	2	54	21	--	--	--	--	--	--
Fagus grandifolia	61	2	28	17	--	17	2	3	0	--
Festuca subverticillata	78	2	18	14	--	50	2	4	2	--
Fraxinus pennsylvanica	83	2	9	8	--	33	2	1	0	--
Galium aparine	39	2	11	4	--	--	--	--	--	--
Galium circaezans	78	2	35	27	30.2	17	1	3	0	--
Galium triflorum	89	2	28	25	29.7	83	2	9	7	--
Geum canadense	78	2	17	13	--	50	2	4	2	--
Glyceria striata var. striata	39	2	11	4	--	50	2	5	2	--
[Gonolobus + Matelea]	33	2	9	3	--	33	1	3	1	--
Goodyera pubescens	22	1	31	7	--	33	2	15	5	--
Hexastylis arifolia	28	2	19	5	--	67	2	15	10	--
Hypericum hypericoides	6	1	3	0	--	33	2	6	2	--
Ilex decidua	22	2	4	1	--	67	1	4	2	--
Ilex opaca var. opaca	72	2	13	9	--	100	2	6	6	--
Impatiens sp	33	2	13	4	--	17	1	2	0	--
Juglans nigra	39	2	16	6	--	17	1	2	0	--
Juncus coriaceus	28	2	10	3	--	83	2	10	9	--
Juncus effusus	22	2	10	2	--	50	2	7	4	--
Juniperus virginiana	72	2	22	16	--	33	2	3	1	--
Leersia virginica	17	2	5	1	--	33	2	4	1	--
Lespedeza cuneata*	--	--	--	--	--	33	3	15	5	--
Ligustrum sinense*	94	2	11	10	--	50	1	2	1	--
Lindera benzoin	78	3	18	14	--	--	--	--	--	--
Liquidambar styraciflua	78	2	10	8	--	100	2	4	4	--
Liriodendron tulipifera	72	2	19	14	--	100	2	9	9	25.6
Lonicera japonica	100	4	11	11	--	100	2	4	4	--
Luzula echinata	28	2	24	7	--	50	2	14	7	--

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Type	Ia.					Ib.				
Lycopus virginicus	28	2	9	2	--	50	2	5	3	--
Lysimachia ciliata	11	2	8	1	--	33	1	8	3	--
Magnolia macrophylla	6	2	50	3	--	17	2	50	8	--
Maianthemum racemosum ssp. racemosum	28	2	33	9	--	17	2	7	1	--
Microstegium vimineum*	94	6	12	11	--	83	6	3	3	--
Mitchella repens	22	2	8	2	--	67	2	8	5	--
Murdannia keisak*	6	1	6	0	--	50	3	17	8	--
Nyssa sylvatica	22	2	6	1	--	50	2	4	2	--
Osmorhiza longistylis	33	2	27	9	--	--	--	--	--	--
Ostrya virginiana	22	2	17	4	--	67	2	17	12	27.7
Oxalis sp	61	2	15	9	--	100	2	8	8	--
Parthenocissus quinquefolia	100	3	10	10	--	100	2	3	3	--
Passiflora lutea var. lutea	39	2	13	5	--	67	2	8	5	--
Persicaria virginiana	50	2	9	5	--	50	2	3	2	--
Phryma leptostachya	72	2	68	49	58.5	--	--	--	--	--
Pinus taeda	6	1	3	0	--	50	2	9	5	--
Poa [autumnalis + cuspidata]	50	5	10	5	--	50	2	3	2	--
Polygonatum biflorum	56	2	18	10	--	67	2	7	5	--
Polystichum acrostichoides	100	4	20	20	30.1	100	3	7	7	--
Potentilla [simplex + canadensis]	17	2	11	2	--	33	1	7	2	--
Potentilla indica	22	2	11	2	--	17	2	3	0	--
Prenanthes [altissima + serpentaria + trifoliolata]	33	2	21	7	--	50	2	11	5	--
Prunus serotina	100	2	19	19	20.5	83	2	5	4	--
Quercus alba	44	2	19	8	--	50	2	7	4	--
Quercus michauxii	6	2	2	0	--	33	2	5	2	--
Quercus nigra	17	2	5	1	--	33	2	3	1	--
Quercus rubra	44	2	29	13	--	33	2	7	2	--
Ranunculus abortivus	44	2	14	6	--	17	1	2	0	--
Ranunculus recurvatus	17	2	20	3	--	33	1	13	4	--
Rhododendron group 1[1]	--	--	--	--	--	50	2	40	13	--
Rosa sp	50	2	15	8	--	--	--	--	--	--
Rubus sp	94	2	13	13	--	50	2	2	1	--
Ruellia caroliniensis	33	2	19	6	--	17	1	3	1	--
Salvia lyrata	50	2	32	16	--	50	2	11	5	--
Sambucus canadensis	44	2	13	6	--	--	--	--	--	--
Sanicula canadensis var. canadensis	89	2	15	13	--	100	2	5	5	--
Saururus cernuus	6	2	2	0	--	33	2	4	1	--
Sceptridium [biternatum + dissectum]	67	2	14	9	--	50	2	3	2	--
Scutellaria integrifolia	11	2	9	1	--	50	2	13	7	--
Smilax bona-nox	94	2	11	11	--	67	2	3	2	--
Smilax glauca	89	2	15	13	--	100	2	6	6	--
Smilax hispida	56	2	20	11	--	17	2	2	0	--
Smilax [rotundifolia + walterii]	72	2	8	6	--	83	2	3	3	--
Solidago sp	89	2	11	10	--	100	2	4	4	--
Stellaria pubera	33	4	55	18	--	--	--	--	--	--
Styrax [americanus + grandifolius]	--	--	--	--	--	33	2	67	22	--
Thelypteris noveboracensis	--	--	--	--	--	33	6	67	22	32.3
Toxicodendron radicans	100	3	10	10	--	100	2	3	3	--

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Type	Ia.					Ib.				
Ulmus alata	44	2	8	3	--	17	2	1	0	--
Ulmus [americana + rubra]	50	2	8	4	--	67	2	4	3	--
Uvularia perfoliata	33	2	67	22	--	17	2	11	2	--
Vaccinium stamineum	--	--	--	--	--	33	2	50	17	--
Verbesina alternifolia	39	2	9	3	--	33	2	2	1	--
Verbesina occidentalis	50	2	13	6	--	33	5	3	1	--
Viburnum prunifolium	78	2	16	12	--	--	--	--	--	--
Viola sp	94	2	11	11	--	100	2	4	4	--
Vitis [cinerea + vulpina]	78	2	17	13	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	100	2	13	13	--	100	3	4	4	--
Xanthorhiza simplicissima	--	--	--	--	--	33	2	40	13	--

Appendix 4

Average cover by strata, constancy (const.), fidelity, diagnostic value (DV), and indicator value (IV) of prevalent species in the three oak-hickory flat types. Prevalence is calculated separately for each stratum, and species must be prevalent in at least one type to be included in table (see text for definition of terms and calculation of metrics). Species may be in the table more than once as they receive cover in every stratum in which they were observed. Non-native species are identified by an *.

Type Name	IIa.					IIb.					IIc.				
Plot Count	32					3					8				
Avg Spp Richness (400m^2)	70.7					53					84.9				
Avg Spp Richness (100m^2)	42.3					33.9					48.2				
Avg Spp Richness (10m^2)	22.4					17.8					28.6				
Avg Spp Richness (1m^2)	9.6					8.1					12.7				
Homotoneity	59					78					65				
Tree stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	19	7	11	2	--	--	--	--	--	--	100	7	15	15	38.1
Acer negundo var. *negundo*	--	--	--	--	--	33	2	2	1	--	--	--	--	--	--
Acer rubrum	78	7	22	17	--	100	6	3	3	--	38	5	3	1	--
Asimina triloba	--	--	--	--	--	33	3	7	2	--	--	--	--	--	--
Bignonia capreolata	28	2	18	5	--	67	2	4	3	--	13	1	2	0	--
Carpinus caroliniana	88	7	26	23	--	100	7	3	3	--	75	7	6	4	--
Carya carolinae-septentrionalis	--	--	--	--	--	--	--	--	--	--	100	7	80	80	93.4
Carya cordiformis	25	6	15	4	--	67	7	4	2	--	25	5	4	1	--
Carya glabra	16	5	38	6	--	--	--	--	--	--	38	5	23	9	--
Carya ovata	38	6	30	11	--	67	5	5	3	--	38	4	8	3	--
Celtis laevigata	--	--	--	--	--	67	5	4	3	--	--	--	--	--	--
Cornus florida	44	5	23	10	--	--	--	--	--	--	50	4	7	3	--
Fagus grandifolia	50	6	47	24	--	--	--	--	--	--	13	3	3	0	--
Fraxinus pennsylvanica	53	5	14	7	--	67	3	2	1	--	63	6	4	3	--
Ilex opaca var. *opaca*	53	6	37	20	--	--	--	--	--	--	13	4	2	0	--
Juglans nigra	3	4	3	0	--	--	--	--	--	--	38	4	9	3	--
Juniperus virginiana	9	5	20	2	--	--	--	--	--	--	38	5	20	8	--
Liquidambar styraciflua	97	6	21	20	--	100	5	2	2	--	100	6	5	5	--
Liriodendron tulipifera	66	5	27	18	--	--	--	--	--	--	25	6	3	1	--
Nyssa sylvatica	56	5	38	21	--	33	7	2	1	--	75	5	13	9	--
Ostrya virginiana	22	6	28	6	--	--	--	--	--	--	38	7	12	5	--
Parthenocissus quinquefolia	22	2	12	3	--	67	2	3	2	--	13	2	2	0	--
Quercus alba	41	6	35	14	--	33	6	3	1	--	63	5	14	8	--
Quercus michauxii	28	6	22	6	--	67	6	5	3	--	--	--	--	--	--

Type Name	IIa.					IIb.					IIc.				
Quercus nigra	69	6	49	34	--	67	6	4	3	--	13	5	2	0	--
Quercus pagoda	47	6	38	18	--	67	7	5	3	--	--	--	--	--	--
Quercus phellos	56	6	34	19	--	--	--	--	--	--	38	6	6	2	--
Quercus shumardii var. shumardii	22	6	23	5	--	--	--	--	--	--	50	7	13	6	--
Toxicodendron radicans	50	4	14	7	--	100	4	3	3	--	38	4	3	1	--
Ulmus alata	56	6	23	13	--	33	3	1	0	--	100	5	10	10	21.0
Ulmus [americana + rubra]	44	5	11	5	--	33	4	1	0	--	38	6	2	1	--
Vitis [cinerea + vulpina]	6	3	6	0	--	33	3	3	1	--	25	3	6	1	--
Vitis aestivalis var. aestivalis	--	--	--	--	--	33	2	8	3	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	69	4	28	19	--	--	--	--	--	--	38	3	4	1	--
Shrub stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	28	4	15	4	--	--	--	--	--	--	100	6	14	14	37.6
Acer negundo var. negundo	6	4	4	0	--	33	1	2	1	--	--	--	--	--	--
Acer rubrum	53	4	22	12	--	--	--	--	--	--	13	2	1	0	--
Aesculus sylvatica	9	2	9	1	--	--	--	--	--	--	63	4	14	9	--
Arundinaria tecta	6	4	12	1	--	100	6	18	18	71.3	--	--	--	--	--
Asimina triloba	19	4	16	3	--	100	5	8	8	36.8	--	--	--	--	--
Bignonia capreolata	44	2	19	9	--	100	2	4	4	26.4	25	2	3	1	--
Carpinus caroliniana	91	6	23	21	--	67	4	2	1	--	75	6	5	4	--
Carya ovate	19	3	30	6	--	33	2	5	2	--	--	--	--	--	--
Crataegus flabellata group	13	2	44	6	--	33	2	11	4	--	--	--	--	--	--
Elaeagnus umbellata*	9	6	14	1	--	--	--	--	--	--	38	6	14	5	--
Fagus grandifolia	44	4	36	16	--	--	--	--	--	--	13	3	3	0	--
Fraxinus pennsylvanica	44	4	16	7	--	33	2	1	0	--	13	3	1	0	--
Ilex decidua	72	4	25	18	--	67	3	2	1	--	63	4	5	3	--
Ilex opaca var. opaca	78	5	31	24	--	--	--	--	--	--	25	4	2	1	--
Juniperus virginiana	28	3	39	11	--	--	--	--	--	--	50	2	17	9	--
Ligustrum sinense*	22	2	9	2	--	33	3	1	0	--	--	--	--	--	--
Liquidambar styraciflua	53	4	25	13	--	33	1	1	0	--	25	4	3	1	--
Lonicera japonica*	38	2	16	6	--	--	--	--	--	--	13	2	1	0	--
Parthenocissus quinquefolia	25	2	11	3	--	100	2	4	4	21.6	13	2	1	0	--
Quercus michauxii	13	3	15	2	--	33	2	4	1	--	--	--	--	--	--
Quercus nigra	16	3	33	5	--	33	2	7	2	--	--	--	--	--	--
Smilax bona-nox	9	2	13	1	--	33	2	4	1	--	13	2	4	1	--
Smilax glauca	13	2	31	4	--	33	1	8	3	--	--	--	--	--	--
Smilax [rotundifolia + walterii]	47	2	17	8	--	100	2	3	3	--	13	2	1	0	--
Toxicodendron radicans	53	2	15	8	--	100	2	3	3	--	25	2	2	0	--
Ulmus alata	66	4	26	17	--	33	2	1	0	--	50	4	5	2	--
Viburnum prunifolium	50	4	25	12	--	67	4	3	2	--	50	4	6	3	--

Type Name	IIa.					IIb.					IIc.				
Vitis aestivalis var. aestivalis	--	--	--	--	--	33	2	8	3	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	72	2	26	18	--	--	--	--	--	--	38	2	3	1	--
Herb stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	34	2	14	5	--	--	--	--	--	--	100	2	11	11	28.5
Acer negundo var. negundo	28	2	9	3	--	67	2	2	1	--	13	2	1	0	--
Acer rubrum	91	2	24	22	--	100	2	2	2	--	63	2	4	3	--
Aesculus sylvatica	13	2	10	1	--	--	--	--	--	--	75	2	15	11	--
Allium canadense var. canadense	16	2	13	2	--	33	1	3	1	--	50	3	10	5	--
Amphicarpaea bracteata	44	2	22	10	--	--	--	--	--	--	63	2	8	5	--
Arisaema dracontium	3	1	3	0	--	67	2	6	4	26.4	13	1	3	0	--
Arisaema triphyllum	19	2	8	2	--	--	--	--	--	--	75	2	8	6	--
Arundinaria tecta	28	6	20	6	--	100	5	7	7	37.5	25	2	4	1	--
Asarum canadense	16	2	17	3	--	100	2	10	10	44.2	--	--	--	--	--
Asimina triloba	25	2	16	4	--	67	5	4	3	25.7	13	1	2	0	--
Athyrium asplenioides	47	2	44	21	--	--	--	--	--	--	--	--	--	--	--
Bidens frondosa	13	2	11	1	--	33	1	3	1	--	25	1	5	1	--
Bignonia capreolata	94	4	20	19	--	100	5	2	2	22.6	100	2	5	5	--
Boehmeria cylindrica	47	2	12	6	--	100	2	2	2	--	25	2	2	0	--
Botrypus virginianus	34	2	20	7	--	--	--	--	--	--	25	2	4	1	--
Brachyelytrum erectum	--	--	--	--	--	--	--	--	--	--	50	4	33	17	29.6
Bromus [nottowayanus + pubescens]	9	2	10	1	--	--	--	--	--	--	75	2	21	16	28.1
Campsis radicans	66	2	16	11	--	33	1	1	0	--	38	2	2	1	--
Carex [amphibola+grisea+corrugata]	66	5	19	13	--	100	3	3	3	--	50	3	4	2	--
Carex [radiata + rosea]	66	3	21	14	--	67	2	2	1	--	63	2	5	3	--
Carex blanda	41	3	17	7	--	--	--	--	--	--	63	3	6	4	--
Carex caroliniana	41	3	33	13	--	--	--	--	--	--	25	2	5	1	--
Carex crebriflora	--	--	--	--	--	33	3	11	4	--	13	2	11	1	--
Carex debilis	66	3	38	25	--	67	2	4	2	--	--	--	--	--	--
Carex gracillima	28	4	23	6	--	--	--	--	--	--	50	3	10	5	--
Carex grayi	13	2	8	1	--	--	--	--	--	--	38	2	6	2	--
Carex intumescens	41	2	33	13	--	100	2	8	8	28.3	--	--	--	--	--
Carex laxiculmis var. laxiculmis	9	2	20	2	--	--	--	--	--	--	63	3	33	21	35.3
Carex laxiflora	--	--	--	--	--	33	2	100	33	--	--	--	--	--	--
Carex oxylepis	22	3	19	4	--	--	--	--	--	--	75	3	16	12	--
Carex tribuloides	25	2	9	2	--	33	1	1	0	--	13	1	1	0	--
Carex typhina	13	2	8	1	--	100	2	6	6	--	--	--	--	--	--
Carpinus caroliniana	97	4	23	22	--	67	2	1	1	--	100	2	6	6	--
Carya alba	38	2	46	17	--	--	--	--	--	--	38	2	12	4	--
Carya carolinae-septentrionalis	--	--	--	--	--	--	--	--	--	--	75	2	75	56	70.7

Type Name	IIa.					IIb.					IIc.				
Carya cordiformis	59	2	19	11	--	100	2	3	3	--	50	2	4	2	--
Carya glabra	22	2	39	9	--	--	--	--	--	--	38	2	17	6	--
Carya ovata	41	3	27	11	--	67	3	4	3	--	38	2	6	2	--
Celtis laevigata	47	2	13	6	--	67	2	2	1	--	38	2	3	1	--
Cercis canadensis var. canadensis	9	2	13	1	--	--	--	--	--	--	50	1	17	9	--
Chasmanthium latifolium	69	4	21	15	--	100	5	3	3	--	75	6	6	4	--
Chasmanthium [sessiliflorum + laxum]	31	4	43	14	--	33	2	4	1	--	38	4	13	5	--
Clematis viorna	25	1	28	7	--	33	2	3	1	--	13	1	3	0	--
Commelina virginica	6	2	4	0	--	33	1	2	1	--	25	2	4	1	--
Cornus florida	59	2	29	17	--	--	--	--	--	--	63	2	8	5	--
Crataegus flabellata group	34	2	79	27	--	--	--	--	--	--	13	2	7	1	--
Cryptotaenia canadensis	9	1	9	1	--	33	2	3	1	--	13	1	3	0	--
Danthonia spicata	22	3	54	12	--	--	--	--	--	--	63	5	38	24	46.7
Dichanthelium boscii	16	2	31	5	--	--	--	--	--	--	63	5	31	20	37.5
Dichanthelium commutatum var. commutatum	78	3	26	20	--	100	2	3	3	--	100	3	8	8	--
Dichanthelium dichotomum	47	2	47	22	--	--	--	--	--	--	50	4	13	6	--
Dichanthelium laxiflorum	34	2	41	14	--	--	--	--	--	--	75	2	22	17	37.5
Dichanthelium polyanthes	9	2	30	3	--	--	--	--	--	--	38	3	30	11	--
Dichanthelium yadkinense	6	2	14	1	--	--	--	--	--	--	38	3	21	8	--
Dioscorea [quaternata + villosa]	56	2	39	22	--	33	2	2	1	--	63	2	11	7	--
Diospyros virginiana	50	2	36	18	--	--	--	--	--	--	25	1	5	1	--
Elaeagnus umbellata	13	2	15	2	--	--	--	--	--	--	38	2	11	4	--
Elephantopus carolinianus	6	2	40	3	--	67	2	40	27	55.2	--	--	--	--	--
Elymus [glabriflorus + macgregorii + virginicus]	47	4	16	8	--	--	--	--	--	--	38	2	3	1	--
Elymus hystrix	9	2	10	1	--	--	--	--	--	--	100	3	26	26	44.6
Endodeca serpentaria	41	2	41	17	--	33	1	3	1	--	25	2	6	2	--
Erechtites hieracifolia	16	1	8	1	--	100	2	5	5	--	13	1	2	0	--
Eubotrys racemosa	22	2	54	12	--	33	2	8	3	--	--	--	--	--	--
Euonymus americanus	100	2	25	25	14.9	100	2	2	2	--	100	2	6	6	--
Fagus grandifolia	50	2	41	21	--	--	--	--	--	--	13	2	3	0	--
Festuca subverticillata	44	3	18	8	--	--	--	--	--	--	38	2	4	1	--
Fraxinus pennsylvanica	100	2	20	20	--	100	2	2	2	--	88	2	4	4	--
Galium aparine	3	1	2	0	--	--	--	--	--	--	50	2	6	3	--
Galium circaezans	50	2	40	20	--	--	--	--	--	--	63	2	13	8	--
Galium obtusum var. obtusum	3	2	33	1	--	33	2	33	11	--	--	--	--	--	--
Galium tinctorium	38	2	29	11	--	--	--	--	--	--	38	2	7	3	--
Galium triflorum	44	2	25	11	--	--	--	--	--	--	50	2	7	4	--
Gelsemium sempervirens	47	2	68	32	--	--	--	--	--	--	--	--	--	--	--
Geum canadense	34	2	14	5	--	--	--	--	--	--	50	1	5	2	--

Type Name	IIa.					IIb.					IIc.				
[Gonolobus + Matelea]	34	2	16	5	--	67	2	3	2	--	25	2	3	1	--
Hamamelis virginiana var. virginiana	6	2	33	2	--	--	--	--	--	--	50	2	67	33	42.9
Hexastylis arifolia	22	2	26	6	--	33	1	4	1	--	100	2	30	30	42.6
Houstonia purpurea	6	2	25	2	--	--	--	--	--	--	50	2	50	25	39.5
Hypericum hypericoides	59	2	59	35	--	--	--	--	--	--	88	2	22	19	38.4
Ilex decidua	91	2	25	23	--	100	2	3	3	--	100	2	7	7	--
Ilex opaca var. opaca	91	2	29	26	--	33	2	1	0	--	100	2	8	8	--
Impatiens sp	3	1	2	0	--	67	2	4	3	--	38	1	6	2	--
Ipomoea sp	6	1	40	3	--	33	1	20	7	--	25	2	40	10	--
Juncus coriaceus	28	2	19	5	--	--	--	--	--	--	88	2	15	13	--
Juniperus virginiana	56	2	30	17	--	--	--	--	--	--	100	2	13	13	31.9
Justicia ovata var. ovata	--	--	--	--	--	33	1	50	17	--	--	--	--	--	--
Lactuca sp	9	1	23	2	--	33	1	8	3	--	--	--	--	--	--
Leersia virginica	31	2	18	5	--	--	--	--	--	--	63	4	9	5	--
Lespedeza cuneata*	6	1	15	1	--	--	--	--	--	--	50	2	31	15	--
Ligustrum sinense*	84	2	17	14	--	100	2	2	2	--	100	2	5	5	--
Lindera benzoin	22	2	9	2	--	--	--	--	--	--	63	2	7	4	--
Liquidambar styraciflua	100	2	24	24	--	100	2	2	2	--	100	2	6	6	--
Liriodendron tulipifera	50	2	23	12	--	--	--	--	--	--	25	1	3	1	--
Lonicera japonica*	97	4	19	18	--	33	2	1	0	--	88	2	4	4	--
Luzula echinata	22	2	33	7	--	--	--	--	--	--	50	2	19	10	--
Lycopus virginicus	19	2	11	2	--	67	2	4	2	--	25	1	4	1	--
Lysimachia ciliata	22	2	28	6	--	33	1	4	1	--	38	2	12	5	--
Melica mutica	56	2	55	31	24.5	--	--	--	--	--	25	2	6	2	--
Microstegium vimineum*	66	2	15	10	--	--	--	--	--	--	100	3	6	6	--
Mitchella repens	91	2	56	51	27.8	67	2	4	3	--	38	2	6	2	--
Morus rubra	47	2	47	22	--	33	1	3	1	--	--	--	--	--	--
Nyssa sylvatica	75	2	35	26	--	67	2	3	2	--	75	2	9	7	--
Oxalis sp	31	2	14	4	--	--	--	--	--	--	88	2	10	8	--
Parthenocissus quinquefolia	100	3	18	18	--	100	3	2	2	--	100	2	4	4	--
Passiflora lutea var. lutea	38	2	23	9	--	67	1	4	3	--	50	2	8	4	--
Persicaria sp	--	--	--	--	--	33	1	3	1	--	--	--	--	--	--
Persicaria virginiana	19	2	6	1	--	33	2	1	0	--	25	1	2	1	--
Phytolacca americana	--	--	--	--	--	67	2	6	4	--	--	--	--	--	--
Pinus taeda	31	2	31	10	--	--	--	--	--	--	25	2	6	2	--
Poa [autumnalis + cuspidata]	78	4	27	21	--	--	--	--	--	--	63	3	5	3	--
Polygonatum biflorum	53	2	31	16	--	33	2	2	1	--	50	2	7	4	--
Polystichum acrostichoides	63	3	22	14	--	--	--	--	--	--	100	2	9	9	--
Potentilla [simplex + canadensis]	34	2	41	14	--	--	--	--	--	--	75	2	22	17	24.8

Type Name	IIa.					IIb.					IIc.				
Prenanthes [altissima + serpentaria + trifoliolata]	25	2	29	7	--	--	--	--	--	--	50	2	14	7	--
Prunus serotina	81	2	28	23	--	--	--	--	--	--	75	2	6	5	--
Quercus alba	66	2	50	33	--	--	--	--	--	--	50	2	10	5	--
Quercus michauxii	25	2	20	5	--	67	2	5	3	--	13	2	2	0	--
Quercus nigra	66	2	36	24	--	100	2	5	5	--	38	2	5	2	--
Quercus pagoda	28	2	29	8	--	33	2	3	1	--	--	--	--	--	--
Quercus phellos	75	2	28	21	--	--	--	--	--	--	75	2	7	5	--
Quercus shumardii var. shumardii	22	2	28	6	--	--	--	--	--	--	75	2	24	18	33.7
Ranunculus abortivus	6	1	4	0	--	100	2	5	5	30.5	50	1	7	4	--
Ranunculus recurvatus	9	1	20	2	--	--	--	--	--	--	38	2	20	8	--
Rosa sp	34	2	18	6	--	33	2	2	1	--	13	1	2	0	--
Rubus sp	94	2	24	22	--	100	2	2	2	--	38	1	2	1	--
Rudbeckia laciniata	22	2	26	6	--	33	2	4	1	--	25	2	7	2	--
Ruellia caroliniensis	31	2	31	10	--	--	--	--	--	--	75	2	19	14	36.0
Salvia lyrata	22	2	25	5	--	--	--	--	--	--	88	2	25	22	42.9
Sambucus canadensis	13	2	7	1	--	33	1	2	1	--	--	--	--	--	--
Sanicula canadensis var. canadensis	72	2	21	15	--	67	2	2	1	--	88	2	6	6	--
Sceptridium [biternatum + dissectum]	78	2	29	22	--	33	1	1	0	--	50	2	5	2	--
Scutellaria integrifolia	34	2	48	16	--	--	--	--	--	--	13	2	4	1	--
Smilax bona-nox	84	2	18	15	--	100	2	2	2	30.5	100	2	5	5	--
Smilax glauca	91	2	27	25	--	100	2	3	3	--	88	2	7	6	--
Smilax [rotundifolia + walterii]	97	2	20	19	--	100	2	2	2	--	88	2	4	4	--
Solanum carolinense var. carolinense	--	--	--	--	--	33	1	50	17	--	--	--	--	--	--
Solidago sp	91	2	19	18	--	100	2	2	2	--	100	2	5	5	--
Stellaria media	6	2	10	1	--	33	2	5	2	--	--	--	--	--	--
Symphoricarpos orbiculatus	13	2	15	2	--	--	--	--	--	--	63	2	19	12	24.3
Toxicodendron radicans	97	4	17	17	--	100	5	2	2	--	100	2	4	4	--
Trachelospermum difforme	50	2	37	19	--	--	--	--	--	--	38	2	7	3	--
Ulmus alata	84	2	26	22	--	67	2	2	1	--	100	2	8	8	17.2
Ulmus [americana + rubra]	31	2	9	3	--	33	2	1	0	--	38	2	3	1	--
Uvularia sessilifolia	16	2	38	6	--	33	2	8	3	--	38	2	23	9	--
Verbesina alternifolia	38	2	15	6	--	--	--	--	--	--	100	2	10	10	--
Verbesina occidentalis	28	2	13	4	--	--	--	--	--	--	50	3	6	3	--
Viburnum dentatum	75	2	39	29	--	--	--	--	--	--	38	1	5	2	--
Viburnum prunifolium	81	2	30	24	--	33	2	1	0	--	75	2	7	5	--
Viola sp	81	2	18	14	--	100	2	2	2	--	88	2	5	4	--
Vitis [cinerea + vulpina]	38	2	15	6	--	--	--	--	--	--	38	2	4	1	--
Vitis aestivalis var. aestivalis	--	--	--	--	--	33	2	5	2	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	100	3	23	23	--	100	2	2	2	--	75	2	4	3	--

Type Name	IIa.					IIb.					IIc.				
Zizia aurea	--	--	--	--	--	--	--	--	--	--	**75**	2	100	75	75.0

Appendix 5

Average cover by strata, constancy (const.), fidelity, diagnostic value (DV), and indicator value (IV) of prevalent species in the two large river levee forest types. Prevalence is calculated separately for each stratum, and species must be prevalent in at least one type to be included in table (see text for definition of terms and calculation of metrics). Species may be in the table more than once as they receive cover in every stratum in which they were observed. Non-native species are identified by an *.

Type Name	IIIa.					IIIb.				
Plot Count	33					30				
Avg Species Richness (400m^2)	58.2					51.9				
Avg Species Richness (100m^2)	36.3					28.5				
Avg Species Richness (10m^2)	18.9					15.2				
Avg Species Richness (1m^2)	8.7					7.1				
Homotoneity	61					58				
Tree stratum	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	55	7	33	18	--	27	6	15	4	--
Acer negundo var. negundo	64	6	38	24	--	97	7	53	51	53.1
Betula nigra	24	4	13	3	--	43	6	21	9	--
Bignonia capreolata	42	3	27	12	--	17	2	10	2	--
Campsis radicans	18	2	18	3	--	20	3	18	4	--
Carpinus caroliniana	52	6	16	8	--	43	6	12	5	--
Carya cordiformis	76	6	45	34	--	20	6	11	2	--
Celtis laevigata	73	7	47	34	26.5	60	6	35	21	--
Cornus florida	42	5	23	10	--	13	4	7	1	--
Fraxinus pennsylvanica	58	6	15	9	--	90	7	22	19	--
Juglans nigra	45	6	44	20	--	23	5	21	5	--
Liquidambar styraciflua	94	6	21	20	--	40	6	8	3	--
Liriodendron tulipifera	58	6	25	14	--	27	6	10	3	--
*Lonicera japonica**	30	2	30	9	--	30	2	27	8	--
Parthenocissus quinquefolia	64	2	36	23	--	27	2	14	4	--
Platanus occidentalis var. occidentalis	58	6	25	15	--	90	6	36	32	21.9
Toxicodendron radicans	64	4	18	12	--	70	5	18	13	--
Ulmus [americana + rubra]	82	6	22	18	--	77	6	19	14	--
Vitis [cinerea + vulpina]	24	5	22	5	--	47	4	39	18	--
Vitis rotundifolia var. rotundifolia	73	3	30	22	--	20	3	8	2	--
taxon name	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	55	5	31	17	--	23	4	12	3	--
Acer negundo var. negundo	67	5	41	27	--	63	5	35	22	--
Aesculus sylvatica	42	4	40	17	--	17	4	14	2	--
Asimina triloba	45	6	39	18	--	7	4	5	0	--
Bignonia capreolata	52	2	24	12	--	30	2	13	4	--
Carpinus caroliniana	64	5	17	11	--	37	4	9	3	--
Celtis laevigata	39	4	33	13	--	50	4	38	19	--
Fraxinus pennsylvanica	33	3	13	4	--	47	4	16	8	--
Ilex decidua	52	4	18	9	--	20	4	6	1	--
Ilex opaca var. opaca	58	4	23	14	--	20	3	7	1	--
*Ligustrum sinense**	64	5	28	18	--	73	4	30	22	--
Lindera benzoin	67	6	39	26	--	43	6	23	10	--
Liquidambar styraciflua	27	3	13	4	--	33	3	15	5	--
*Lonicera japonica**	61	2	26	16	--	43	3	17	7	--
Parthenocissus quinquefolia	73	2	32	23	--	37	2	14	5	--

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Type Name	IIIa.					IIIb.				
Smilax [rotundifolia + walterii]	45	2	17	8	--	40	3	14	5	--
Toxicodendron radicans	73	3	21	15	--	60	3	15	9	--
Ulmus alata	39	5	16	6	--	23	4	9	2	--
Ulmus [americana + rubra]	27	5	15	4	--	30	4	15	5	--
Vitis [cinerea + vulpina]	15	2	16	2	--	37	2	34	13	--
Vitis rotundifolia var. rotundifolia	76	2	28	21	--	30	2	10	3	--
taxon name	const.	cover	fidelity	DV	IV	const.	cover	fidelity	DV	IV
Acer floridanum	64	2	28	18	--	43	2	17	7	--
Acer negundo var. negundo	94	3	31	29	--	97	3	29	28	21.8
Aesculus sylvatica	42	3	35	15	--	13	2	10	1	--
Amphicarpaea bracteata	39	2	21	8	--	27	2	13	3	--
Arisaema dracontium	42	2	45	19	--	17	2	16	3	--
Arisaema triphyllum	39	2	18	7	--	37	2	15	5	--
Arundinaria tecta	39	5	29	11	--	13	6	9	1	--
Asimina triloba	58	3	38	22	--	3	1	2	0	--
Bignonia capreolata	97	2	22	21	--	70	3	14	10	--
Boehmeria cylindrica	64	2	17	11	--	83	3	20	17	--
Botrypus virginianus	45	2	28	13	--	17	2	9	2	--
Campsis radicans	55	2	14	8	--	67	2	16	10	--
Carex [amphibola+grisea+corrugata]	73	4	22	16	--	73	4	20	15	--
Carex [radiata + rosea]	67	5	22	15	--	33	4	10	3	--
Carex blanda	67	3	28	19	--	33	3	13	4	--
Carex grayi	61	3	38	23	--	40	5	23	9	--
Carex tribuloides	42	2	15	7	--	60	4	20	12	--
Carpinus caroliniana	67	3	16	11	--	60	2	13	8	--
Carya cordiformis	94	2	31	29	19.4	60	2	18	11	--
Celtis laevigata	94	3	26	25	17.4	87	2	22	19	--
Chasmanthium latifolium	45	5	14	7	--	77	6	22	17	--
Cinna arundinacea	9	4	9	1	--	43	4	38	17	--
Clematis viorna	15	2	17	3	--	33	2	34	11	--
Commelina virginica	27	2	16	4	--	57	2	31	18	--
Cryptotaenia canadensis	27	2	26	7	--	43	2	38	17	--
Dichanthelium clandestinum	3	3	6	0	--	37	2	65	24	--
Dichanthelium commutatum var. commutatum	45	3	16	7	--	23	2	7	2	--
Elymus [glabriflorus + macgregorii + virginicus]	67	5	24	16	--	63	6	21	13	--
Erechtites hieracifolia	30	2	15	5	--	37	2	17	6	--
Euonymus americanus	58	2	15	9	--	30	2	7	2	--
Festuca subverticillata	39	5	17	7	--	60	3	24	14	--
Fraxinus sp	82	2	17	14	--	90	2	17	15	--
Galium aparine	64	2	32	20	--	70	4	32	22	--
Geum canadense	48	2	20	10	--	43	2	16	7	--
Glechoma hederacea	33	6	48	16	--	37	6	48	18	--
Glyceria striata var. striata	15	2	8	1	--	37	2	18	7	--
[Gonolobus + Matelea]	73	2	34	25	--	60	2	26	15	--
Ilex decidua	48	2	14	7	--	33	2	9	3	--
Ilex opaca var. opaca	52	2	17	9	--	27	2	8	2	--
Juglans nigra	52	2	40	20	--	37	2	26	9	--
Laportea canadensis	52	5	43	22	--	57	4	43	24	--
Leersia virginica	9	3	5	0	--	53	2	28	15	--
Ligustrum sinense*	94	3	19	18	--	97	2	18	18	--
Lindera benzoin	70	3	30	21	--	53	2	21	11	--
Liquidambar styraciflua	45	2	11	5	--	53	2	12	6	--
Lonicera japonica*	100	4	20	20	--	90	4	16	15	--
Microstegium vimineum*	85	6	19	16	--	93	7	19	18	--

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Type Name		IIIa.					IIIb.			
Osmorhiza longistylis	45	2	68	31	28.3	--	--	--	--	--
Oxalis sp	48	2	22	11	--	60	2	25	15	--
Parthenocissus quinquefolia	100	2	18	18	--	100	2	17	17	--
Persicaria sp	6	2	5	0	--	40	2	32	13	--
Persicaria virginiana	76	2	26	20	--	87	2	27	23	--
Phytolacca americana	21	2	21	4	--	53	2	47	25	--
Pilea pumila	27	2	18	5	--	63	2	37	24	--
Poa [autumnalis + cuspidata]	45	3	16	7	--	27	2	9	2	--
Polygonatum biflorum	39	2	24	9	--	17	1	9	2	--
Polystichum acrostichoides	52	2	19	10	--	37	2	12	4	--
Potentilla indica	39	3	36	14	--	40	2	33	13	--
Prunus serotina	45	2	16	7	--	43	2	14	6	--
Ranunculus abortivus	39	2	23	9	--	33	2	18	6	--
Rosa sp	39	2	22	9	--	30	2	15	5	--
Rubus sp	55	2	14	8	--	40	2	10	4	--
Sambucus canadensis	36	2	20	7	--	67	2	33	22	--
Sanicula canadensis var. canadensis	70	2	21	15	--	37	2	10	4	--
Smilax bona-nox	91	2	20	18	--	83	2	17	14	--
Smilax hispida	27	2	18	5	--	40	2	24	9	--
Smilax [rotundifolia + walterii]	73	2	15	11	--	70	2	13	9	--
Solidago sp	52	2	11	6	--	77	2	15	12	--
Staphylea trifolia	45	2	48	22	--	20	2	19	4	--
Toxicodendron radicans	100	2	18	18	--	100	2	17	17	--
Ulmus alata	45	2	14	6	--	30	2	9	3	--
Ulmus [americana + rubra]	55	2	17	9	--	70	2	20	14	--
Verbesina alternifolia	70	3	28	20	--	80	3	30	24	--
Verbesina occidentalis	70	2	32	23	--	67	2	28	19	--
Viola sp	88	2	20	17	--	73	3	15	11	--
Vitis [cinerea + vulpina]	33	2	14	5	--	73	2	27	20	--
Vitis rotundifolia var. rotundifolia	82	2	19	16	--	47	2	10	5	--

Appendix 6

Average cover by strata, constancy (const), fidelity (fid), diagnostic value (DV), and indicator value (IV) of prevalent species in the five bottomland and swamp forest types. Prevalence is calculated separately for each stratum, and species must be prevalent in at least one type to be included in table (see text for definition of terms and calculation of metrics). Species may be in the table more than once as they receive cover in every stratum in which they were observed. Non-native species are identified by an *.

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Plot Count	17					24					6					3					2				
Avg Spp Richness (400m^2)	56.2					53.5					54.8					33.3					35.0				
Avg Spp Richness (100m^2)	36.1					31.8					27.6					18.7					16.6				
Avg Spp Richness (10m^2)	17.6					15,7					17.3					7.8					5.9				
Avg Spp Richness (1m^2)	7.4					6.6					7.4					3.5					2.1				
Homotoneity	58					62					59					63					62				
Tree stratum	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV
Acer floridanum	35	6	11	4	--	4	5	2	0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Acer negundo var. negundo	6	5	2	0	--	--	--	--	--	--	17	3	2	0	--	--	--	--	--	--	--	--	--	--	--
Acer rubrum	88	6	13	12	--	100	8	21	21	--	100	7	5	5	--	100	7	3	3	--	100	6	2	2	--
Betula nigra	41	6	11	5	--	29	6	11	3	--	83	6	8	7	--	--	--	--	--	--	50	4	2	1	--
Bignonia capreolata	41	2	14	6	--	38	2	18	7	--	17	2	2	0	--	--	--	--	--	--	--	--	--	--	--
Campsis radicans	53	2	27	14	--	29	2	21	6	--	17	2	3	1	--	--	--	--	--	--	50	2	3	2	--
Carpinus caroliniana	71	6	11	8	--	33	7	7	2	--	17	6	1	0	--	33	3	1	0	--	50	6	1	0	--
Carya aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100	6	100	100	100.0
Carya ovata	41	6	18	7	--	17	5	10	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Crataegus viridis	--	--	--	--	--	13	5	75	9	--	--	--	--	--	--	--	--	--	--	--	50	4	25	13	38.7
Fraxinus pennsylvanica	71	6	10	7	--	96	7	18	18	--	100	8	5	5	17.7	100	6	2	2	--	50	4	1	0	--
Liquidambar styraciflua	100	7	11	11	--	88	6	14	12	--	67	6	3	2	--	67	5	1	1	--	100	5	1	1	--
Lonicera japonica*	24	2	12	3	--	8	3	6	1	--	33	2	6	2	--	--	--	--	--	--	--	--	--	--	--
Nyssa aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	100	8	100	100	100.0
Nyssa sylvatica	35	5	13	4	--	29	4	15	4	--	--	--	--	--	--	33	5	2	1	--	--	--	--	--	--
Parthenocissus quinquefolia	53	2	15	8	--	25	2	10	3	--	33	2	3	1	--	--	--	--	--	--	--	--	--	--	--
Pinus taeda	18	5	12	2	--	8	5	8	1	--	--	--	--	--	--	33	3	4	1	--	--	--	--	--	--
Platanus occidentalis var. occidentalis	24	4	5	1	--	25	6	8	2	--	67	6	5	4	--	33	4	1	0	--	50	2	1	1	--
Populus deltoides	6	7	10	1	--	4	2	10	0	--	--	--	--	--	--	--	--	--	--	--	50	5	10	5	--
Quercus alba	41	5	19	8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus lyrata	12	7	12	1	--	17	6	24	4	--	--	--	--	--	--	100	6	18	18	42.9	100	6	12	12	--
Quercus michauxii	41	6	17	7	--	33	6	20	7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus nigra	35	5	13	5	--	8	4	4	0	--	33	6	4	1	--	--	--	--	--	--	--	--	--	--	--
Quercus pagoda	53	6	23	12	--	33	5	20	7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Quercus phellos	76	7	25	19	--	54	6	25	13	--	--	--	--	--	--	100	6	6	6	27.9	--	--	--	--	--
Salix nigra	--	--	--	--	--	13	3	43	5	--	50	5	43	21	40.5	--	--	--	--	--	--	--	--	--	--
Toxicodendron radicans	94	5	14	13	--	71	5	15	10	--	83	5	4	4	--	--	--	--	--	--	50	3	1	0	--
Ulmus alata	76	6	17	13	--	46	6	14	7	--	17	5	1	0	--	--	--	--	--	--	--	--	--	--	--
Ulmus [americana + rubra]	94	6	13	12	--	88	6	17	15	--	67	5	3	2	--	67	5	2	1	--	100	4	2	2	--
Vitis rotundifolia var. rotundifolia	53	3	11	6	--	13	2	4	0	--	17	4	1	0	--	--	--	--	--	--	--	--	--	--	--
Shrub stratum	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV
Acer floridanum	41	6	12	5	--	8	2	3	0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Acer rubrum	65	4	14	9	--	88	4	27	24	--	83	4	6	5	--	67	4	3	2	--	--	--	--	--	--
Aesculus sylvatica	24	4	11	3	--	4	3	3	0	--	--	--	--	--	--	33	2	3	1	--	--	--	--	--	--
Alnus serrulata	--	--	--	--	--	--	--	--	--	--	67	5	50	33	54.3	--	--	--	--	--	--	--	--	--	--
Bignonia capreolata	71	2	17	12	--	42	2	14	6	--	17	2	1	0	--	--	--	--	--	--	--	--	--	--	--
Campsis radicans	65	2	27	17	--	29	2	17	5	--	17	2	2	0	--	33	2	2	1	--	50	1	2	1	--
Carpinus caroliniana	88	5	12	11	--	71	4	14	10	--	50	6	2	1	--	67	4	2	1	--	--	--	--	--	--
Cephalanthus occidentalis	--	--	--	--	--	8	3	67	6	--	--	--	--	--	--	--	--	--	--	--	50	2	33	17	41.4
Cornus amomum	--	--	--	--	--	--	--	--	--	--	33	4	67	22	--	--	--	--	--	--	--	--	--	--	--
Fraxinus pennsylvanica	71	5	14	10	--	79	4	22	17	--	67	6	5	3	--	33	3	1	0	--	--	--	--	--	--
Ilex decidua	88	5	16	14	--	71	5	18	13	--	--	--	--	--	--	100	3	3	3	--	100	4	2	2	--
Ilex opaca var. opaca	47	5	10	5	--	25	4	7	2	--	33	3	2	1	--	--	--	--	--	--	--	--	--	--	--
Ilex verticillata	18	3	43	8	--	4	2	14	1	--	--	--	--	--	--	33	2	14	5	--	--	--	--	--	--
Ligustrum sinense*	47	4	11	5	--	33	2	11	4	--	50	4	4	2	--	--	--	--	--	--	--	--	--	--	--
Liquidambar styraciflua	47	3	12	6	--	25	4	9	2	--	50	5	4	2	--	33	2	1	0	--	--	--	--	--	--
Lonicera japonica*	94	2	21	20	22.9	17	2	5	1	--	50	4	4	2	--	--	--	--	--	--	--	--	--	--	--
Parthenocissus quinquefolia	76	2	17	13	--	42	2	13	5	--	33	2	3	1	--	--	--	--	--	--	--	--	--	--	--
Platanus occidentalis var. occidentalis	--	--	--	--	--	8	5	25	2	--	33	3	25	8	--	--	--	--	--	--	--	--	--	--	--
Quercus lyrata	6	2	33	2	--	4	7	33	1	--	--	--	--	--	--	33	2	33	11	--	--	--	--	--	--
Quercus michauxii	41	3	27	11	--	21	3	19	4	--	17	2	4	1	--	33	2	4	1	--	--	--	--	--	--
Quercus phellos	18	2	20	4	--	17	2	27	4	--	17	2	7	1	--	33	2	7	2	--	--	--	--	--	--
Rubus sp	--	--	--	--	--	13	2	43	5	--	--	--	--	--	--	33	2	14	5	--	--	--	--	--	--
Smilax [rotundifolia + walterii]	88	4	17	15	--	71	3	19	14	--	67	3	5	3	--	67	3	2	2	--	50	2	1	1	--
Toxicodendron radicans	94	3	14	13	--	75	3	15	12	--	50	3	3	1	--	67	2	2	1	--	100	2	2	2	--
Ulmus alata	88	5	18	16	23.0	54	4	16	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ulmus [americana + rubra]	71	4	20	14	--	46	4	19	9	--	17	2	2	0	--	33	2	2	1	--	--	--	--	--	--
Viburnum dentatum	--	--	--	--	--	17	4	22	4	--	33	5	11	4	--	--	--	--	--	--	--	--	--	--	--
Viburnum prunifolium	65	4	17	11	--	38	4	14	5	--	17	2	2	0	--	--	--	--	--	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	59	2	11	7	--	21	2	6	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Herb stratum	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV	const	cover	fid	DV	IV
Acer negundo var. negundo	35	2	6	2	--	29	2	7	2	--	67	3	4	3	--	--	--	--	--	--	--	--	--	--	--
Acer rubrum	100	2	14	14	--	100	2	20	20	--	100	2	5	5	--	100	2	2	2	--	100	2	2	2	--

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Aesculus sylvatica	35	2	15	5	--	8	2	5	0	--	--	--	--	--	--	33	2	3	1	--	--	--	--	--	--
Allium canadense var. canadense	47	2	21	10	--	8	2	5	0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Alnus serrulata	--	--	--	--	--	--	--	--	--	--	33	3	40	13	--	--	--	--	--	--	--	--	--	--	--
Apios americana	--	--	--	--	--	4	1	20	1	--	33	1	40	13	--	--	--	--	--	--	--	--	--	--	--
Arisaema triphyllum	88	2	20	18	--	17	2	5	1	--	33	1	3	1	--	--	--	--	--	--	--	--	--	--	--
Betula nigra	--	--	--	--	--	8	2	22	2	--	33	2	22	7	--	33	2	11	4	--	--	--	--	--	--
Bidens frondosa	24	2	11	2	--	29	2	18	5	--	50	3	8	4	--	67	2	5	4	--	100	2	5	5	--
Bignonia capreolata	100	3	12	12	--	79	3	13	10	--	67	2	3	2	--	--	--	--	--	--	50	1	1	0	--
Boehmeria cylindrica	76	2	10	8	--	92	3	17	16	--	100	6	5	5	23.6	100	2	2	2	--	50	1	1	0	--
Bromus [nottowayanus + pubescens]	6	2	3	0	--	--	--	--	--	--	--	--	--	--	--	33	2	3	1	--	--	--	--	--	--
Callitriche heterophylla	--	--	--	--	--	4	1	50	2	--	--	--	--	--	--	33	2	50	17	--	--	--	--	--	--
Campsis radicans	100	2	13	13	--	83	2	16	13	--	100	2	5	5	--	100	2	2	2	--	50	2	1	0	--
Carex [amphibola+grisea+corrugata]	59	4	9	5	--	38	4	8	3	--	33	1	2	1	--	--	--	--	--	--	50	3	1	0	--
Carex [radiata + rosea]	53	2	9	5	--	42	2	10	4	--	17	1	1	0	--	--	--	--	--	--	--	--	--	--	--
Carex blanda	35	2	8	3	--	29	2	9	3	--	--	--	--	--	--	--	--	--	--	--	50	1	1	1	--
Carex bromoides	--	--	--	--	--	46	5	73	34	31.9	--	--	--	--	--	--	--	--	--	--	50	1	7	3	--
Carex caroliniana	41	2	18	7	--	25	2	15	4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carex crinita	29	2	17	5	--	33	3	27	9	--	83	6	17	14	41.9	67	2	7	4	--	--	--	--	--	--
Carex cumberlandensis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33	2	13	4	--	--	--	--	--	--
Carex debilis	41	3	13	5	--	50	4	21	11	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carex flaccosperma	12	2	8	1	--	33	2	33	11	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carex gracillima	18	3	8	1	--	33	3	21	7	--	17	2	3	0	--	--	--	--	--	--	--	--	--	--	--
Carex grayi	12	3	4	0	--	33	5	15	5	--	17	3	2	0	--	--	--	--	--	--	50	2	2	1	--
Carex hirsutella	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	2	50	25	48.5
Carex intumescens	47	3	20	9	--	29	5	18	5	--	--	--	--	--	--	67	2	5	3	--	--	--	--	--	--
Carex louisianica	6	2	8	0	--	38	4	69	26	23.9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carex lupulina	29	2	16	5	--	58	4	45	26	--	67	4	13	9	--	33	5	3	1	--	--	--	--	--	--
Carex lurida	6	1	10	1	--	13	3	30	4	--	--	--	--	--	--	33	2	10	3	--	--	--	--	--	--
Carex stipata	6	2	3	0	--	50	3	39	19	--	33	3	6	2	--	33	2	3	1	--	50	1	3	2	--
Carex tribuloides	76	3	14	11	--	88	4	23	20	--	100	4	7	7	22.2	33	2	1	0	--	50	2	1	1	--
Carex typhina	47	2	15	7	--	88	4	40	35	27.0	33	4	4	1	--	67	2	4	3	--	--	--	--	--	--
Carpinus caroliniana	76	2	9	7	--	63	2	11	7	--	67	2	3	2	--	67	3	1	1	--	50	2	1	0	--
Carya cordiformis	41	2	7	3	--	29	2	7	2	--	17	2	1	0	--	--	--	--	--	--	--	--	--	--	--
Carya ovata	41	2	14	6	--	29	2	14	4	--	17	2	2	0	--	--	--	--	--	--	--	--	--	--	--
Celtis laevigata	71	2	10	7	--	42	2	9	4	--	17	1	1	0	--	--	--	--	--	--	50	1	1	0	--
Cephalanthus occidentalis	--	--	--	--	--	29	2	58	17	--	33	1	17	6	--	33	1	8	3	--	50	1	8	4	--
Chasmanthium latifolium	47	2	8	4	--	54	4	13	7	--	67	4	4	3	--	--	--	--	--	--	50	1	1	0	--
Cicuta maculata	--	--	--	--	--	4	1	25	1	--	33	3	50	17	30.6	--	--	--	--	--	--	--	--	--	--

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Cinna arundinacea	12	4	6	1	--	33	4	24	8	--	50	6	9	4	--	--	--	--	--	--	--	--	--	--	--
Clematis virginiana	--	--	--	--	--	--	--	--	--	--	33	2	12	4	--	--	--	--	--	--	--	--	--	--	--
Commelina virginica	24	1	7	2	--	54	2	24	13	--	67	6	7	5	--	33	3	2	1	--	--	--	--	--	--
Cornus amomum	--	--	--	--	--	4	2	17	1	--	33	2	33	11	--	33	2	17	6	--	--	--	--	--	--
Dichanthelium commutatum[2]	29	2	5	2	--	46	2	11	5	--	33	2	2	1	--	33	1	1	0	--	50	2	1	1	--
Dichanthelium dichotomum	18	2	9	2	--	17	2	13	2	--	--	--	--	--	--	33	2	3	1	--	--	--	--	--	--
Dichanthelium yadkinense	--	--	--	--	--	8	2	14	1	--	--	--	--	--	--	--	--	--	--	--	50	2	7	4	--
Diospyros virginiana	12	2	5	1	--	21	2	11	2	--	67	2	9	6	--	67	2	5	3	--	--	--	--	--	--
Elymus[1]	65	3	12	8	--	42	2	11	5	--	33	1	2	1	--	--	--	--	--	--	--	--	--	--	--
Erechtites hieracifolia	59	2	15	9	--	63	1	23	14	--	17	1	2	0	--	33	1	2	1	--	100	1	3	3	--
Euonymus americanus	76	2	10	8	--	71	2	13	9	--	33	2	2	1	--	--	--	--	--	--	--	--	--	--	--
Festuca subverticillata	35	2	8	3	--	17	4	5	1	--	--	--	--	--	--	33	2	1	0	--	--	--	--	--	--
Fraxinus pennsylvanica	94	2	10	9	--	92	2	14	13	--	100	2	4	4	--	100	2	2	2	--	50	1	1	0	--
Galium aparine	18	2	5	1	--	17	2	6	1	--	67	2	6	4	--	33	1	2	1	--	--	--	--	--	--
Galium tinctorium	65	2	26	17	--	42	2	24	10	--	--	--	--	--	--	--	--	--	--	--	50	1	2	1	--
Gelsemium sempervirens	12	2	9	1	--	4	1	5	0	--	17	1	5	1	--	67	2	9	6	30.7	--	--	--	--	--
Geum canadense	29	2	6	2	--	50	2	15	7	--	50	2	4	2	--	--	--	--	--	--	--	--	--	--	--
Glyceria striata var. striata	65	2	18	11	--	50	4	19	10	--	83	4	8	7	--	67	2	3	2	--	--	--	--	--	--
Gratiola virginiana	--	--	--	--	--	4	2	33	1	--	17	1	33	6	--	33	3	33	11	--	--	--	--	--	--
Hydrocotyle umbellata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	2	100	50	50.0
Hypericum punctatum	6	1	8	0	--	4	1	8	0	--	17	3	8	1	--	33	2	8	3	--	--	--	--	--	--
Hypoxis hirsuta	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ilex decidua	100	2	15	15	--	88	2	18	16	--	--	--	--	--	--	--	--	--	--	--	100	2	2	2	--
Ilex opaca var. opaca	47	2	8	4	--	33	2	8	3	--	33	2	2	1	--	--	--	--	--	--	--	--	--	--	--
Ilex verticillata	29	2	19	6	--	21	2	19	4	--	17	2	4	1	--	67	2	8	5	27.6	--	--	--	--	--
Impatiens sp	29	4	10	3	--	38	2	19	7	--	33	2	4	1	--	67	2	4	3	--	50	1	2	1	--
Juncus acuminatus	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33	1	100	33	33.3	--	--	--	--	--
Juncus coriaceus	35	2	13	4	--	33	3	17	6	--	33	2	4	1	--	33	2	2	1	--	--	--	--	--	--
Juncus effusus	24	2	10	2	--	54	3	32	17	--	33	4	5	2	--	--	--	--	--	--	--	--	--	--	--
Juncus elliottii	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33	2	100	33	33.3	--	--	--	--	--
Leersia oryzoides	--	--	--	--	--	--	--	--	--	--	33	4	50	17	--	--	--	--	--	--	--	--	--	--	--
Leersia virginica	18	2	5	1	--	50	3	21	11	--	50	3	5	3	--	--	--	--	--	--	--	--	--	--	--
*Ligustrum sinense**	94	2	10	9	--	79	2	12	9	--	67	2	3	2	--	33	1	1	0	--	50	2	1	0	--
Lindera benzoin	47	2	11	5	--	4	2	1	0	--	33	2	3	1	--	--	--	--	--	--	--	--	--	--	--
Liquidambar styraciflua	88	2	11	10	--	88	2	15	14	--	67	3	3	2	--	33	2	1	0	--	50	2	1	0	--
Liriodendron tulipifera	29	2	7	2	--	17	1	6	1	--	67	2	6	4	--	33	1	1	0	--	--	--	--	--	--
Lobelia cardinalis	12	1	14	2	--	13	2	21	3	--	67	2	29	19	27.3	33	2	7	2	--	--	--	--	--	--
Lobelia siphilitica var. siphilitica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33	2	100	33	33.3	--	--	--	--	--
*Lonicera japonica**	100	2	10	10	--	79	2	11	9	--	100	3	4	4	--	33	1	1	0	--	50	1	1	0	--
Ludwigia alternifolia	--	--	--	--	--	4	1	25	1	--	17	1	25	4	--	33	1	25	8	--	--	--	--	--	--

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Ludwigia palustris	6	1	8	0	--	21	2	42	9	--	--	--	--	--	--	100	2	25	25	60.1	50	2	8	4	--
Lycopus virginicus	24	2	7	2	--	54	2	23	13	--	100	3	11	11	--	100	2	5	5	--	100	2	4	4	--
Microstegium vimineum*	82	4	10	8	--	67	4	11	7	--	83	7	3	3	--	33	2	1	0	--	50	1	1	0	--
Mikania scandens	--	--	--	--	--	21	2	42	9	--	50	2	25	13	31.4	--	--	--	--	--	--	--	--	--	--
Murdannia keisak*	6	1	6	0	--	29	3	39	11	--	33	6	11	4	--	33	4	6	2	--	50	1	6	3	--
Nyssa aquatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	2	100	50	50.0
Nyssa sylvatica	47	2	12	6	--	38	2	13	5	--	33	1	3	1	--	33	1	1	0	--	--	--	--	--	--
Onoclea sensibilis	24	2	24	6	--	8	2	12	1	--	33	4	12	4	--	--	--	--	--	--	--	--	--	--	--
Packera aurea	--	--	--	--	--	--	--	--	--	--	33	1	50	17	--	--	--	--	--	--	--	--	--	--	--
Parthenocissus quinquefolia	100	3	9	9	--	96	2	13	12	--	100	2	3	3	--	33	1	1	0	--	100	2	1	1	--
Peltandra virginica	--	--	--	--	--	29	2	58	17	--	83	4	42	35	68.5	--	--	--	--	--	--	--	--	--	--
Persicaria sp	12	2	5	1	--	46	3	29	13	--	83	3	13	11	26.1	33	1	3	1	--	50	2	3	1	--
Persicaria virginiana	53	2	9	5	--	42	2	10	4	--	67	2	4	3	--	33	2	1	0	--	--	--	--	--	--
Phytolacca americana	6	1	3	0	--	17	1	12	2	--	50	2	9	4	--	--	--	--	--	--	--	--	--	--	--
Pilea pumila	29	2	10	3	--	38	2	18	7	--	33	3	4	1	--	33	2	2	1	--	100	2	4	4	31.8
Pinus taeda	24	1	13	3	--	17	2	13	2	--	--	--	--	--	--	33	2	3	1	--	--	--	--	--	--
Platanus occidentalis var. occidentalis	--	--	--	--	--	8	2	15	1	--	17	2	8	1	--	33	1	8	3	--	--	--	--	--	--
Pleopeltis polypodioides	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	33	2	33	11	--	--	--	--	--	--
Pluchea camphorata	--	--	--	--	--	--	--	--	--	--	17	1	50	8	--	33	2	50	17	--	--	--	--	--	--
Poa [autumnalis + cuspidata]	82	3	15	12	--	42	3	11	4	--	50	2	3	2	--	--	--	--	--	--	50	2	1	1	--
Polystichum acrostichoides	35	2	7	2	--	13	2	3	0	--	17	1	1	0	--	--	--	--	--	--	--	--	--	--	--
Prunus serotina	18	2	3	1	--	13	1	3	0	--	67	2	4	3	--	--	--	--	--	--	--	--	--	--	--
Quercus lyrata	12	2	17	2	--	13	2	25	3	--	--	--	--	--	--	67	3	17	11	45.7	--	--	--	--	--
Quercus michauxii	53	2	22	12	--	38	2	22	8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus nigra	35	2	10	4	--	29	2	12	4	--	33	2	3	1	--	--	--	--	--	--	--	--	--	--	--
Quercus pagoda	41	2	23	9	--	25	2	19	5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus phellos	82	2	16	13	--	75	2	21	16	--	50	2	3	2	--	33	2	1	0	--	--	--	--	--	--
Ranunculus abortivus	41	2	13	5	--	17	2	7	1	--	50	1	5	3	--	--	--	--	--	--	50	2	2	1	--
Rosa sp	35	2	10	4	--	25	2	10	3	--	67	2	7	4	--	--	--	--	--	--	--	--	--	--	--
Rubus sp	71	3	10	7	--	79	2	15	12	--	100	2	5	5	--	67	2	2	1	--	50	2	1	0	--
Sambucus canadensis	29	2	8	2	--	29	2	12	3	--	50	2	5	3	--	--	--	--	--	--	--	--	--	--	--
Samolus parviflorus	6	2	50	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	2	50	25	44.7
Sanicula canadensis var. canadensis	47	2	7	3	--	33	2	7	2	--	67	1	4	2	--	--	--	--	--	--	100	1	2	2	--
Saururus cernuus	29	2	10	3	--	71	6	33	24	--	33	6	4	1	--	100	7	6	6	33.0	100	2	4	4	--
Sceptridium [biternatum + dissectum]	53	2	10	5	--	54	2	15	8	--	17	2	1	0	--	--	--	--	--	--	50	1	1	1	--
Sisyrinchium angustifolium	6	1	10	1	--	8	1	20	2	--	33	2	20	7	--	33	1	10	3	--	50	2	10	5	--
Smilax bona-nox	82	2	9	8	--	75	2	12	9	--	50	2	2	1	--	--	--	--	--	--	--	--	--	--	--
Smilax glauca	59	2	9	5	--	50	2	11	6	--	67	2	4	2	--	--	--	--	--	--	50	1	1	0	--

Type Name	IVa.					IVb.					IVc.					IVd.					IVe.				
Smilax rotundifolia + walterii	**100**	3	11	11	--	**100**	3	15	15	--	**100**	2	4	4	--	**100**	2	2	2	--	**100**	3	1	1	--
Solidago sp	**88**	2	10	9	--	**96**	3	15	15	--	**83**	4	3	3	--	**67**	2	1	1	--	**100**	2	1	1	--
Toxicodendron radicans	**100**	4	9	9	--	**100**	4	13	13	--	**100**	4	3	3	--	**100**	2	2	2	--	**100**	2	1	1	--
Trachelospermum difforme	**59**	2	23	14	--	29	2	16	5	--	17	1	2	0	--	--	--	--	--	--	--	--	--	--	--
Triadenum walteri	--	--	--	--	--	4	1	20	1	--	**50**	4	60	30	45.8	--	--	--	--	--	--	--	--	--	--
Ulmus alata	**88**	2	14	13	--	**71**	2	16	11	--	17	1	1	0	--	**33**	1	1	0	--	50	1	1	0	--
Ulmus [americana + rubra]	**76**	2	12	9	--	**83**	2	19	16	--	**67**	2	4	3	--	**67**	2	2	1	--	50	1	1	0	--
Viburnum dentatum	**41**	2	11	5	--	**42**	2	16	7	--	**50**	2	5	2	--	**33**	1	2	1	--	--	--	--	--	--
Viburnum prunifolium	**76**	2	15	11	--	**38**	2	10	4	--	17	1	1	0	--	--	--	--	--	--	--	--	--	--	--
Viola sp	**100**	2	11	11	--	**67**	2	11	7	--	**50**	2	2	1	--	--	--	--	--	--	**100**	2	1	1	--
Vitis [cinerea + vulpina]	**35**	2	7	3	--	**46**	2	14	6	--	**33**	2	2	1	--	--	--	--	--	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	**88**	2	11	9	--	**54**	2	9	5	--	**67**	2	3	2	--	--	--	--	--	--	**100**	2	1	1	--

[1] *var. heterophylla*
[2] *var. commutatum*
[3] *[glabriflorus + macgregorii + virginicus]*

Appendix 7

Average cover, constancy, fidelity, and diagnostic value (DV) of prevalent species in the two riparian herbaceous vegetation types. Species may be in the table more than once as they receive cover in every stratum in which they were observed. Non-native species are identified by an *.

Type Name	Va.				Vb.			
Plot Count	10				2			
Avg Spp Richness (10m^2)	20				13			
Homotoneity	53				81			
taxon name	const.	cover	fidelity	DV	const.	cover	fidelity	DV
Acalypha rhomboidea	10	1	100	10	--	--	--	--
Acer negundo var. negundo	40	3	100	40	--	--	--	--
Acer rubrum	20	2	67	13	50	1	33	17
Betula nigra	70	3	100	70	--	--	--	--
Bidens frondosa	30	2	60	18	100	2	40	40
Boehmeria cylindrica	80	2	89	71	50	2	11	6
Cardamine pensylvanica	10	2	50	5	50	2	50	25
Cephalanthus occidentalis	30	4	100	30	--	--	--	--
Commelina communis*	--	--	--	--	50	1	100	50
Diodia virginiana	30	2	100	30	--	--	--	--
Eclipta prostrata	70	3	100	70	--	--	--	--
Fraxinus pennsylvanica	50	4	100	50	--	--	--	--
Galium sp.	--	--	--	--	50	1	100	50
Gratiola neglecta	--	--	--	--	100	1	100	100
Hymenocallis coronaria	--	--	--	--	100	8	100	100
Hypericum mutilum	--	--	--	--	50	3	100	50
Hypericum mutilum var. mutilum	40	2	100	40	--	--	--	--
Justicia americana	100	7	83	83	100	7	17	17
Leersia oryzoides	--	--	--	--	50	1	100	50
Ludwigia alternifolia	--	--	--	--	50	2	100	50
Ludwigia palustris	50	2	71	36	100	2	29	29
Microstegium vimineum*	70	2	100	70	--	--	--	--
Murdannia keisak*	80	4	80	64	100	2	20	20
Oxalis sp.	40	2	100	40	--	--	--	--
Persicaria setacea	--	--	--	--	100	2	100	100
Persicaria virginiana	60	2	100	60	--	--	--	--
Platanus occidentalis var. occidentalis	80	2	100	80	--	--	--	--
Rumex crispus	--	--	--	--	100	1	100	100
Saururus cernuus	40	3	100	40	--	--	--	--
Toxicodendron radicans var. radicans	30	2	100	30	--	--	--	--
Ulmus alata	30	3	100	30	--	--	--	--
Ulmus americana var. americana	30	2	100	30	--	--	--	--
Viola sp.	40	2	100	40	--	--	--	--

Appendix 8

Species attributes (growth habit, nativity, habitat, and dispersal mode) for 530 taxa recognized in Chapters 3 and 4. Growth habit information is from USDA PLANTS 2010. Nativity and habitat is from Weakley 2010. References for dispersal mode information are included in table.

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
1	*Acalypha gracilens*	Forb	Native	Ruderal	Unassisted	Minor et al 2009
2	*Acalypha rhomboidea*	Forb	Native	Ruderal	Unassisted	Minor et al 2009; Hooper et al 2004
3	*Acer floridanum*	Tree	Native	General bottomland	Wind	Inferred from morphology and con-geners
4	*Acer negundo*	Tree	Native	General bottomland	Wind; Water	Minor et al 2009; Cain et al 1998
5	*Acer rubrum*	Tree	Native	General forest	Wind	Inferred from morphology and con-geners
6	*Acer saccharinum*	Tree	Native	General bottomland	Wind	Inferred from morphology and con-geners
7	*Actaea racemosa*	Forb	Native	Rich Cove	Vertebrate	Thompson 1979; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
8	*Adiantum pedatum*	Forb	Native	Lowland Mesic Forest	Wind	Flinn et al 2010
9	*Aesculus sylvatica*	Shrub	Native	Lowland Mesic Forest	Vertebrate; Water	Howard 1992
10	*Ageratina altissima*	Forb	Native	Lowland Mesic Forest	Unknown	
11	*Agrimonia [bicknellii + microcarpa + pubescens]*	Forb	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
12	*Agrimonia parviflora*	Forb	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
13	*Agrimonia rostellata*	Forb	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
14	*Agrostis perennans*	Graminoid	Native	Gen Woodland	Unknown	
15	*Ailanthus altissima*	Tree	Exotic	No natural habitat	Wind	Inferred from morphology and con-geners

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
16	*Albizia julibrissin*	Tree	Exotic	No natural habitat	Wind; Vertebrate; Water	Meyer 2009
17	*Alisma subcordatum*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
18	*Allium canadense var. canadense*	Forb	Native	General bottomland	Water; Unassisted	Mehrhoff et al 2003
19	*Allium cuthbertii*	Forb	Native	Granite Glade	Water; Unassisted	Mehrhoff et al 2003
20	*Alnus serrulata*	Shrub	Native	General wet acidic	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
21	*Ambrosia artemisiifolia*	Forb	Native	Ruderal	Unassisted	Minor et al 2009; Lavoie et al 2007
22	*Amelanchier arborea*	Shrub	Native	Lowland Acid Dry Forest	Vertebrate	USDA, NRCS 2010
23	*Amianthium muscitoxicum*	Forb	Native	Lowland Mesic Forest	Unknown	
24	*Amorpha fruticosa*	Shrub	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
25	*Amphicarpaea bracteata*	Vine	Native	Lowland Mesic Forest	Unassisted	Trapp 1988
26	*Amsonia tabernaemontana*	Forb	Native	General bottomland	Unknown	
27	*Anemone americana*	Forb	Native	Lowland Mesic Forest	Unknown	
28	*Anemone virginiana*	Forb	Native	General bottomland	Unknown	
29	*Anemonella thalictroides*	Forb	Native	General bottomland	Unassisted	Minor et al 2009; Sitzia 2007
30	*Antennaria sp.*	Forb	Native	Lowland Acid Dry Forest	Unknown	
31	*Apios americana*	Vine	Native	General bottomland	Unknown	
32	*Arisaema dracontium*	Forb	Native	General bottomland	Vertebrate	Minor et al 2009; Matlack 1994
33	*Arisaema triphyllum*	Forb	Native	General bottomland	Vertebrate	Minor et al 2009; Matlack 1994
34	*Arnoglossum atriplicifolium*	Forb	Native	Lowland Mesic Forest	Unknown	
35	*Aronia arbutifolia*	Shrub	Native	General wet acidic	Vertebrate	Rossell and Kesgen 2003
36	*Artemisia sp.*	Forb	Exotic	No natural habitat	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
37	*Arundinaria tecta*	Graminoid	Native	General bottomland	Unassisted	Hughes 1951
38	*Asarum canadense*	Forb	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Matlack 1994
39	*Asclepias incarnata*	Forb	Native	General bottomland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
40	*Asclepias quadrifolia*	Forb	Native	Rich Cove	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
41	*Asimina triloba*	Shrub	Native	General bottomland	Vertebrate; Water	Minor et al 2009; Thompson 1981
42	*Asplenium platyneuron*	Forb	Native	Lowland Acid Dry Forest	Wind	Minor et al 2009
43	*Athyrium asplenioides*	Forb	Native	Lowland Mesic Forest	Wind	Flinn et al 2010
44	*Aureolaria virginica*	Forb	Native	Lowland Acid Dry Forest	Unknown	
45	*Berchemia scandens*	Vine	Native	General bottomland	Unknown	
46	*Betula nigra*	Tree	Native	General bottomland	Wind; Water	Inferred from morphology and con-geners
47	*Bidens frondosa*	Forb	Native	Aquatic	Vertebrate; Water	Cain et al 1998; Neff and Baldwin 2005
48	*Bignonia capreolata*	Vine	Native	General bottomland	Unknown	
49	*Boechera canadensis*	Forb	Native	Mafic Glade	Unknown	
50	*Boehmeria cylindrica*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
51	*Botrypus virginianus*	Forb	Native	Lowland Mesic Forest	Wind	Minor et al 2009; Matlack 1994
52	*Brachyelytrum erectum*	Graminoid	Native	Lowland Mesic Forest	Wind	Montgomery 1977
53	*Bromus [nottowayanus + pubescens]*	Graminoid	Native	General bottomland	Unassisted	Minor et al 2009; Cain et al 1998
54	*Callitriche heterophylla var. heterophylla*	Forb	Native	General bottomland	Vertebrate; Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
55	*Callitriche terrestris*	Forb	Native	Ruderal	Vertebrate; Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
56	*Calycanthus floridus*	Shrub	Native	Lowland Mesic Forest	Unknown	
57	*Campsis radicans*	Vine	Native	General bottomland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
58	*Cardamine debilis*	Forb	Exotic	No natural habitat	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
59	*Cardamine hirsuta*	Forb	Exotic	No natural habitat	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
60	*Cardamine pensylvanica*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
61	*Carex [amphibola + grisea + corrugata]*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
62	*Carex [radiata + rosea]*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
63	*Carex alata*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
64	*Carex albolutescens*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
65	*Carex allegheniensis*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
66	*Carex blanda*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
67	*Carex bromoides*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
68	*Carex caroliniana*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
69	*Carex cephalophora*	Graminoid	Native	General forest	Unassisted	Minor et al 2009; Cain et al 1998
70	*Carex complanata*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
71	*Carex crebriflora*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
72	*Carex crinita*	Graminoid	Native	General wet acidic	Water	Flinn et al 2010
73	*Carex crus-corvi*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
74	*Carex cumberlandensis*	Graminoid	Native	Rich Cove	Unassisted	Inferred from con-geners
75	*Carex debilis*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
76	*Carex digitalis*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
77	*Carex festucacea*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
78	*Carex flaccosperma*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
79	*Carex folliculata*	Graminoid	Native	Mont Bog	Unassisted	Inferred from con-geners
80	*Carex glaucescens*	Graminoid	Native	Black Bottom	Unassisted	Inferred from con-geners
81	*Carex glaucodea*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
82	*Carex gracilescens*	Graminoid	Native	Rich Cove	Unassisted	Inferred from con-geners
83	*Carex gracillima*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
84	*Carex grayi*	Graminoid	Native	General bottomland	Water	Flinn et al 2010; Inferred from con-geners
85	*Carex hirsutella*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
86	*Carex impressinervia*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
87	*Carex intumescens*	Graminoid	Native	General wet acidic	Water	Flinn et al 2010
88	*Carex laevivaginata*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
89	*Carex laxiculmis var. laxiculmis*	Graminoid	Native	Rich Cove	Unassisted	Inferred from con-geners
90	*Carex laxiflora*	Graminoid	Native	General bottomland	Unassisted	Minor et al 2009; Cain et al 1998
91	*Carex leavenworthii*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
92	*Carex louisianica*	Graminoid	Native	CP Calc wet	Unassisted	Inferred from con-geners
93	*Carex lupulina*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
94	*Carex lurida*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
95	*Carex mitchelliana*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
96	*Carex nigromarginata*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
97	*Carex normalis*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
98	*Carex oblita*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
99	*Carex oligosperma*	Graminoid	Native	Mont Bog	Unassisted	Inferred from con-geners
100	*Carex oxylepis*	Graminoid	Native	CP Calc wet	Unassisted	Inferred from con-geners
101	*Carex pigra*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
102	*Carex planispicata*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
103	*Carex retroflexa*	Graminoid	Native	General forest	Unassisted	Inferred from con-geners

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
104	*Carex scoparia var. scoparia*	Graminoid	Native	General wet acidic	Unassisted	Inferred from con-geners
105	*Carex seorsa*	Graminoid	Native	Black Bottom	Unassisted	Inferred from con-geners
106	*Carex squarrosa*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
107	*Carex stipata*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
108	*Carex striatula*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
109	*Carex tenera var. tenera*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
110	*Carex tribuloides*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
111	*Carex typhina*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
112	*Carex willdenowii*	Graminoid	Native	Lowland Acid Dry Forest	Unassisted	Inferred from con-geners
113	*Carpinus caroliniana*	Tree	Native	General bottomland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
114	*Carya alba*	Tree	Native	General forest	Vertebrate	Minor et al 2009
115	*Carya aquatica*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
116	*Carya carolinae-septentrionalis*	Tree	Native	Lowland Calc Dry Forest	Vertebrate	Minor et al 2009
117	*Carya cordiformis*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
118	*Carya glabra*	Tree	Native	General forest	Vertebrate	Minor et al 2009
119	*Carya laciniosa*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
120	*Carya ovalis*	Tree	Native	General forest	Vertebrate	Minor et al 2009
121	*Carya ovata*	Tree	Native	General forest	Vertebrate	Minor et al 2009
122	*Carya pallida*	Tree	Native	Lowland Acid Dry Forest	Vertebrate	Minor et al 2009
123	*Celastrus orbiculatus*	Vine	Exotic	No natural habitat	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
124	*Celtis laevigata*	Tree	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
125	*Cephalanthus occidentalis*	Shrub	Native	General wet acidic	Water	Schneider and Shartiz 1988
126	*Cerastium fontanum*	Forb	Exotic	No natural habitat	Unknown	
127	*Cercis canadensis*	Tree	Native	Gen Woodland	Wind	Minor et al 2009; Wilson et al 1990
128	*Chaerophyllum procumbens var. procumbens*	Forb	Native	General bottomland	Unassisted	Minor et al 2009; Romermann et al 2005
129	*Chamaecrista sp.*	Forb	Native	Ruderal	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
130	*Chamaelirium luteum*	Forb	Native	Lowland Mesic Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
131	*Chasmanthium [laxum + sessiliflorum]*	Graminoid	Native	General bottomland	Unknown	
132	*Chasmanthium latifolium*	Graminoid	Native	General bottomland	Unknown	
133	*Chelone glabra*	Forb	Native	General wet acidic	Wind	Flinn et al 2010
134	*Chenopodium album*	Forb	Native	Ruderal	Unassisted	Minor et al 2009
135	*Chimaphila maculata*	Subshrub	Native	Lowland Acid Dry Forest	Unknown	
136	*Chionanthus virginicus*	Shrub	Native	Gen Woodland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
137	*Chrysogonum virginianum*	Forb	Native	Lowland Mesic Forest	Unknown	
138	*Cicuta maculata*	Forb	Native	Aquatic	Unknown	
139	*Cinna arundinacea*	Graminoid	Native	General bottomland	Wind	Montgomery 1977
140	*Circaea canadensis*	Forb	Native	Lowland Mesic Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
141	*Clematis terniflora*	Vine	Exotic	No natural habitat	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
142	*Clematis viorna*	Vine	Native	General forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
143	*Clematis virginiana*	Vine	Native	General forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
144	*Clitoria mariana*	Vine	Native	Gen Woodland	Unknown	
145	*Collinsonia canadensis*	Forb	Native	Rich Cove	Unknown	
146	*Collinsonia tuberosa*	Forb	Native	Lowland Mesic Forest	Unknown	
147	*Commelina communis*	Forb	Exotic	No natural habitat	Unassisted	Minor et al 2009; Ohtsuka and Ohsawa 1994
148	*Commelina virginica*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
149	*Conoclinium coelestinum*	Forb	Native	Ruderal	Unknown	
150	*Conyza canadensis*	Forb	Native	Ruderal	Unknown	
151	*Coreopsis auriculata*	Forb	Native	Lowland Mesic	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
				Forest		
152	*Cornus amomum*	Shrub	Native	General bottomland	Vertebrate	Stiles 1980
153	*Cornus florida*	Tree	Native	General forest	Vertebrate	Minor et al 2009; Czarnecka 2005
154	*Cornus foemina*	Shrub	Native	General bottomland	Vertebrate	Stiles 1980
155	*Corydalis flavula*	Forb	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
156	*Corylus americana*	Shrub	Native	General forest	Unassisted	Minor et al 2009; Beattie and Culver 1981
157	*Crataegus [flabellata group]*	Shrub	Native	General bottomland	Vertebrate	Stiles 1980
158	*Crataegus marshallii*	Shrub	Native	General bottomland	Vertebrate	Stiles 1980
159	*Crataegus phaenopyrum*	Shrub	Native	General forest	Vertebrate	Stiles 1980
160	*Crataegus viridis*	Shrub	Native	General bottomland	Vertebrate	Stiles 1980
161	*Cryptotaenia canadensis*	Forb	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Williams 1994
162	*Cynoglossum virginianum var. virginianum*	Forb	Native	Lowland Mesic Forest	Unknown	
163	*Cyrilla racemiflora*	Shrub	Native	CP Pocosin	Unknown	
164	*Danthonia spicata*	Graminoid	Native	Gen Woodland	Vertebrate	Minor et al 2009; McIntyre et al. 1995
165	*Decumaria barbara*				Unknown	
166	*Dendrolycopodium obscurum*	Forb	Native	Lowland Mesic Forest	Unknown	
167	*Desmodium [glabellum + perplexum]*	Forb	Native	General forest	Unknown	
168	*Desmodium nudiflorum*	Forb	Native	General forest	Unknown	
169	*Desmodium paniculatum var. paniculatum*	Forb	Native	Gen Woodland	Vertebrate	Minor et al 2009; Matlack 1994*
170	*Desmodium rotundifolium*	Forb	Native	Gen Woodland	Unknown	
171	*Dichanthelium acuminatum var. acuminatum*	Graminoid	Native	Gen Woodland	Unassisted	Inferred from con-geners
172	*Dichanthelium boscii*	Graminoid	Native	General forest	Unassisted	Inferred from con-geners
173	*Dichanthelium clandestinum*	Graminoid	Native	Gen Woodland	Unassisted	Inferred from con-geners
174	*Dichanthelium commutatum*	Graminoid	Native	General forest	Unassisted	Kirkman et al 2004

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
175	*Dichanthelium dichotomum*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
176	*Dichanthelium erectifolium*	Graminoid	Native	CP Pond	Unassisted	Inferred from con-geners
177	*Dichanthelium laxiflorum*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Inferred from con-geners
178	*Dichanthelium polyanthes*	Graminoid	Native	Gen Woodland	Unassisted	Inferred from con-geners
179	*Dichanthelium yadkinense*	Graminoid	Native	General bottomland	Unassisted	Inferred from con-geners
180	*Dichondra carolinensis*	Forb	Native	Ruderal	Unknown	
181	*Dicliptera brachiata*	Forb	Native	General bottomland	Unknown	
182	*Dioscorea [quaternata + villosa]*	Vine	Native	Lowland Mesic Forest	Unknown	
183	*Dioscorea polystachya*	Vine	Exotic	No natural habitat	Unassisted	Minor et al 2009; Harrison et al. 2001
184	*Diospyros virginiana*	Tree	Native	General forest	Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
185	*Diphasiastrum digitatum*	Forb	Native	Lowland Acid Dry Forest	Unknown	
186	*Diphasiastrum tristachyum*	Forb	Native	Lowland Acid Dry Forest	Unknown	
187	*Dryopteris cristata*	Forb	Mixed	Mont Bog	Wind	Flinn et al 2010
188	*Eclipta prostrata*	Forb	Native	Ruderal	Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
189	*Elaeagnus umbellata*	Shrub	Exotic	No natural habitat	Vertebrate	Minor et al 2009; Swearington et al. 2002
190	*Elephantopus carolinianus*	Forb	Native	Lowland Acid Dry Forest	Wind	Kirkman et al 2004
191	*Elephantopus tomentosus*	Forb	Native	Lowland Acid Dry Forest	Wind	Kirkman et al 2004
192	*Elymus [glabriflorus + macgregorii + virginicus]*	Graminoid	Native	General bottomland	Unknown	
193	*Elymus canadensis var. canadensis*	Graminoid	Native	General bottomland	Unassisted	Minor et al 2009; Bockelmann et al 2003
194	*Elymus hystrix*	Graminoid	Native	General bottomland	Unknown	
195	*Elymus repens*	Graminoid	Exotic	No natural habitat	Unknown	
196	*Elymus riparius*	Graminoid	Native	General bottomland	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
197	*Elymus villosus*	Graminoid	Native	General bottomland	Unassisted	Minor et al 2009; Bockelmann et al 2003
198	*Endodeca serpentaria*	Forb	Native	Lowland Acid Dry Forest	Unassisted	Kirkman et al 2004
199	*Epilobium coloratum*	Forb	Native	Mont Bog	Unknown	
200	*Equisetum arvense*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
201	*Equisetum hyemale ssp. affine*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
202	*Erechtites hieracifolia*	Forb	Native	Ruderal	Wind	based on morphology
203	*Erigeron strigosus var. strigosus*	Forb	Native	Ruderal	Unknown	
204	*Eubotrys racemosa*	Shrub	Native	Black Bottom	Unknown	
205	*Euonymus americanus*	Subshrub	Native	General forest	Vertebrate	Stiles 1980
206	*Euonymus fortunei var. radicans*	Shrub	Exotic	No natural habitat	Vertebrate	Stiles 1980
207	*Eupatorium capillifolium*	Forb	Native	Ruderal	Wind	Flinn et al 2010; Montgomery 1975
208	*Eupatorium compositifolium*	Forb	Native	Dry Pine	Wind	Flinn et al 2010; Montgomery 1976
209	*Eupatorium perfoliatum*	Forb	Native	General wet acidic	Wind	Flinn et al 2010; Montgomery 1977
210	*Eupatorium serotinum*	Forb	Native	Barrier	Wind	Flinn et al 2010; Montgomery 1978
211	*Euphorbia corollata*	Forb	Native	Gen Woodland	Unknown	
212	*Eurybia divaricata*	Forb	Native	Lowland Mesic Forest	Wind	Flinn et al 2010; Britton and Brown 1913
213	*Eutrochium fistulosum*	Forb	Native	General wet acidic	Unknown	
214	*Fagus grandifolia*	Tree	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009;
215	*Fallopia scandens*	Vine	Native	General wet acidic	Unknown	
216	*Festuca subverticillata*	Graminoid	Native	Lowland Mesic Forest	Wind	Minor et al 2009; Cain et al 1998
217	*Fragaria vesca var. americana*	Forb	Native	Ruderal	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
218	*Fragaria virginiana*	Forb	Native	Ruderal	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2009
219	*Frangula caroliniana*	Shrub	Native	Mafic Glade	Unknown	
220	*Fraxinus caroliniana*	Tree	Native	Black Bottom	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
221	*Fraxinus pennsylvanica*	Tree	Native	General bottomland	Wind	Minor et al 2009; Cain et al 1998
222	*Galium aparine*	Forb	Native	Ruderal	Vertebrate	Minor et al 2009; Fischer et al 1996
223	*Galium circaezans*	Forb	Native	Lowland Mesic Forest	Unknown	
224	*Galium latifolium*	Forb	Native	Rich Cove	Unknown	
225	*Galium obtusum*	Forb	Native	General forest	Unknown	
226	*Galium pilosum*	Forb	Native	Lowland Mesic Forest	Unknown	
227	*Galium tinctorium*	Forb	Native	General bottomland	Unknown	
228	*Galium triflorum*	Forb	Native	General forest	Vertebrate	Minor et al 2009; Fischer et al 1996
229	*Gaultheria procumbens*	Forb	Native	Montane Dry Forest	Unknown	
230	*Gelsemium sempervirens*	Vine	Native	General forest	Unknown	
231	*Gentiana saponaria*	Forb	Native	General wet acidic	Unknown	
232	*Geranium maculatum*	Forb	Native	Rich Cove	Unassisted	Minor et al 2009; Matlack 1994
233	*Geum canadense*	Forb	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Thompson 1981
234	*Geum virginianum*	Forb	Native	General bottomland	Unknown	
235	*Glechoma hederacea*	Forb	Exotic	No natural habitat	Unassisted	Minor et al 2009; Hutchings and Price 1999
236	*Gleditsia triacanthos*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009Royal Botanic Gardens Kew Seed Information Database (SID) 2008
237	*Glyceria septentrionalis*	Graminoid	Native	General bottomland	Unknown	
238	*Glyceria striata var. striata*	Graminoid	Native	General wet acidic	Wind; Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
239	*Gonolobus suberosus*	Vine	Native	Lowland Mesic	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
				Forest		
240	*Goodyera pubescens*	Forb	Native	Lowland Acid Dry Forest	Unknown	
241	*Gratiola virginiana*	Forb	Native	General wet acidic	Unknown	
242	*Halesia tetraptera var. tetraptera*	Tree	Native	General bottomland	Wind	based on morphology
243	*Hamamelis virginiana*	Shrub	Native	General forest	Vertebrate; Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
244	*Hedera helix*	Vine	Exotic	No natural habitat	Vertebrate	Minor et al 2009; Swearington et al. 2002
245	*Heliopsis helianthoides*	Forb	Native	Lowland Mesic Forest	Wind	based on morphology
246	*Hexastylis arifolia*	Forb	Native	Lowland Acid Dry Forest	Unassisted	Padgett 2004. Dissertation at ASU.
247	*Hibiscus moscheutos*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
248	*Houstonia caerulea*	Forb	Native	Lowland Acid Dry Forest	Unknown	
249	*Houstonia purpurea*	Forb	Native	Gen Woodland	Unknown	
250	*Humulus japonicus*	Vine	Exotic	No natural habitat	Wind; Water	PA Department of Conservation and Natural Resources 2009
251	*Huperzia lucidula*	Forb	Native	Acid Cove	Unknown	
252	*Hydrangea arborescens*	Shrub	Native	General forest	Unknown	
253	*Hydrocotyle umbellata*	Forb	Native	Ruderal	Water	Flinn et al 2010
254	*Hypericum crux-andreae*	Subshrub	Native	General forest	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
255	*Hypericum densiflorum*	Shrub	Native	Gen Woodland	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
256	*Hypericum hypericoides*	Subshrub	Native	Lowland Acid Dry Forest	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
257	*Hypericum mutilum*	Forb	Native	General wet acidic	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
258	*Hypericum nudiflorum*	Subshrub	Native	General wet acidic	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
259	*Hypericum prolificum*	Subshrub	Native	General forest	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
260	*Hypericum punctatum*	Forb	Native	Ruderal	Wind; Vertebrate; Water	Tisdale et al 1959; Comes et al 1978
261	*Hypoxis hirsuta*	Forb	Native	Gen Woodland	Unknown	
262	*Ilex decidua*	Tree	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
263	*Ilex opaca var. opaca*	Tree	Native	Lowland Mesic Forest	Vertebrate	Stiles 1980
264	*Ilex verticillata*	Tree	Native	General wet acidic	Vertebrate	Stiles 1980
265	*Impatiens capensis*	Forb	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
266	*Impatiens pallida*	Forb	Native	Rich Cove	Unassisted	Minor et al 2009; Cain et al 1998
267	*Ipomoea sp.*	Vine	Exotic	No natural habitat	Wind; Vertebrate	Erwin 2010
268	*Iris sp.*	Forb	Native	Lowland Mesic Forest	Unknown	
269	*Itea virginica*	Shrub	Native	General bottomland	Unknown	
270	*Juglans nigra*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009; Cain et al 1998
271	*Juncus abortivus*	Graminoid	Native	Wet Pine	Unknown	
272	*Juncus acuminatus*	Graminoid	Native	Ruderal	Unknown	
273	*Juncus coriaceus*	Graminoid	Native	General bottomland	Unknown	
274	*Juncus dichotomus*	Graminoid	Native	Ruderal	Unknown	
275	*Juncus effusus*	Graminoid	Native	General wet acidic	Wind; Vertebrate; Water	Flinn et al 2010; Pakeman et al 2002; Neff and Baldwin 2005
276	*Juncus elliottii*	Graminoid	Native	Wet Pine	Unknown	
277	*Juncus tenuis*	Graminoid	Native	Ruderal	Wind	Minor et al 2009; Cain et al. 1998
278	*Juniperus virginiana*	Tree	Native	General forest	Vertebrate	Minor et al 2009; Stiles 1980

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
279	*Justicia americana*	Forb	Native	General bottomland	Unknown	
280	*Justicia ovata var. ovata*	Forb	Native	General bottomland	Unknown	
281	*Kalmia latifolia*	Shrub	Native	Montane Dry Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
282	*Krigia sp.*	Forb	Native	Ruderal	Unknown	
283	*Lactuca sp.*	Forb	Native	Ruderal	Unknown	
284	*Lamium purpureum*	Forb	Native	Ruderal	Unknown	
285	*Laportea canadensis*	Forb	Native	General bottomland	Unassisted	Montgomery 1977
286	*Leersia [oryzoides + virginica]*	Graminoid	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Ridley 1930
287	*Lespedeza cuneata*	Subshrub	Exotic	No natural habitat	Vertebrate	Eddy et al 2003
288	*Leucothoe axillaris*	Shrub	Native	Black Bottom	Unknown	
289	*Ligusticum canadense*	Forb	Native	Montane Dry Forest	Unknown	
290	*Ligustrum sinense*	Shrub	Exotic	No natural habitat	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
291	*Lilium superbum*	Forb	Native	Rich Cove	Unknown	
292	*Lindera benzoin*	Shrub	Native	General bottomland	Vertebrate	Minor et al 2009; Matlack 1994
293	*Linum striatum*	Forb	Native	General wet acidic	Unknown	
294	*Liquidambar styraciflua*	Tree	Native	General bottomland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
295	*Liriodendron tulipifera*	Tree	Native	Lowland Mesic Forest	Wind; Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
296	*Lobelia cardinalis*	Forb	Native	General bottomland	Unassisted	Inferred from con-geners
297	*Lobelia inflata*	Forb	Native	Ruderal	Unassisted	Minor et al 2009; Simons and Johnston 2000
298	*Lobelia puberula*	Forb	Native	Ruderal	Unassisted	Minor et al 2009; Simons and Johnston 2000
299	*Lonicera japonica*	Vine	Exotic	No natural habitat	Vertebrate	Minor et al 2009; Sewarington et al 2002
300	*Lonicera sempervirens*	Vine	Native	General forest	Vertebrate	Stiles 1980
301	*Ludwigia alternifolia*	Forb	Native	General wet acidic	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
302	*Ludwigia glandulosa*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
303	*Ludwigia palustris*	Forb	Native	Ruderal	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
304	*Luzula acuminata var. acuminata*	Forb	Native	Lowland Mesic Forest	Unknown	
305	*Luzula echinata*	Graminoid	Native	Lowland Mesic Forest	Unknown	
306	*Lycopus sp.*	Forb	Native	General bottomland	Unknown	
307	*Lysimachia ciliata*	Forb	Native	General bottomland	Water	Andersson et al 2000
308	*Lysimachia nummularia*	Forb	Exotic	No natural habitat	Unassisted	Minor et al 2009; Suzuki et al. 2003
309	*Magnolia macrophylla*	Tree	Native	Rich Cove	Vertebrate	Stiles 1980
310	*Magnolia virginiana var. virginiana*	Tree	Native	CP Pocosin	Vertebrate	Stiles 1980
311	*Maianthemum racemosum ssp. racemosum*	Forb	Native	General forest	Vertebrate	Thompson 1979
312	*Marshallia obovata var. obovata*	Forb	Native	Mafic Glade	Unknown	
313	*Matelea sp.*	Vine	Native	Lowland Mesic Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
314	*Medeola virginiana*	Forb	Native	Lowland Mesic Forest	Unknown	
315	*Melica mutica*	Graminoid	Native	General forest	Unknown	
316	*Melothria pendula*	Vine	Native	General bottomland	Unknown	
317	*Menispermum canadense*	Vine	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
318	*Micranthemum umbrosum*	Forb	Native	General bottomland	Unknown	
319	*Microstegium vimineum*	Graminoid	Exotic	No natural habitat	Wind; Vertebrate; Water	Swearingen 2004
320	*Mikania scandens*	Vine	Native	General bottomland	Unknown	
321	*Mimulus sp.*	Forb	Native	General wet acidic	Unassisted	Montgomery 1977
322	*Mitchella repens*	Forb	Native	General forest	Vertebrate	Stiles 1980
323	*Mollugo verticillata*	Forb	Exotic	No natural habitat	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
324	*Monotropa uniflora*	Forb	Native	Lowland Acid Dry Forest	Unassisted	Montgomery 1977
325	*Morus rubra*	Tree	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Stiles 1980
326	*Muhlenbergia sp*	Graminoid	Native	General bottomland	Unassisted	Minor et al 2009; Kirkman et al. 2004
327	*Murdannia keisak*	Forb	Exotic	No natural habitat	Vertebrate	Dunn and Sharitz 1990
328	*Myosotis sp.*	Forb	Native	General bottomland	Unknown	
329	*Nandina domestica*	Shrub	Exotic	No natural habitat	Vertebrate; Water	Meisenburg and Fox 2002
330	*Nemophila aphylla*	Forb	Native	General bottomland	Unknown	
331	*Nyssa aquatica*	Tree	Native	General bottomland	Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
332	*Nyssa biflora*	Tree	Native	Black Bottom	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
333	*Nyssa sylvatica*	Tree	Native	Lowland Acid Dry Forest	Vertebrate	Minor et al 2009;
334	*Onoclea sensibilis*	Forb	Native	General bottomland	Wind	Flinn et al 2010
335	*Ophioglossum pycnostichum*	Forb	Native	General bottomland	Unknown	
336	*Osmorhiza longistylis*	Forb	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Matlack 1994
337	*Osmunda cinnamomea*	Forb	Native	General wet acidic	Wind	Flinn et al 2010
338	*Ostrya virginiana*	Tree	Native	Lowland Mesic Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
339	*Oxalis sp.*	Forb	Native	NA	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
340	*Oxydendrum arboreum*	Tree	Native	Lowland Acid Dry Forest	Wind	Schwartz et al 2001
341	*Packera aurea*	Forb	Native	General bottomland	Unknown	
342	*Panicum anceps var. rhizomatum*	Graminoid	Native	Dry Pine	Unassisted	Kirkman et al 2004
343	*Parthenocissus quinquefolia*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
344	*Passiflora lutea var. lutea*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
345	*Pedicularis canadensis*	Forb	Native	Gen Woodland	Unknown	
346	*Peltandra virginica*	Forb	Native	Aquatic	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
347	*Penstemon sp.*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
348	*Penthorum sedoides*	Forb	Native	Ruderal	Unassisted	Montgomery 1977
349	*Perilla frutescens*	Forb	Exotic	No natural habitat	Unknown	
350	*Persicaria arifolia*	Vine	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
351	*Persicaria hydropiperoides*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
352	*Persicaria lapathifolia*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
353	*Persicaria punctata*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
354	*Persicaria sagittata*	Forb	Native	General wet acidic	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
355	*Persicaria setacea*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
356	*Persicaria virginiana*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
357	*Phacelia covillei*	Forb	Native	General bottomland	Unknown	
358	*Phryma leptostachya*	Forb	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Holm 1913
359	*Phytolacca americana*	Forb	Native	Ruderal	Vertebrate	Minor et al 2009; Matlack 1994
360	*Pilea pumila*	Forb	Native	General bottomland	Water	Neff and Baldwin 2005
361	*Pinus echinata*	Tree	Native	Lowland Acid Dry Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
362	*Pinus strobus*	Tree	Native	Montane Dry Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
363	*Pinus taeda*	Tree	Native	General bottomland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
364	*Pinus virginiana*	Tree	Native	Montane Dry Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
365	*Piptochaetium avenaceum*	Graminoid	Native	Gen Woodland	Unknown	
366	*Platanthera sp.*	Forb	Native	General bottomland	Wind	Minor et al 2009; Cain et al 1998
367	*Platanus occidentalis*	Tree	Native	General bottomland	Unknown	
368	*Pleopeltis polypodioides*	Forb	Native	General forest	Unknown	
369	*Pluchea camphorata*	Forb	Native	General bottomland	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
370	*Poa [autumnalis + cuspidata]*	Graminoid	Native	General bottomland	Unassisted	
371	*Poa sylvestris*	Graminoid	Native	Lowland Mesic Forest	Unassisted	Minor et al 2009; Cain et al 1998
372	*Poa trivialis*	Graminoid	Exotic	No natural habitat	Unassisted	Minor et al 2009; Cain et al 1998
373	*Podophyllum peltatum*	Forb	Native	Lowland Mesic Forest	Unknown	
374	*Podostemum ceratophyllum*	Forb	Native	General bottomland	Vertebrate	Minor et al 2009; Matlack 1994
375	*Polygonatum biflorum*	Forb	Native	General forest	Wind	Flinn et al 2010
376	*Polypodium virginianum*	Forb	Native	Acid Outcrop	Wind	Minor et al 2009
377	*Polystichum acrostichoides*	Forb	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Matlack 1994
378	*Populus deltoides*	Tree	Native	General bottomland	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
379	*Potentilla [simplex + canadensis]*	Forb	Native	Gen Woodland	Unknown	
380	*Potentilla indica*	Forb	Exotic	No natural habitat	Unknown	
381	*Potentilla norvegica*	Forb	Mixed	Ruderal	Vertebrate	Minor et al 2009
382	*Potentilla simplex*	Forb	Native	Gen Woodland	Unknown	
383	*Prenanthes sp.*	Forb	Native	Lowland Mesic Forest	Unknown	
384	*Prunella vulgaris*	Forb	Native	Ruderal	Vertebrate	Minor et al 2009; Cain et al 1998
385	*Prunus americana*	Tree	Native	General forest	Unknown	
386	*Prunus caroliniana*	Tree	Native	Hammock	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
387	*Prunus serotina*	Tree	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
388	*Pseudognaphalium sp.*	Forb	Native	Gen Woodland	Unknown	
389	*Ptelea trifoliata*	Shrub	Native	Mafic Glade	Unknown	
390	*Ptilimnium capillaceum*	Forb	Native	Ruderal	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
391	*Pycnanthemum pycnanthemoides*	Forb	Native	General forest	Unknown	
392	*Pyrularia pubera*	Shrub	Native	Montane Dry Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
393	*Pyrus communis*	Tree	Exotic	No natural habitat	Unknown	
394	*Quercus alba*	Tree	Native	General forest	Vertebrate	Minor et al 2009
395	*Quercus falcata*	Tree	Native	Lowland Acid Dry Forest	Vertebrate	Minor et al 2009
396	*Quercus laurifolia*	Tree	Native	Black Bottom	Vertebrate	Minor et al 2009
397	*Quercus lyrata*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
398	*Quercus michauxii*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
399	*Quercus muehlenbergii*	Tree	Native	Calc Glade	Vertebrate	Minor et al 2009
400	*Quercus nigra*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
401	*Quercus pagoda*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
402	*Quercus phellos*	Tree	Native	General bottomland	Vertebrate	Minor et al 2009
403	*Quercus rubra*	Tree	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009
404	*Quercus shumardii var. shumardii*	Tree	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009
405	*Quercus stellata*	Tree	Native	Lowland Acid Dry Forest	Vertebrate	Minor et al 2009
406	*Quercus velutina*	Tree	Native	Lowland Acid Dry Forest	Vertebrate	Minor et al 2009
407	*Ranunculus abortivus*	Forb	Native	General bottomland	Unassisted	Minor et al 2009; Matlack 1994
408	*Ranunculus arvensis*	Forb	Exotic	No natural habitat	Unknown	
409	*Ranunculus recurvatus*	Forb	Native	General bottomland	Vertebrate	Montgomery 1977
410	*Ranunculus repens*	Forb	Native	General bottomland	Unknown	
411	*Rhododendron [periclymenoides+arborescens+viscosum+calendulaceum]*	Shrub	Native	Lowland Mesic Forest	Unknown	
412	*Robinia pseudoacacia*	Tree	Native	Montane Dry Forest	Vertebrate	Minor et al 2009; Zalba and Villamil 2002
413	*Rosa sp.*	Subshrub	NA	NA	Vertebrate	Minor et al 2009
414	*Rubus sp.*	Subshrub	Native	NA	Vertebrate	Minor et al 2009
415	*Rudbeckia laciniata*	Forb	Native	General bottomland	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
416	*Ruellia caroliniensis*	Forb	Native	Lowland Acid Dry Forest	Unassisted	Kirkman et al 2004
417	*Rumex sp.*	Forb	Exotic	No natural habitat	Wind; Vertebrate; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
418	*Sagittaria australis*	Forb	Native	Aquatic	Unknown	
419	*Salix nigra*	Tree	Native	General bottomland	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
420	*Salvia lyrata*	Forb	Native	Ruderal	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
421	*Sambucus canadensis*	Shrub	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
422	*Samolus parviflorus*	Forb	Native	General wet acidic	Unknown	
423	*Sanguinaria canadensis*	Forb	Native	Lowland Mesic Forest	Vertebrate	Minor et al 2009; Matlack 1994
424	*Sanicula canadensis*	Forb	Native	Lowland Mesic Forest	Vertebrate	Montgomery 1977
425	*Sanicula smallii*	Forb	Native	Lowland Mesic Forest	Vertebrate	Montgomery 1977
426	*Sassafras albidum*	Tree	Native	Gen Woodland	Vertebrate	Minor et al 2009; Stiles 1980
427	*Saururus cernuus*	Forb	Native	General bottomland	Unknown	
428	*Sceptridium [dissectum+biternatum]*	Forb	Native	General bottomland	Wind	infered from morphology
429	*Schizachyrium scoparium*	Graminoid	Native	Gen Woodland	Unknown	
430	*Scirpus atrovirens*	Graminoid	Native	General wet acidic	Water	Flinn et al 2010; Aubin et al 2007
431	*Scirpus cyperinus*	Graminoid	Native	General wet acidic	Unknown	
432	*Scleria oligantha*	Graminoid	Native	Gen Woodland	Unknown	
433	*Scutellaria elliptica*	Forb	Native	Lowland Acid Dry Forest	Unknown	
434	*Scutellaria integrifolia*	Forb	Native	General wet acidic	Unknown	
435	*Scutellaria lateriflora*	Forb	Native	General bottomland	Unassisted; Water	Minor et al 2009; Kirkman et al. 2004
436	*Scutellaria nervosa*	Forb	Native	General bottomland	Unknown	
437	*Scutellaria serrata*	Forb	Native	Rich Cove	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
438	*Sedum ternatum*	Forb	Native	General bottomland	Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
439	*Sideroxylon lycioides*	Shrub	Native	Lowland Mesic Forest	Unknown	
440	*Silene stellata*	Forb	Native	Lowland Mesic Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
441	*Sisyrinchium sp.*	Forb	Native	Gen Woodland	Unknown	
442	*Sium suave*	Forb	Native	General bottomland	Water	Montgomery 1977
443	*Smallanthus uvedalius*	Forb	Native	General bottomland	Unknown	
444	*Smilax [rotundifolia + walterii]*	Vine	Native	General forest	Vertebrate	Minor et al 2009; Schneider and Sharitz 1988
445	*Smilax bona-nox*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988
446	*Smilax glauca*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988
447	*Smilax herbacea*	Vine	Native	Rich Cove	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988
448	*Smilax hispida*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988
449	*Smilax laurifolia*	Vine	Native	Black Bottom	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988
450	*Smilax pulverulenta*	Vine	Native	Lowland Mesic Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Shcneider and Shartiz 1988

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
451	*Smilax smallii*	Vine	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
452	*Solanum carolinense var. carolinense*	Forb	Native	Ruderal	Unknown	
453	*Solidago altissima*	Forb	Native	Ruderal	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
454	*Solidago arguta*	Forb	Native	Gen Woodland	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
455	*Solidago caesia*	Forb	Native	Lowland Mesic Forest	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
456	*Solidago curtisii*	Forb	Native	Rich Cove	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
457	*Solidago gigantea*	Forb	Native	NA	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
458	*Solidago rugosa*	Forb	Native	Ruderal	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
459	*Solidago sp.*	Forb	Native	NA	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
460	*Sonchus asper*	Forb	Exotic	No natural habitat	Unknown	
461	*Sorghastrum sp.*	Forb	Native	Gen Woodland	Unknown	
462	*Sphenopholis obtusata*	Graminoid	Native	General forest	Unknown	
463	*Sporobolus clandestinus*	Graminoid	Native	Gen Woodland	Unknown	
464	*Stachys cordata*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
465	*Stachys latidens*	Forb	Native	Rich Cove	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
466	*Staphylea trifolia*	Shrub	Native	General bottomland	Wind; Vertebrate	Minor et al 2009; Garwood and Horvitz 1985; Willson et al 1990
467	*Stellaria media*	Forb	Exotic	No natural habitat	Unassisted	Minor et al 2009; Harvey 2000
468	*Stellaria pubera*	Forb	Native	Rich Cove	Unassisted	Minor et al 2009; Harvey 2000
469	*Styrax americanus var. americanus*	Tree	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
470	*Symphoricarpos orbiculatus*	Shrub	Native	Gen Woodland	Wind	Minor et al 2009
471	*Symphyotrichum divaricatum*	Forb	Mixed	Ruderal	Wind	Minor et al 2009

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
472	*Symphyotrichum pilosum*	Forb	Native	Ruderal	Wind	Minor et al 2009
473	*Symphyotrichum puniceum*	Forb	Native	General wet acidic	Wind	Minor et al 2009
474	*Symphyotrichum racemosum var. racemosum*	Forb	Native	General bottomland	Wind	Minor et al 2009
475	*Symphyotricum [lateriflorum + lanceolatum]*	Forb	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
476	*Symplocos tinctoria*	Shrub	Native	General forest	Unknown	
477	*Taxodium distichum*	Tree	Native	General bottomland	Water	Schneider and Sharitz 1988
478	*Tephrosia sp.*	Forb	Native	Gen Woodland	Unknown	
479	*Teucrium canadense*	Forb	Native	General wet acidic	Unknown	Minor et al 2009
480	*Thalictrum revolutum*	Forb	Native	Mafic Glade	Unassisted	infer from morphology
481	*Thaspium trifoliatum*	Forb	Native	Rich Cove	Unknown	
482	*Thelypteris noveboracensis*	Forb	Native	Lowland Mesic Forest	Wind	Flinn et al 2010
483	*Tiarella cordifolia*	Forb	Native	Rich Cove	Unassisted	Flinn et al 2010; Montgomery 1977
484	*Tiarella wherryi*	Forb	Native	Lowland Mesic Forest	Unassisted	Flinn et al 2010; Montgomery 1977
485	*Tilia americana*	Tree	Native	Lowland Mesic Forest	Wind	Flinn et al 2010
486	*Tipularia discolor*	Forb	Native	Lowland Acid Dry Forest	Unknown	
487	*Toxicodendron radicans*	Vine	Native	General bottomland	Vertebrate	Minor et al 2009; Cain et al 1998
488	*Trachelospermum difforme*	Vine	Native	Lowland Mesic Forest	Unknown	
489	*Triadenum walteri*	Forb	Native	General bottomland	Unassisted	Flinn et al 2010; Britton and Brown 1913
490	*Trillium catesbaei*	Forb	Native	Lowland Mesic Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
491	*Trillium cuneatum*	Forb	Native	Rich Cove	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
492	*Trillium sulcatum*	Forb	Native	Rich Cove	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
493	*Triodanis perfoliata*	Forb	Native	Ruderal	Unknown	

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
494	*Tripsacum dactyloides*	Graminoid	Native	General bottomland	Unknown	
495	*Ulmus alata*	Tree	Native	Gen Woodland	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Young and Young 1992
496	*Ulmus [americana + rubra]*	Tree	Native	General bottomland	Wind; Water	Royal Botanic Gardens Kew Seed Information Database (SID) 2008; Young and Young 1992
497	*Uvularia perfoliata*	Forb	Native	Lowland Mesic Forest	Unassisted	Thompson 1979
498	*Uvularia sessilifolia*	Forb	Native	General bottomland	Unassisted	Thompson 1979
499	*Vaccinium arboreum*	Shrub	Native	Gen Woodland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
500	*Vaccinium elliottii*	Shrub	Native	Black Bottom	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
501	*Vaccinium fuscatum*	Shrub	Native	General wet acidic	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
502	*Vaccinium pallidum*	Shrub	Native	Montane Dry Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
503	*Vaccinium stamineum*	Shrub	Native	Gen Woodland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
504	*Valerianella radiata*	Forb	Native	Ruderal	Unknown	
505	*Verbesina alternifolia*	Forb	Native	General bottomland	Wind: Vertebrate	Minor et al 2009; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
506	*Verbesina occidentalis*	Forb	Native	Lowland Mesic Forest	Wind: Vertebrate	Minor et al 2009; Royal Botanic Gardens Kew Seed Information Database (SID) 2008
507	*Vernonia sp.*	Forb	Native	Ruderal	Wind	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
508	*Veronica sp.*	Forb	Exotic	No natural habitat	Wind; Vertebrate	Flinn et al 2010; Minor et al 2009
509	*Viburnum acerifolium*	Shrub	Native	Lowland Mesic Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
510	*Viburnum [dentatum + rafinesquianum]*	Shrub	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008

	Taxon name	Growth Habit	Nativity	Habitat	Dispersal mode	Dispersal mode references
511	*Viburnum nudum*	Shrub	Native	CP Pocosin	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
512	*Viburnum prunifolium*	Shrub	Native	General bottomland	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
513	*Viburnum rufidulum*	Shrub	Native	Lowland Calc Dry Forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
514	*Vinca minor*	Vine	Exotic	No natural habitat	Unassisted	Sonday 2010
515	*Viola bicolor*	Forb	Native	Ruderal	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
516	*Viola palmata*	Forb	Native	General bottomland	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
517	*Viola pubescens*	Forb	Native	Lowland Mesic Forest	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
518	*Viola sororia*	Forb	Native	General forest	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
519	*Viola sp.*	Forb	Native	NA	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
520	*Viola striata*	Forb	Native	Lowland Mesic Forest	Unassisted	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
521	*Vitis [cinerea + vulpina]*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
522	*Vitis aestivalis var. aestivalis*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
523	*Vitis labrusca*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
524	*Vitis riparia*	Vine	Native	NA	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
525	*Vitis rotundifolia*	Vine	Native	General forest	Vertebrate	Royal Botanic Gardens Kew Seed Information Database (SID) 2008
526	*Woodwardia areolata*	Forb	Native	General wet acidic	Wind	infered from morphology
527	*Xanthorhiza simplicissima*	Forb	Native	General bottomland	Unknown	
528	*Yucca filamentosa*	Forb	Native	Granite Glade	Unassisted	Massey and Hamrick 1998
529	*Zephyranthes atamasca*	Forb	Native	General bottomland	Unknown	
530	*Zizia aurea*	Forb	Native	Rich Cove	Unassisted	Farnsworth 2003

Appendix 9

Forward selected environmental variables for variation partitioning analyses (Chapter 4).

Table 1. Forward selected environmental variables for all plant species and all plots, across all 5 river basins.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	*P*-value
1	Ca/Mg (ppm)	0.063	0.063	0.058	12.187	0.001
2	Clay (A horizon)	0.040	0.103	0.093	7.949	0.001
3	Levee (geomorphic position)	0.030	0.134	0.119	6.240	0.001
4	Fe (ppm)	0.025	0.159	0.140	5.263	0.001
5	Distance to river mouth	0.018	0.177	0.154	3.949	0.001
6	Floodplain width	0.015	0.192	0.165	3.313	0.001
7	S	0.015	0.207	0.175	3.272	0.001
8	Al (ppm)	0.015	0.222	0.186	3.273	0.001
9	Cu (ppm)	0.014	0.236	0.196	3.157	0.001
10	Mean annual precipitation	0.010	0.246	0.201	2.165	0.001
11	Silt (A horizon)	0.009	0.255	0.207	2.146	0.001
12	N	0.010	0.265	0.213	2.392	0.001
13	K (ppm)	0.009	0.274	0.218	1.974	0.001
14	Flat (geomorphic position)	0.008	0.282	0.222	1.947	0.001
15	Mean annual temperature	0.008	0.291	0.226	1.924	0.001
16	Upstream area drained	0.008	0.298	0.230	1.794	0.001
17	Mn (ppm)	0.007	0.305	0.233	1.717	0.002
18	Stream order	0.007	0.313	0.237	1.727	0.001
19	Mg (ppm)	0.007	0.320	0.240	1.688	0.001
20	Cation exchange capacity	0.008	0.327	0.244	1.832	0.001
21	Small stream (geomorphic position)	0.007	0.335	0.247	1.725	0.002
22	Backswamp (geomorphic position)	0.007	0.341	0.250	1.610	0.003
23	Bulk density	0.006	0.347	0.252	1.462	0.009
24	P	0.006	0.353	0.254	1.446	0.005
25	Organic matter	0.006	0.359	0.257	1.494	0.006
26	Ca (ppm)	0.006	0.365	0.259	1.430	0.015
27	Zn (ppm)	0.005	0.371	0.260	1.332	0.033

Table 2. Forward selected variables for all species in the Catawba river basin.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	*P*-value
1	Floodplain width	0.120	0.120	0.068	2.316	0.001
2	Cu (ppm)	0.096	0.216	0.118	1.958	0.002
3	Small stream (geomorphic position)	0.074	0.290	0.148	1.564	0.015
4	Mean annual temperature	0.073	0.363	0.181	1.599	0.018
5	P	0.068	0.431	0.212	1.559	0.030
6	Ca/Mg (ppm)	0.067	0.498	0.248	1.613	0.016

Table 3. Forward selected variables for all species in the Yadkin river basin.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	P-value
1	Ca/Mg (ppm)	0.103	0.103	0.084	5.390	0.001
2	Clay (A horizon)	0.058	0.161	0.124	3.172	0.001
3	Fe (ppm)	0.050	0.211	0.158	2.849	0.001
4	Levee (geomorphic position)	0.040	0.251	0.183	2.357	0.001
5	Floodplain width	0.034	0.285	0.202	2.038	0.001
6	Mean annual precipitation	0.034	0.319	0.222	2.119	0.001
7	Small stream (geomorphic position)	0.027	0.346	0.234	1.674	0.005
8	Backswamp (geomorphic position)	0.026	0.372	0.246	1.668	0.004
9	Organic matter	0.025	0.397	0.258	1.636	0.005
10	P	0.025	0.422	0.270	1.629	0.005
11	pH	0.023	0.445	0.280	1.517	0.011
12	Al (ppm)	0.022	0.467	0.289	1.484	0.017
13	Bulk density	0.020	0.487	0.297	1.386	0.038
14	Stream order	0.020	0.507	0.304	1.372	0.046
15	Upstream area drained	0.024	0.531	0.318	1.682	0.005

Table 4. Forward selected variables for all species in the Cape Fear river basin.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	P-value
1	Ca/Mg (ppm)	0.108	0.108	0.092	6.694	0.001
2	Floodplain width	0.053	0.162	0.131	3.442	0.001
3	Distance to river mouth	0.040	0.202	0.156	2.631	0.001
4	Cu (ppm)	0.035	0.237	0.178	2.407	0.001
5	N	0.033	0.270	0.198	2.279	0.001
6	S	0.026	0.296	0.211	1.845	0.002
7	Levee (geomorphic position)	0.024	0.320	0.223	1.743	0.002
8	Silt (A horizon)	0.024	0.344	0.234	1.765	0.002
9	Mean annual temperature	0.025	0.369	0.248	1.859	0.001
10	Stream order	0.020	0.389	0.256	1.521	0.008
11	Small stream (geomorphic position)	0.020	0.409	0.265	1.555	0.011
12	B (ppm)	0.019	0.428	0.272	1.427	0.038
13	basesatA	0.019	0.447	0.280	1.476	0.019
14	Fe (ppm)	0.019	0.466	0.288	1.514	0.012
15	Mean annual precipitation	0.018	0.484	0.295	1.411	0.033

Table 5. Forward selected environmental variables in the Neuse river basin.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	P-value
1	Cu (ppm)	0.110	0.110	0.078	3.450	0.001
2	Backswamp (geomorphic position)	0.093	0.203	0.144	3.156	0.001
3	Small stream (geomorphic position)	0.079	0.282	0.199	2.868	0.001
4	Floodplain width	0.052	0.334	0.227	1.933	0.003
5	Ca (ppm)	0.046	0.380	0.251	1.797	0.004
6	Distance to river mouth	0.043	0.423	0.273	1.728	0.008
7	N	0.039	0.462	0.291	1.581	0.017
8	Upstream area drained	0.036	0.498	0.307	1.520	0.028
9	Flat (geomorphic position)	0.035	0.534	0.324	1.518	0.037
10	Levee (geomorphic position)	0.035	0.569	0.342	1.551	0.033

| 11 | Mg (ppm) | | | 0.034 | 0.602 | | 0.359 | 1.517 | 0.038 |

Table 6. Forward selected environmental variables in the Tar river basin.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	*P*-value
1	Flat (geomorphic position)	0.119	0.119	0.084	3.389	0.001
2	Levee (geomorphic position)	0.091	0.210	0.144	2.755	0.001
3	Upstream area drained	0.066	0.276	0.181	2.091	0.001
4	Backswamp (geomorphic position)	0.064	0.340	0.219	2.121	0.002
5	Distance to river mouth	0.054	0.394	0.249	1.881	0.004
6	Small stream (geomorphic position)	0.040	0.434	0.264	1.404	0.049

Table 7. Forward selected environmental variables for wind-dispersed species, across all river basins.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	*P*-value
1	Levee (geomorphic position)	0.078	0.078	0.073	15.151	0.001
2	Clay (A horizon)	0.045	0.123	0.113	9.207	0.001
3	Ca/Mg (ppm)	0.039	0.162	0.148	8.302	0.001
4	Fe (ppm)	0.027	0.189	0.171	5.993	0.001
5	Distance to river mouth	0.025	0.214	0.192	5.530	0.001
6	Cu (ppm)	0.023	0.237	0.211	5.334	0.001
7	N	0.020	0.257	0.228	4.734	0.001
8	Floodplain width	0.014	0.272	0.238	3.383	0.001
9	S	0.014	0.286	0.248	3.397	0.001
10	Silt (A horizon)	0.011	0.296	0.255	2.583	0.001
11	Mean annual precipitation	0.011	0.307	0.262	2.613	0.001
12	Flat (geomorphic position)	0.010	0.317	0.268	2.447	0.003
13	K (ppm)	0.009	0.326	0.274	2.319	0.002
14	Small stream (geomorphic position)	0.009	0.335	0.280	2.254	0.005
15	basesatA	0.009	0.344	0.285	2.178	0.003
16	P	0.008	0.352	0.289	1.967	0.007
17	Bulk density	0.007	0.359	0.292	1.807	0.026
18	Mean annual temperature	0.006	0.365	0.295	1.657	0.032
19	Upstream area drained	0.007	0.372	0.298	1.728	0.024
20	Al (ppm)	0.006	0.378	0.301	1.667	0.030
21	Organic matter	0.006	0.385	0.304	1.647	0.034
22	Mn (ppm)	0.006	0.391	0.307	1.693	0.041
23	Mg (ppm)	0.006	0.398	0.310	1.704	0.034

Table 8. Forward selected environmental variables for vertebrate-dispersed species, across all river basins.

Order	Variable	R^2	Cumulative R^2	Adj. Cumulative R^2	F	*P*-value
1	Ca/Mg (ppm)	0.080	0.080	0.075	15.647	0.001
2	Clay (A horizon)	0.047	0.127	0.117	9.567	0.001
3	Fe (ppm)	0.026	0.153	0.139	5.494	0.001
4	Levee (geomorphic position)	0.022	0.175	0.157	4.803	0.001
5	Floodplain width	0.020	0.195	0.172	4.407	0.001
6	Distance to river mouth	0.016	0.212	0.185	3.644	0.001
7	Al (ppm)	0.019	0.231	0.200	4.408	0.001
8	S	0.013	0.244	0.209	2.974	0.001
9	Cu (ppm)	0.010	0.254	0.215	2.255	0.001

Order	Variable	R²	Cumulative R²	Adj. Cumulative R²	F	P-value
10	N	0.011	0.265	0.222	2.656	0.001
11	Mean annual precipitation	0.009	0.275	0.228	2.207	0.001
12	Silt (A horizon)	0.009	0.284	0.233	2.198	0.001
13	basesatA	0.008	0.292	0.237	1.918	0.001
14	Zn (ppm)	0.007	0.300	0.241	1.742	0.005
15	Flat (geomorphic position)	0.007	0.307	0.244	1.724	0.005
16	Mean annual temperature	0.007	0.314	0.247	1.661	0.017
17	Stream order	0.008	0.322	0.251	1.915	0.001
18	Small stream (geomorphic position)	0.007	0.329	0.255	1.771	0.002
19	Upstream area drained	0.007	0.336	0.258	1.734	0.005
20	P	0.007	0.343	0.261	1.670	0.012
21	Na (ppm)	0.006	0.349	0.264	1.554	0.025
22	Cation exchange capacity	0.006	0.355	0.266	1.521	0.020
23	Mg (ppm)	0.006	0.361	0.269	1.537	0.032
24	Ca (ppm)	0.007	0.368	0.272	1.697	0.008
25	pH	0.006	0.374	0.274	1.498	0.034

Table 9. Forward selected environmental variables for water dispersal species, across all river basins.

Order	Variable	R²	Cumulative R²	Adj. Cumulative R²	F	P-value
1	Ca/Mg (ppm)	0.083	0.083	0.078	16.302	0.001
2	Levee (geomorphic position)	0.036	0.119	0.110	7.389	0.001
3	S	0.035	0.154	0.140	7.358	0.001
4	Mn (ppm)	0.026	0.180	0.162	5.611	0.001
5	Clay (A horizon)	0.019	0.200	0.177	4.260	0.001
6	Cu (ppm)	0.015	0.215	0.188	3.456	0.001
7	Backswamp (geomorphic position)	0.014	0.229	0.198	3.077	0.001
8	Al (ppm)	0.013	0.241	0.206	2.874	0.001
9	Distance to river mouth	0.016	0.257	0.218	3.680	0.001
10	Upstream area drained	0.013	0.270	0.227	2.931	0.001
11	Mean annual temperature	0.009	0.278	0.232	2.025	0.016
12	Flat (geomorphic position)	0.009	0.288	0.237	2.244	0.011
13	Silt (A horizon)	0.009	0.297	0.243	2.236	0.007
14	P	0.008	0.306	0.247	2.001	0.019

Table 10. Forward selected environmental variables for unassissted dispersal species, across all river basins.

Order	Variable	R²	Cumulative R²	Adj. Cumulative R²	F	P-value
1	Levee (geomorphic position)	0.041	0.041	0.035	7.608	0.001
2	Backswamp (geomorphic position)	0.034	0.075	0.065	6.674	0.001
3	Ca/Mg (ppm)	0.020	0.095	0.080	3.899	0.001
4	Clay (A horizon)	0.018	0.113	0.093	3.645	0.001
5	S	0.014	0.127	0.102	2.820	0.001
6	Mn (ppm)	0.015	0.142	0.113	3.033	0.001
7	SandA	0.013	0.155	0.121	2.637	0.001
8	Mean annual precipitation	0.013	0.168	0.129	2.673	0.001
9	Mean annual temperature	0.013	0.180	0.137	2.630	0.001
10	K (ppm)	0.011	0.191	0.144	2.361	0.001
11	Stream order	0.011	0.202	0.151	2.343	0.001
12	Fe (ppm)	0.009	0.212	0.156	1.987	0.002
13	Organic matter	0.009	0.221	0.160	1.938	0.003

14	Zn (ppm)	0.009	0.230	0.165	1.948	0.006
15	Floodplain width	0.008	0.237	0.168	1.698	0.014
16	Upstream area drained	0.008	0.245	0.172	1.666	0.02
17	Al (ppm)	0.007	0.252	0.175	1.555	0.034

References

Andersson, E., Nilsson, C. and M.E. Johansson. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. Journal of Biogeography 27: 1095-1106.

Aubin, I., Gachet, S., Messier, C. and A. Bouchard. 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience 14: 259-271.

Beattie, A. J., and D. C. Culver. 1981. The Guild of Myrmecochores in the Herbaceous Flora of West Virginia Forests. Ecology 62:107–115.

Bockelmann, A. -C., T. B. H. Reusch, R. Bijlsma, and J. P. Bakker. 2003. Habitat differentiation vs. isolationby-distance: the genetic population structure of *Elymus athericus* in European salt marshes. Molecular Ecology 12:505–515.

Boyce, Richard L. 2009. Invasive shrubs and forest tree regeneration. Journal of Sustainable Forestry. 28(1-2): 152-217.

Britton, N.L., and A. Brown. 1913. *An Illustrated Flora of the Northern United States, Canada, and the British Possessions.* Charles Scriber's Sons, New York, NY.

Cain, M. L., H. Damman, and A. Muir. 1998. Seed dispersal and the Holocene migration of woodland herbs. Ecological Monographs 68:325–247.

Comes, R. D., Bruns, V. F., Kelley, A.D. 1978. Longevity of certain weed and crop seeds in fresh water. Weed Science. 26(4): 336-344.

Czarnecka, J. 2005. Seed dispersal effectiveness in three adjacent plant communities: xerothermic grassland, brushwood and woodland. Annales Botanici. Fennici 42:161–171.

Dunn, C.P. and R.R. Sharitz. 1990. The history of Murdannia keisak in the Southeastern United States. Castanea 55: 122-129.

Eddy, T.A., Davidson, J., Obermeyer, B. 2003. Invasion dynamics and biological control prospects for sericea lespedeza in Kansas. Great Plains Research. 13: 217-230.

Erwin, A. with Sonday, R. and R.J. Burnham. 2010. Michigan Plant Diversity: Ipomoea purpurea. http://www-personal.umich.edu/~rburnham/SpeciesAccountspdfs/IpompurpCONVFINAL.pdf

Farnsworth, E.J. 2003. Zizia aptera (Gray) Fern. Heart-leaved Golden Alexanders: Conservation and Research Plant for New England. http://www.newfs.org/docs/pdf/Ziziaaptera.PDF

Fischer, S. F., P. Poschlod, and B. Beinlich. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology 33:1206–1222.

Flinn, K.M., Gouhier, T.C., Lechowicz, M.J., and M.J. Waterway. 2010. The role of dispersal in shaping plant community composition of wetlands within an old-growth forest. Journal of Ecology 98: 1292-1299.

Garwood, N. C., and C. C. Horvitz. 1985. Factors limiting fruit and seed production of a temperate shrub, Staphylea trifolia L. (Staphyleaceae). American Journal of Botany 72:453–466.

Harrison, R. D., R. Banka, I. W. B. Thornton, M. Shanahan, and R. Yamuna. 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera la ke. II. The vascular flora. Journal of Biogeography 28:1311–1337.

Harvey, C. A. 2000. Windbreaks enchance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. Ecological Applications 10:155–173.

Holm, T. 1913. *Phryma leptostachya* L., a morphological study. Botanical Gazette 56: 306–318.

Hooper, E. R., P. Legendre, and R. Condit. 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. Ecology 85:3313–3326.

Howard, J. L. 1992. Aesculus californica. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2010, November 28].

Hughes, R.H. 1951. Observations of cane (Arundinaria) flowers, seed, and seedlings in the North Carolina Coastal Plain. Bulletin of the Torrey Botanical Club. 78(2): 113-121.

Kirkman, L. K., K. L. Coffey, R. J. Mitchell, and E. B. Moser. 2004. Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna. Journal of Ecology 92:409–421.

Lavoie, C., Y. Jodoin, and A. G. de Merlis. 2007. How did common ragweed (Ambrosia artemisiifolia L.) spread in Quebec? A historical analysis using herbarium records. Journal of Biogeography 34:1751–1761.

McIntyre, S., S. Lavorel, and R.M. Tremont. 1995. Plant life- history a ttributes: their relationship to disturbance response in herbaceous vegetation. Journal of Ecology 83:31–44.

Massey and Hamrick 1998. Genetic diversity and population structure of Yucca filamentosa. American Journal of botany 85: 340-345.

Matlack, G. 1994. Plant species migration in a mixed-history forest landscape in Eastern North America. Ecology 75:1491–1502.

Mehrhoff, L. J., J. A. Silander, Jr., S. A. Leicht, E. S. Mosher and N. M. Tabak. 2003. IPANE: Invasive Plant Atlas of New England. Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT, USA.URL: http://www.ipane.org

Meisenburg, M.J., and A.M. Fox. 2002.What role do birds play in dispersal of invasive plants? Wildland Weeds 6: 8-14.

Meyer, R. 2009. Albizia julibrissin. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2010, November 28].

Minor, E.S., Tessel, S.M., Engelhardt, K.A.M., and T.R. Lookingbill. 2009. The role of landscape connectivity in assembly exotic plant communities: a network analysis. Ecology 90: 1802-1809.

Montgomery, F.H. 1977. Seeds and fruits of plants of eastern Canada and northeastern United States. University of Toronto Press, Toronto, Ontario, Canada.

Neff, K.P. and Baldwin, A.H. 2005. Seed dispersal into wetlands: Techniques and results for a restored tidal freshwater marsh. Wetlands, 25, 392-404.

Ohtsuka, T., and M. Ohsawa. 1994. Accumulation of buried seeds and establishment of ruderal therophytic communities in disturbed habitat, central Japan. Vegetatio 110:83–96.

Pakeman, R.J., Digneffe, G. and Small, J. L. (2002) Ecological correlates of endozoochory by herbivores. Functional Ecology, 16, 296-304.

Pennsylvania Department of Conservation and Natural Resources. 2009. Japanese hops. http://www.dcnr.state.pa.us/forestry/invasivetutorial/japanese_hops.htm

Römermann, C., Tackenberg, O., and P. Poschlod. 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. Oikos 110:219–230.

Rossell, I.M. and J.M. Kesgen. 2003. The distribution and fruiting of red and balck chokeberry (Aronia arbutifolia and A. melanocarpa) in a southern Appalachian fen.

Journal of the Torrey Botnaical Society 130: 202-205.

Royal Botanic Gardens Kew. 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (May 2008)

Schneider, R.L. and R.R. Sharitz. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. Ecology 69:1055-1063.

Schwartz, Iverson, and Prasad. 2001. Predicting the potnetial future distribution of four tree species in ohio using current habitat availability and climatic forcing. Ecosystems 4: 568-581.

Simons, A. M., and M. O. Johnston. 2000. Variation in seed traits of *Lobelia inflata* (Campanulaceae): sources and fitness consequences. American Journal of Botany 87:124–132.

Sitzia, T. 2007. Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. Plant Ecology 188:235–252.

Sonday, R. with R.J. Burnham. 2010. Michigan Plant Diversity: Vinca minor. http://www-personal.umich.edu/~rburnham/SpeciesAccountspdfs/VincminoAPOCFINAL.pdf

Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. American Naturalist 116: 670- 688.

Suzuki, R.O., H. Kudoh, and N. Kachi. 2003. Spatial and temporal variations in mortality of the biennial plant, *Lysimachia rubida*: Effects of intraspecific competition and environmental heterogeneity. Journal of Ecology 91:114–125.

Swearington, J., K. Reshetiloff, B. Slattery, and S. Zwicker. 2002. *Plant invaders of Mid-Atlantic natural areas.* National Park Service and U.S. Fish and Wildlife Service Washington, D.C., USA.

Thompson, J. 1979. Elaiosomes and fleshy fruits: phenology and selection pressures for ant-dispersed seeds. The American Naturalist 117: 104-108.

Tisdale, E.W., Hironaka, M., and W.L. Pringle. 1959. Observations on the autecology of *Hypericum perforatum*. Ecology 40: 54-62.

Trapp, E.J. 1988. Dispersal of heteromorphic seeds in *Amphicarpaea bracteata* (Fabaceae). American Journal of Botany 75: 1535-1539.

Williams, C. F. 1994. Genetic consequences of seed dispersal in t hree sympatric forest herbs. II. Microspatial genetic structure within populations. Evolution 48:1959–1972.

Willson, M. F., Michaels, H.J., Bertin, R.I., Benner, B., Ricke, S., Lee, T.D., and A. P. Hartgerink. 1990. Introspecific variation in seed packaging. American Midland Naturalist 123:179–185.

Young, J.A. and C.G. Young. 1992. *Seeds of woody plants in North America*. Discorides Press. Portland, Oregon.